

**New delimitations and phylogenetic relationships  
of Sabiceae (Ixoroideae, Rubiaceae) and revision  
of the Neotropical species of *Sabicea* Aubl.**

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## 1. GENERAL INTRODUCTION

The tropical regions, comprising about 40% of the earth's land surface between the Tropic of Cancer (23°27' N) and the Tropic of Capricorn (23°27' S) (Longman & Jeník, 1987; Forero & Mori, 1995), are the most important domiciles for world's plant species. About two-third of the roughly 265,000 species of bryophytes and vascular plants of the world including 250,000 species of flowering plants, are believed to occur in the tropics (Prance, 1977; Raven, 1988). The Neotropics are supposed to provide shelter for more than 94,500 species of plants including 90,000 species of flowering plants (Prance, 1977; Maas & Westra, 1998; Thomas, 1999), Tropical Africa for about 35,000 species (Raven, 1988) including 30,152 species of flowering plants (African Flowering Plants Database), and tropical and subtropical Asia for about 40,000 or more species (Raven, 1988). Despite the presence of overwhelmingly large numbers of living species in the tropics, the natural habitats are being destroyed rapidly due to the uncontrolled activities of increasing human population. In respect to this circumstance, the limited studies by the woefully small pool of plant systematists indicate that many plant species will disappear before they are described and classified, a process that Campbell (1989) designated as "anonymous extinction". Once plant species are extinct, their role in maintaining healthy ecosystems and a livable planet, as well as, their potential use to mankind, would never be known (Mori, 1992). In this regard, plant systematics has a lot to contribute in knowing, especially in identifying, describing, and classifying plant species, as well as in investigating their relationships.

The plant species of the tropics, especially of the Latin America, have been encompassed very limitedly in both descriptive and phylogenetic works. On the other hand, our understanding of descriptions and phylogenetic relationships of angiosperms have been dramatically changed during the last decade. Many groups of plants based on morphological characters and presumed relationships derived on the basis of cladistic analyses of morphological characters do not correspond to the results of modern studies including more comprehensive sampling and collaborative analyses of molecular data sets. As a consequence, recent expectations are also largely driven by the intention to make better and more efficient use of earlier research (Pullan & al., 2005). Therefore, there is an urgent need to continue comprehensive botanical exploration and the evaluation of phylogenetic relationships among the flowering plants, especially in the tropics.

The recent classification of the angiosperm order Rubiales (Superorder Lamianae) includes four principal families: Apocynaceae, Gentianaceae, Loganiaceae, and Rubiaceae (Thorne, 1992), in which Rubiaceae (Bluets, Coffees, Madder, Quaker-ladies, Madders, Madder family), comprising more than 630 to 650 genera (Robbrecht, 1996; Delprete, 2004) and 11,000 (Robbrecht, 1996) or 10,200 (Mabberley, 1997) to 13,000 species (Delprete, 2004), is the largest one. Rubiaceae, the fourth largest family after Asteraceae, Orchidaceae and Fabaceae (Leguminosae), comprises also many endemic genera in the tropics. The

Neotropics harbor roughly 4,555 species under 225 genera of the family (Andersson, 1992). Notable endemism occurs in the northern Andean countries of Colombia, Ecuador, and Peru, where the most remarkable concentration of species in the world is found (Raven, 1988). Plant diversity of South America remarkably converges also to the Amazonian regions of Brazil and Venezuela, and the Guiana Highlands. Approximately 2,575 species under 247 genera occur in subsaharan Africa, most of which ( $\pm$  197 genera) occur in tropical Africa including Madagascar and other islands close to the continent. Tropical Africa, especially the Guineo-Congolian and Madagascan regions, harbor numerous endemic Rubiaceae as well. The remainders of the Rubiaceae are distributed in other floristic regions (Holarctic, Indomalasian, Polynesian, Australian, and Holarctic regions; Takhtajan, 1986; Robbrecht, 1988). The origin and diversification of the family is still insufficiently known. Hallé (1967) hypothesized a rain forest origin of Rubiaceae. He recognized Gardenieae, as the most primitive tribe as its endemic genera occur in almost all tropical islands and archipelagos. Robbrecht (1996), in contrast, interpreted the extremely rich representation of the Afro-Madagascan or Madagascan element of Rubiaceae as evidence to a possible Afro-Madagascan origin of the family and postulated a “secondary differentiation under other climatic condition”. None of these hypothetical interpretations is based on fossil records.

In the tropics, Rubiaceae is predominantly represented by woody species making up an important component of all tropical woody vegetation, especially the rain forest understory, whereas, in the temperate regions only by herbaceous species (Robbrecht, 1988). Numerous Rubiaceae are socio-economically important, especially as the source of foods (e.g., *Coffea* L. for coffee), medicines (e.g., quinine, *Cinchona* L.; ipecac, *Cephaelis* Sw.), “ayahuasca admixture” (e.g., vine of the souls, *Psychotria* L.), dyes (e.g., *Galium* L., *Rubia* L.), ornamentals (e.g., *Ixora* L.), perfumes (e.g., *Gardenia* Ellis.), ecologically and economically important weeds (e.g., *Paederia* L.), and some trees for plantation. But, there are notable inadequacies in knowledge of morphology and current understanding of phylogeny within the family, mainly because of the meager number of Rubiaceae systematists in contrast to the large size of the family and its very wide distribution. The family has been variously classified into different subfamilies and numerous tribes since the classical period. However, in the 20<sup>th</sup> century it has been classified into eight (Bremekamp, 1934, 1952, 1966), three (Verdcourt, 1958), and recently four subfamilies- Cinchonoideae, Ixoroideae, Antirheoideae, and Rubioideae, comprising a total of 44 tribes (Robbrecht, 1988, 1993). On the other hand, the recent phylogenetic studies based on molecular data (e.g., *rbcl*, Bremer & al., 1995; *rps16*, Andersson & Rova, 1999; *trnL-F*, Rova & al., 2002) strongly support three subfamilies, excluding Robbrecht’s Antirheoideae. The subfamilial circumscriptions for Rubiaceae appear to be established, but till now, there is a little agreement or lack of support from intensive morphological as well as molecular data sets concerning the tribal, generic, and infrageneric circumscriptions within the family, although some recent studies have confirmed the delimitation of some tribes and a notable number of genera and the ongoing studies are

reducing the conflicts as well. Sabiceae and Virectarieae are two tribes of the subfamily Ixoroideae that are presently established with strong controversies, especially in their tribal delimitation, generic limits, intergeneric relationships, and relationships within their type genera *Sabicea* Aubl. and *Virectaria* Bremek., respectively, for which both phylogenetic and descriptive studies are earnestly needed.

This study was undertaken with six goals: 1) to investigate the present circumscription of the tribes Sabiceae and Virectarieae, 2) to establish the monophyly of *Sabicea* and new tribal limit of Sabiceae, 3) to explore the phylogenetic relationships within the tribe Sabiceae, 4) to examine the monophyly and phylogeography of the genus *Virectaria*, and relationships between its species, 5) taxonomic revision of Neotropical *Sabicea*, and 6) assessment of taxonomically useful characters for Neotropical *Sabicea*.

**1.1 Circumscription of Sabiceae and Virectarieae.** — The pantropical tribe Sabiceae Bremek. (subfamily Ixoroideae) showing African-Asian-American disjunction is one of the least understood rubiaceous tribes comprised of ca. 177 species of lianas, vines, straggling (sub-) shrubs, and erect herbs or rarely trees. In tropical Africa, it is mainly centered the Guineo-Congolian and Zambezi Region (White, 1979, 1993) with 112 species under 5 genera (*Ecpoma* K. Schum., *Hekistocarpa* Hook. f., *Pseudosabicea* N. Hallé, *Sabicea*, *Virectaria*) with two disjunct assemblages – one in Madagascar with 6 species and another in São Tomé and Príncipe with 3 species, all of which are endemic and belong to the type genus *Sabicea*. Only two species of this tribe occur in Asia, one on the island of Socotra (Yemen), which belongs to the monospecific genus *Tamridaea* Thulin & B. Bremer, and the other in Sri Lanka, which belongs to the monotypic genus *Schizostigma* Arn. ex Meisn., and these are endemic as well. The Neotropics harbor 54 species of this tribe, all of which belong to *Sabicea*. In classical systems, the tribe Sabiceae has been included in the subfamily Cinchonoideae (Candolle, 1830; Hooker, 1873; Schumann, 1891), but in modern systems its position has been confirmed in the subfamily Ixoroideae (Bremekamp, 1952; Verdcourt, 1958; Robbrecht, 1988; Andersson, 1996; Bremer & Thulin, 1998). However, there are strong conflicts among the Rubiaceae experts in circumscribing and delimiting the tribe Sabiceae.

The tribe Sabiceae was monogeneric and characterized by simple stipules, axillary inflorescences, and very narrow testa cells when Bremekamp (1934, 1966) proposed or established it. But its tribal status was not accepted by most of the rubiaceous taxonomists (Verdcourt, 1958; Hallé, 1961; Hallé, 1966; Steyermark, 1972, 1974; Kirkbride, 1982; Robbrecht, 1988) until 1996, when Andersson resurrected it based on phylogenetic analysis of morphological data. Before Bremekamp's (1934) recognition of Sabiceae, the type genus *Sabicea* was placed in Hamelieae (Don, 1834), treated as a monogeneric subtribe Sabicieae under the tribe Cinchonaceae (Grisebach, 1861) or included in Mussaendeae (Candolle 1830; Hooker, 1873; Schumann, 1891). Its placement in Mussaendeae has been maintained also in some modern systems (Verdcourt, 1958; Steyermark, 1972, 1974). Hallé (1963) introduced a

new genus *Pseudosabicea* based on some *Sabicea* species with bilocular ovaries and placed his new genus in Mussaendeae. In other modern classifications, *Sabicea* and *Pseudosabicea* were included in Isertieae (Kirkbride, 1982; Robbrecht, 1988, 1993) until Andersson's (1996) broadened circumscription of Sabiceeae including the genera *Acranthera* Arn. ex Meisn., *Amphidasya* Standl., *Ecpoma*, *Pentaloncha* Hook. f., *Pittierothamnus* Steyerm., *Pseudosabicea*, *Sabicea*, *Schizostigma*, and *Temnopteryx* Hook. f. All of these classifications are exclusively based on morphological data. Bremer & Thulin (1998), conducting the first molecular study including this group, delimited Sabiceeae with *Pseudosabicea*, *Sabicea*, *Tamridaea*, and *Virectaria* under the subfamily Ixoroideae, although Verdcourt (1975) established the monogeneric tribe Virectarieae Verdc. to accommodate the genus *Virectaria* and placed the tribe in the subfamily Cinchonoideae. The morphological and anatomical studies of Dessein & al. (2001b) supported the tribal circumscription of Sabiceeae sensu Bremer & Thulin.

On the other hand, Dessein & al. (2001a) based on *rbcL* and *rps16* data segregated Sabiceeae sensu Bremer & Thulin into two tribes – Sabiceeae s.s. to include five genera (*Ecpoma*, *Pentaloncha*, *Pseudosabicea*, *Sabicea*, *Stipularia* P. Beauv.) and Virectarieae to include three genera (*Tamridaea*, *Hekistocarpa* and *Virectaria*). Corresponding to Dessein & al. (2001a), Robbrecht & Manen (2006) classified Sabiceeae into two subtribes – Sabiceinae (Bremek.) Robbr. & Manen (to include *Ecpoma*, *Pseudosabicea*, *Sabicea*, *Schizostigma*, *Stipularia*) and Virectariinae (Verdc.) Robbr. & Manen (to include *Hekistocarpa*, *Tamridaea*, *Virectaria*). All of the previous and recent studies, circumscribing or rejecting the tribe Sabiceeae or Virectarieae, have a major shortcoming– they are either exclusively based on morphological data or on molecular data but their analysis used very few samples (e.g., 2.5 to 4.5 % of the species of *Virectaria*), which hardly represent the existing variation ranges of the tribe. These conflicting treatments of Sabiceeae and Virectarieae create the scope for the present study to thoroughly investigate these tribes and subtribes using molecular data sets.

This study has established the monophyly of the tribe Sabiceeae and Virectarieae based on parsimony and Bayesian analyses of the sequence data from *trnT-F* region of chloroplast DNA (Chapter 6.1), collected from the representative samples of three subfamilies of Rubiaceae (Cinchonoideae, Ixoroideae, Rubioideae) and all established genera associated with the existing circumscriptions of these tribes. The resolved clade/s for the tribes or subtribes are further investigated through the combined analyses of sequence data sets from *trnT-F* region and internal transcribed spacer (ITS) of nuclear rDNA (Chapter 6.1), collected through relatively wider sampling of the genera of Sabiceeae and Virectarieae, recognized in the recent studies. Both markers used in this study have never been used before in studying these tribes but have been proved as useful tools for inferring phylogenetic relationships at tribal and generic levels in the family by previous phylogenetic studies on some Rubiaceae groups (e.g., Andreasen & al., 1999; Razafimandimbison & Bremer, 2002; Alejandro & al., 2005).

**1.2 Generic limit of *Sabicea* and tribal limit of Sabiceae.** — The pantropical *Sabicea* is the largest genus of the tribe Sabiceae comprising ca. 145 species of scandent shrubs, woody climbers and scramblers or twiners. It is the only one genus of the family Rubiaceae displaying an African-Asian-American disjunction. In mainland tropical Africa this genus includes ca. 82 species, mainly centered in the Lower- and Upper Guinea of Guineo-Congolian Region, spreading notably towards the upper Guineo-Congolian/Sudania regional transition zone (White, 1993). With six (Razafimandimbison & Miller, 1999), and three (Joffroy, 2001) species, this genus is the sole representative of the tribe Sabiceae in Madagascar and São Tomé and Príncipe, respectively. In Asia it is restricted to Sri Lanka with one species, *S. ceylanica* Puff (Puff & al., 1998). In the Neotropics, *Sabicea* represents the tribe Sabiceae with ca. 54 species, mainly centered in southeastern, central western to northwestern, northern and northeastern South America including the Amazonas-Río Negro basin, but extending north as far as southern Mexico. Aublet (1775) originally described *Sabicea* from South America with two species (*S. aspera* Aubl. and *S. cinerea* Aubl.). Wernham (1914) proposed the first and only broad circumscription of *Sabicea* to include 105 species of Africa and South America under two subgenera (*Sabicea* subgenus *Stipulariopsis* Wernham with nine species and *Sabicea* subgen. *Eusabicea* Wernham with 96 species).

Hiern (1877), endorsed by Wernham (1914), Hallé (1963), Andersson (1996), Bremer & Thulin (1998), and Dessein & al. (2001a), recognized Palisot-Beauvois's (1807) genus *Stipularia* as a well-defined genus closely related to *Sabicea*. But Hepper (1958) and Hepper & Keay (1963) rejected Hiern's (1877) circumscription of *Stipularia*, instead they merged its five species with *Sabicea*. On the other hand, Hallé (1963) viewed *Sabicea* sensu Wernham as morphologically heterogeneous and introduced the new genus *Pseudosabicea* to accommodate some of the previously described African species of *Sabicea*. Hepper & Keay (1963) rejected the generic status of African *Ecpoma*, originally described by Schumann (1896), but Hallé (1963) broadly circumscribed it including five African *Sabicea* species (*S. bicarpellata* K. Schum., *S. cauliflora* Hiern, *S. gigantea* Wernham, *S. gigantostipula* K. Schum., *S. hierniana* Wernham), previously considered under Wernham's (1914) subgenus "*Stipulariopsis*". On the other hand, Hiern (1877) suggested the merging of Hooker's (1873) genera *Pentaloncha* and *Temnopteryx* with the Sri Lankan monotypic genus *Schizostigma*. But Puff & al. (1998) disagreed with Hiern (1877), instead they merged *Schizostigma* with *Sabicea*. These generic circumscriptions of *Sabicea* and its potential allies exhibit clear-cut conflicts. Nevertheless, none of these contrasting circumscriptions of *Sabicea* or its close allies has ever been investigated using molecular-based phylogenies. It means that previously the tribe Sabiceae has been delimited without examining the generic limits for its type genus *Sabicea* and its closely allied genera using molecular data. The biogeographical origin of *Sabicea* is totally unexplored. Therefore, besides establishing the monophyly of the tribe Sabiceae, it appeared as very necessary to investigate the monophyly of its type genus

*Sabicea*, to ascertain a new tribal limit for Sabiceae following the new generic circumscription of *Sabicea* and to examine the biogeographical origins of *Sabicea*.

In this study the monophyly of *Sabicea* and its relationships with its most closely allied genera *Ecpoma*, *Pseudosabicea* sensu Hallé, *Schizostigma*, and *Stipularia* sensu Hiern, has been examined based on parsimony and Bayesian analyses using ITS and *trnT-F* data sets (Chapter 6.1). Based on the new generic circumscription for *Sabicea* and its close allies, the tribe Sabiceae s.l. has been newly delimited. Furthermore, the biogeographical origins of the Malagasy, São Tomean, Asian, and Neotropical *Sabicea* have been explored based on the resolutions of most parsimonious tree (Chapter 6.1).

**1.3 Phylogenetic relationships within Sabiceae.** — The tribe Sabiceae was variously delimited by different Rubiaceae authors (refer to Khan & al., 2007, for more information on tribal limits). Recently Khan & al. (2007) have newly circumscribed the tribe Sabiceae with four genera – *Hekistocarpa*, *Sabicea* s.l., *Tamridaea*, and *Virectaria*. Although, the tribal limit and generic composition of Sabiceae have been discussed in the recent studies, from Andersson (1996) to Khan & al. (2007), but the intergeneric relationships within the tribe have been mostly ignored or only very partially demonstrated.

Before Khan & al. (2007), the molecular study of Bremer & Thulin (1998) revealed that the African *Virectaria* has a close relationship to the monospecific *Tamridaea*, confined to Socotra of Yemen, than with the African *Pseudosabicea* and the species-rich pantropical *Sabicea*. However, the palynological study of Huysmans & al. (1998) did not support the close relationship of *Virectaria* with *Sabicea*, but postulated an affinity to the Neotropical genus *Raritebe* Wernham, which was placed before (Robbrecht, 1993) in the tribe Iseriidae (subfamily Cinchonoideae) but in more recent study (Andersson & Rova, 1999) it has been placed in the tribe Urophyllaeae (subfamily Rubioideae). Rova (1999), based on *rps16* intron data, again suggested a relationship of *Virectaria* with *Sabicea*. Based on morphological and anatomical evidence, Dessein & al. (2001b) postulated “an independent evolutionary line” for the genus *Virectaria* within the tribe Sabiceae. On the other hand, Dessein & al. (2001a), endorsed by Robbrecht & Manen (2006), suggested that *Hekistocarpa*, *Tamridaea*, and *Virectaria* are more closely related to each other than to *Sabicea* and its close allies (e.g., *Ecpoma*, *Pseudosabicea*, *Sabicea*). Khan & al. (2007) showed that the generic circumscriptions of *Ecpoma*, *Pseudosabicea*, *Sabicea*, *Schizostigma*, and *Stipularia*, previously accepted as close allies of *Sabicea*, are untenable due to which they merged all of these genera under *Sabicea* s.l. The previous studies (Bremer & Thulin, 1998; Dessein & al., 2001a; Robbrecht & Manen, 2006) using the molecular data were based on very narrow sampling of the genera. The study of Khan & al. (2007), the first study dealing with relationships within Sabiceae including all established genera associated with the tribe, indicated a close relationship between *Hekistocarpa*, *Tamridaea*, *Virectaria*, and *Sabicea* s.l. But the parsimonious trees of Khan & al. (2007) lack sufficient resolution, especially for



demonstrating relationships between *Hekistocarpa*, *Tamridaea*, and *Virectaria*. Therefore, the controversies regarding the relationships between the genera of Sabiceae are sustaining, but these relationships are largely undiscovered or mostly incompletely demonstrated. These facts suggest that exploring the relationships within Sabiceae s.l. using molecular, as well as morphological data sets from wider sampling especially of the genus *Virectaria*, is still necessary.

In this study the existing knowledge on the intergeneric relationships within Sabiceae sensu Khan & al. (2007) has been amended through investigating the phylogenetic relationships between the genera *Hekistocarpa*, *Sabicea* s.l., *Tamridaea*, and *Virectaria*, based on parsimony and Bayesian analyses of ITS, *rpoC1* and *trnT-F* sequence data (Chapter 6.2). The nucleotide sequence data from *rpoC1* exon of cpDNA and broader sampling for the genus *Virectaria* has been used here for the first time in phylogenetic studies including this tribe.

**1.4 Generic limit of *Virectaria* and relationships within *Virectaria*.** — The genus *Virectaria*, comprised of eight species, is characterized by herbaceous or subshrubby habit, lack of raphides, truncate stigmata, flat internal indument, elongated floral discs, and one persistent and one deciduous valve during fruit dehiscence. This African genus is mainly centered in the Guineo-Congolian and Zambezian Region (White, 1979, 1993). Previously, the genus *Virectaria* was known as *Virecta* Afzel. ex Sm. *Virecta* was in constant use until Bremekamp (1952), who erected the genus *Virectaria* through renaming Smith's (1819) *Virecta* comprising some African species (e.g., *V. multiflora* Sm. and *V. procumbens* Sm.). Bremekamp's recognition of *Virectaria* as a genus has been confirmed by recent morphological (Verdcourt, 1953; Dessein & al. 2001b), and molecular studies (Dessein & al. 2001a, Bremer & Thulin, 1998, Robbrecht & Manen, 2006, Khan & al., 2007). However, controversies on its tribal position were continuing. It has been classified before in the tribe Hedyotideae (Don, 1834; Hepper & Keay, 1963; Hallé, 1966), Oldenlandieae (Schumann, 1891), and Ophiorrhizeae (Bremekamp, 1952). Verdcourt (1975) established the monogeneric tribe Virectarieae to accommodate this genus. But Robbrecht (1988) maintained it under Hedyotideae. Following Verdcourt (1975), Dessein & al. (2001a) placed it in Virectarieae but Robbrecht & Manen (2006) in subtribe Virectariinae of Sabiceae. Corresponding Bremer & Thulin (1998), Khan & al. (2007) confirmed its position in the tribe Sabiceae s.l. Although the recognition and placement of the genus *Virectaria* has been confirmed by molecular and morphological studies and the knowledge on this genus has been notably amended by morphological studies (Verdcourt, 1953; Dessein & al., 2001a), however, its monophyly has never been examined using molecular data from more than two species.

The views of previous authors were apparently inconsistent in delimiting the genus and anticipating its infrageneric relationships. Hiern (1877) presented the genus *Virecta* placing *V. multiflora* at the first, followed by *V. procumbens* and *V. angustifolia* Hiern, but did not

explain the reason for these placements. Schumann (1891) divided the genus into three sections (Bistipulatae, Unistipulatae, Setosostipulatae), based on stipule types without arguing any reason for this partitioning of the genus. Adopting the generic name *Virectaria*, Bremekamp (1952) restricted the genus to six African species without any infrageneric categorization. Verdcourt (1953) delimited *Virectaria* with five species and postulated the relationships within the genus considering *V. major* (K. Schum.) Verdc. as close to *V. procumbens* (Sm.) Bremek., and *V. angustifolia* (Hiern) Bremek. to *V. salicoides* (C. H. Wright) Bremek. but with *V. multiflora* (Sm.) Bremek. further diverged. Additionally he considered Bremekamp's *V. heteromera* (K. Schum.) Bremek. and *V. kaessneri* (S. Moore) Bremek. as conspecific with two of his species (*V. angustifolia* and *V. major*, respectively) and treated two other species (*V. petrophila* and *V. suffruticosa* K. Schum) as conspecific with *Virectaria angustifolia* (Hiern.) Bremek. Hallé (1966) placed *V. procumbens* at first position, followed by *V. angustifolia*, *V. salicoides*, *V. belingana* N. Hallé, *V. multiflora*, and *V. herbacoursi* N. Hallé without explaining the reason. Dessein & al. (2001b) mostly agreed with Verdcourt's explained relationship within the genus and additionally showed that *V. procumbens* is closely related to *V. angustifolia* instead of *V. major*. They recognized two clades within the genus but avoided any sectional division as Schumann (1891) and Verdcourt (1953) envisaged. These previous studies demonstrating the controversial relationships within the genus were solely based on morphological grounds, meaning that the relationships between its species have never been examined using molecular data. Therefore, besides examining the monophyly of *Virectaria*, investigation of the relationships within *Virectaria* using molecular data sets is still necessary.

This study has explored the monophyly of the genus *Virectaria*, resolved the phylogenetic relationships between the species of this genus, and revealed the phylogeographical origins within the genus based on parsimony and Bayesian analyses of both morphological and molecular data for the first time (Chapter 6.2). The morphological data used in this study include 16 new characters and the molecular data from four spacers, ETS and ITS of nrDNA and *rpoC1* and *trnT-F* of cpDNA, as well as a wider sampling for the genus *Virectaria*.

**1.5 Scope of taxonomic revision of the genus *Sabicea*.** — The pantropical genus *Sabicea* was originally coined by Aublet (1775) for *Sabicea aspera* and *S. cinerea* from French Guiana. Aublet (1775) distinguished the genus by its twining habit, ovate to lanceolate and apically acute leaves, appressed indument, 4–5-lobed corolla, and 3–5-locular ovaries. After Aublet (1775), no revisionary work on the genus *Sabicea* was done until Wernham (1914), who published the first monographic work on *Sabicea* consisting of 105 species from Africa and the Neotropics. Wernham's (1914) monographic work on *Sabicea* is a great contribution to plant systematics. However, his revision was based on a small amount of specimens and a narrow typological species concept (Andersson, 1999). Some species

described by Wernham (1914) are found indistinguishable (e.g., *S. asperula* Wernham, *S. colombiana* Wernham, *S. costaricensis* Wernham, *S. robbii* Wernham) when they are compared with their close allies. Wernham's (1914) treatment is scarred by either avoidance in referring to or unawareness in tracing relationships between closely allied species. After the monographic work of Wernham (1914), ca. 46 new species have been published. Furthermore, the species of *Stipularia* (*S. africana* P. Beauv., *S. efulenensis* Hutch., *S. elliptica* Schweinf. ex Hiern, *S. gabonica* Hiern and *S. mollis* Wernham) have been merged with *Sabicea* (Hepper, 1958), and in contrast some species of *Sabicea* have been merged with other genera like *Ecpoma* or transferred to the new genus *Pseudosabicea* (Hallé 1963, 1966). The taxonomic revision of the second major genus of the tribe Sabiceae (*Virectaria*) has been accomplished recently (Dessein & al., 2001b), but its type genus *Sabicea* has never been revised to any extent after Wernham (1914). Although the recent phylogenetic studies have notably reduced the conflicts regarding the generic circumscriptions within the tribe Sabiceae, however, the descriptive knowledge on *Sabicea* has not yet been amended. In these contexts, a modern revision of the genus *Sabicea*, both of Africa and Neotropics, is badly needed (Andersson, 1999). It is believed that plant species of Latin America are relatively poorly known than those of other major tropical regions (Raven, 1988), which appears also true in case of the genus *Sabicea*, if the floristic works of different regions including the genus *Sabicea* are compared. The comparative studies of the specimens of African and Neotropical *Sabicea* indicate that the Neotropical species are morphologically relatively less distinct than those of African *Sabicea*. Therefore, revision of Neotropical *Sabicea* should be prioritized.

Neotropical *Sabicea*, with ca. 54 species, is the only representative of the tribe Sabiceae in the Neotropics. Most of its species occur in South America, especially in southeastern, central western to northwestern, northern and northeastern South America including the Amazonas-Río Negro basin. They are usually vines, lianas or (sub-) shrubs with lianescent branches, which mostly grow on scrubs or thickets in upland tropical humid forests and extend to open areas, especially grasslands including pastures and savannahs. Wernham (1914) described 39 species including 25 new species from the Neotropics. After Wernham (1914), 26 new species of *Sabicea* were published from South America and the Caribbean Islands and the previously published 11 species were transferred elsewhere by different authors. Like Wernham (1914), Steyermark (1967, 1974, 1981), who is notable for studying the genus in South America, has not described the similarities of some of his new species with their close allies. After Wernham, the genus *Sabicea* has been isolatedly studied together with other Rubiaceae of the Neotropics for regional flora treatments (e.g., Dwyer, 1980; Macbride, 1936; Standley, 1930, 1931, 1936; Standley & Williams, 1975; Taylor, 2001; Steyermark, 1967, 1972, 1974, 1988; Taylor & Steyermark, 2004; Urban, 1931; Vásquez, 1997) and checklists or catalogues (Andersson, 1992; Balick & al., 2000; Boggan & al., 1997; Brako & Zarucchi, 1993; Foster, 1958; Molina, 1975; Moraes, 1990; Nelson, 1978) of some

countries or smaller areas. Therefore, a revision of the Neotropical *Sabicea* based on a sufficient number of specimens is indispensable.

This study based on the available specimens of Neotropical *Sabicea* from major world herbaria provides a comprehensive taxonomic treatment of all species of the Neotropics (Chapter 6.3), including a detailed description originally generated from DELTA, distribution maps, illustrations, an indented key to all recognized taxa, lectotype designation, and annotation of the identified specimens of the genus.

### **1.6 Taxonomic implication of morphological characters of *Sabicea*. —**

Neotropical *Sabicea* is the most confusing group of Sabiceae, because most of the Neotropical *Sabicea* species described so far appear morphologically so similar that they seem alike at a glance, although they do not really belong to the same species. The characters used in distinguishing many species of Neotropical *Sabicea* by previous authors are not always useful for certain identification. Some of Wernham's (1914) key characters such as climbing habit, compactness of inflorescence, pedicel lengths, shape, partitioning and arrangements of bracts, length of corolla tubes, and stipule shapes etc. are neither invariant, nor always species-specific. Characters like pedicel lengths, length-width ratios, and apex-types of leaves, used in species delimitation (Andersson, 1999), and number of flowers per inflorescences, used in infraspecific delimitation (Steyermark, 1974), is barely stable. On the other hand, the important characters like colleter's position in calices and indumentum status inside the stipules, bracts and calyces are ignored in the previous studies. Therefore, an overall assessment of the morphological characters of Neotropical *Sabicea* is necessary for their practical implications in identification of its species or varieties.

In this study 620 macromorphological characters of Neotropical *Sabicea* have been thoroughly investigated based on a large bulk of specimens using DELTA. This study has emphasized the concept of using the combination of two or more key characters, rather than single character frequently used by Wernham (1914), in recognizing Neotropical *Sabicea* species, because in most cases a single character, appearing strongly diagnostic, may be revealed as variable if more specimens are compared. Finally, this study has provided a comparative assessment of the usefulness of the easily visible morphological characters of Neotropical *Sabicea* that can be a helpful guide for selecting characters of taxonomic implication (Chapter 6.3).

All parts of this dissertation corresponding the six goals described above are compiled under three major chapters following the headings: 1. Sabiceae and Virectarieae (Rubiaceae): One or two tribes? – New tribal and generic limits of Sabiceae and biogeography of *Sabicea* s.l. (Chapter 6.1), 2. Phylogenetic relationships within Sabiceae s. l. (Ixoroideae, Rubiaceae) - phylogeography of *Virectaria* (Chapter 6.2), and 3. Taxonomic Revision of the Neotropical *Sabicea* (Rubiaceae–Ixoroideae) (Chapter 6.3).

## 2. RESULTS AND DISCUSSION

This study imparts the robust phylogeny of the pantropical tribe Sabiceae based on both nrDNA and cpDNA data sets for the first time and further discloses the limitations of morphological characters in explaining the intergeneric relationships or delimiting the genera of Sabiceae. This study demonstrates the monophyly of *Sabicea*, the type and most species-rich genus of Sabiceae representing the intercontinental (Africa-Asian-American) disjunction, a new generic circumscription for Sabiceae including its closely allied genera and consequently a new tribal limit for Sabiceae. It brings out the biogeographical origins of the major assemblages of *Sabicea*. Using the new combinations of molecular data sets and additionally new sets of morphological characters, this study unfolds the phylogenetic relationships within the tribe Sabiceae s.l., establishes the monophyly of the tropical African genus *Virectaria*, the second major genus of Sabiceae s.l., and reveals the phylogenetic relationships within *Virectaria* with focusing its phylogeography. The present study amends the existing taxonomic understanding on the Neotropical species of *Sabicea*, the most confusing group of the tribe Sabiceae, and provides a concept for taxonomic implications of morphological characters for species delimitation in Neotropical *Sabicea*, through a revisionary work.

**2.1 Circumscription of Sabiceae s.l. and indefensibility of the amended tribe Virectarieae.** — The results of *trnT-F* and combined ITS- *trnT-F* analyses (Chapter 6.1, Figs. 1–3) strongly support a broad circumscription of Sabiceae (Sabiceae s.l.) comprised of eight genera: *Ecpoma*, *Hekistocarpa*, *Pseudosabicea*, *Sabicea*, *Schizostigma*, *Stipularia*, *Tamridaea*, and *Virectaria* that form a strongly supported monophyletic group nested in Ixoroideae s.l., consistent with Robbrecht & Manen (2006). No potential morphological synapomorphy supports this newly delimited Sabiceae s.l. due to which the monophyly of the tribe is entirely based on molecular data.

The results of *trnT-F* analysis (Chapter 6.1, Fig. 1) support the polyphyly of Sabiceae sensu Andersson (1996), as both *Pentaloncha* and *Temnopteryx* are resolved with strong support in the subfamily Rubioideae. The polyphyly of Sabiceae sensu Andersson was disclosed before by Bremer & Manen (2000) and Robbrecht & Manen (2006) classifying *Amphidasya* in the tribe Urophyllae (Rubioideae), and Alejandro & al. (2005) showing *Acranthera* to be associated with Rubioideae, as these two genera are also included with Sabiceae sensu Andersson. Sabiceae sensu Bremer & Thulin (1998) is not monophyletic, unless *Ecpoma*, *Hekistocarpa*, and *Schizostigma* are also included, as revealed in the combined ITS-*trnT-F* tree (Chapter 6.1, Fig. 3). Sabiceae sensu Dessein & al. (2001a) is not monophyletic also, as it includes *Pentaloncha*, which is shown to belong to Rubioideae. This study proves that Virectarieae sensu Dessein & al. (2001a) is not monophyletic, as its

members *Hekistocarpa*, *Virectaria*, and *Tamridaea* never form a clade (Chapter 6.1, Figs. 1–3) and there is no potential support from morphological characters to recognize this tribe. Therefore, the tribal status of Virectarieae sensu Dessein & al. is unaccepted. For the same reason, the new subtribal classification of Sabiceae (Sabiceinae and Virectariinae) by Robbrecht and Manen (2006) is not supported.

**2.2 Monophyly of *Sabicea* s.l., new tribal limit of Sabiceae, and biogeographical origins in *Sabicea* s.l.** — In the ITS and ITS-*trnT-F* trees (Chapter 6.1, Figs. 2 and 3, respectively), *Ecpoma hierniana* (Wernham) N. Hallé & F. Hallé is consistently nested within the moderately supported *Pseudosabicea-Sabicea-Stipularia-Schizostigma-Ecpoma* clade. Although the type species of *Ecpoma* is not included in this study, its character states clearly fall within the range of variation in *Sabicea* s.l. *Pseudosabicea* sensu Hallé (1963) is resolved as para- or polyphyletic, as the sampled species of *Pseudosabicea* group in two separate clades (Chapter 6.1, Figs. 2–3). Neither the characters of *Pseudosabicea*, nor the characters of its species belonging to these two clades were found as distinctive. Most of the species of *Pseudosabicea* [e.g., *P. batesii* (Wernham) N. Hallé, *P. medusula* (K. Schum. ex Wernham) N. Hallé, *P. mildbraedii* (Wernham) N. Hallé, and *P. segregata* (Hiern) N.Hallé] were once included in *Sabicea* (Wernham, 1914). The African genus *Stipularia* has been shown as polyphyletic (Chapter 6.1, Figs. 2–3), as its two species, *S. elliptica* and *S. efulenensis*, are resolved in two separate clades. Hepper (1958), endorsed by Hallé (1966), showed that many African *Sabicea* show a great range of the degree of bract fusion – from inconspicuous to distinct and totally free to partly or completely fused bracts, due to which the generic distinction of *Stipularia* based on the presence of large campanulate involucral bracts is unsupported. Therefore, finally *Ecpoma*, *Pseudosabicea*, and *Stipularia* have been merged here with *Sabicea* based on both molecular and morphological grounds. On the other hand, as the Asian genus *Schizostigma* is deeply nested within the moderately supported *Pseudosabicea-Sabicea-Stipularia-Schizostigma-Ecpoma* clade of both the ITS and ITS-*trnT-F* trees (Chapter 6.1, Figs. 2–3) and its morphological characters completely correspond to Puff & al. (1998), who merged it with *Sabicea*, it is accepted here as the only Asian species of the genus *Sabicea*.

Considering the original descriptions of *Ecpoma* and *Pseudosabicea* and previous merging of *Stipularia* (Hepper, 1958) and *Schizostigma* (Puff & al., 1998) with *Sabicea*, the acceptance of *Sabicea* s.l. (through merging all species of *Ecpoma*, *Pseudosabicea*, *Schizostigma*, and *Stipularia* with *Sabicea*), requires only six new combinations that have been presented here- *Sabicea apocynaceum* (K. Schum.) Razafim., B. Bremer, Liede & Khan, comb. nova., 2., *Sabicea becquetii* (N. Hallé) Razafim., B. Bremer, Liede & Khan, comb. nova., 4. *Sabicea proselyta* (N. Hallé) Razafim., B. Bremer, Liede & Khan, comb. nova., 5. *Sabicea sanguinosa* (N. Hallé) Razafim., B. Bremer, Liede & Khan, comb. nova.,

and 6. *Sabicea sthenula* (N. Hallé) Razafim., B. Bremer, Liede & Khan, comb. nova. Adopting *Sabicea* s.l., the broadly circumscribed Sabiceeae (Sabiceeae s.l.) is finally delimited with four genera only— *Hekistocarpa*, *Sabicea* s.l. *Tamridaea*, and *Virectaria*.

Besides circumscribing *Sabicea* s.l., this study further shows that *Sabicea* sensu Wernham (1914) is only monophyletic if *Pseudosabicea proselyta*, *Schizostigma*, and *Stipularia efulenensis* are also incorporated and the monophyly of Wernham's (1914) two subgenera of *Sabicea* (*Sabicea* subgen. *Eusabicea* and *Sabicea* subgen. *Stipulariopsis*) based on habit and size of leaves and stipules is not supported (Chapter 6.1, Figs. 2–3). This study further reveals that *Sabicea* sensu Hallé (1963) is polyphyletic because *Ecpoma*, represented by *E. hierniana*, *Pseudosabicea*, represented by *P. segregata*, *P. nobilis*, and *P. proselyta*, and *Schizostigma* are all resolved in the large *Sabicea* clade. This study suggests further molecular phylogenetic investigations using multiple markers and much broader sampling of *Ecpoma*, *Pseudosabicea*, *Stipularia*, and *Sabicea* to establish, if possible, new infrageneric classifications for the newly delimited *Sabicea* with ca. 170 species and also to address some evolutionary questions.

This study reveals for the first time that the São Tomean *Sabicea* had African ancestors, as the São Tomean species of *Sabicea* (*S. exellii* G. Taylor, *S. ingrata* K. Schum., *S. thomensis* Joffroy) are consistently nested in the Afro-Asian *Sabicea* clade, and form a subclade together with three African *Sabicea* species (*S. capitellata* Benth., *S. johnstonii* K. Schum. ex Wernham, *S. rosea* Hoyle) (Chapter 6.1, Figs. 2–3). The highly supported Malagasy *Sabicea* clade, comprised of two species – *S. diversifolia* Pers. and *S. seua* Wernham (Razafimandimbison & Miller, 1999), is always nested in the African *Sabicea* clade, which indicates that Malagasy *Sabicea* also had African ancestors. On the other hand, the moderately to highly supported single clade consisting of all sequenced Neotropical *Sabicea* species (Chapter 6.1, Fig. 3), indicates a single origin of all Neotropical *Sabicea* that appear to have originated from an African common ancestor. The results of this study indicate that the African common ancestors of *Sabicea* presumably independently reached in Madagascar, São Tomé & Príncipe, and the Neotropics via three single long-distance dispersal events. Two hypotheses are postulated here for the means of these dispersal events – by wind and/or ocean currents (Hypothesis 1) or by birds transferring the seeds across the Mozambique Channel and the tropical Atlantic (Hypothesis 2). The Neotropics and São Tomé & Príncipe do not share any *Sabicea* species, which indicates that the stepping-stone long-distance dispersal (i.e., dispersal from the mainland Africa to the Neotropics via São Tomé & Príncipe) was excluded from the mode of dispersal responsible for the present trans-Atlantic distribution of *Sabicea* s.l. Among African *Sabicea*, three species (*S. angolensis* Wernham, *S. orientalis* Wernham, *S. venosa* Benth.), constantly appeared as most closely related to the Neotropical *Sabicea* s.l., consistent with morphological indications. It appears that the major diversification of *Sabicea* s.l. started in mainland Africa and a second major radiation has occurred after the

group began to colonize the Neotropics. The presence of only one species— *Sabicea ceylanica* in Asia (restricted to Sri Lanka) indicates the failure of the genus to diversify in Asia.

*Sabicea* s.l. are easily recognizable from other three genera (*Hekistocarpa*, *Tamridaea* and *Virectaria*) of Sabiceae s.l. They are predominantly lianas or vines and occasionally erect woody herbs, straggling herbs, shrubs or erect shrubs, whereas, other three genera of Sabiceae are either only herbs (*Hekistocarpa* and *Virectaria*) or shrubs (*Tamridaea*). *Sabicea* s.l. are morphologically very distinct from *Hekistocarpa*, by their few- to many-flowered fascicles or densely capitulate to laxly paniculate to thyrsoid cymes or solitary flowers, valvate aestivation, 2–5(7)-locular ovaries, rounded-fruits, and few to many perforations in seed exotesta cells, in contrast to many-flowered scorpioid cymes, reduplicate valvate aestivation, ca. 10-locular ovaries, laterally flattened-fruits, and one perforation per exotesta cell of seeds of *Hekistocarpa*. *Sabicea* s.l. are distinct from both *Tamridaea* and *Virectaria* by their axillary inflorescences and indehiscent fruits instead of terminal inflorescence and dehiscent fruits. Additionally they are distinct from *Tamridaea* by their valvate aestivation and ovate corolla lobes with (sub-)acute apices in contrast to reduplicate valvate aestivation and  $\pm$  obcordate corolla lobes with emarginate-mucronate apices of *Tamridaea*. They differs from *Virectaria* by their anthers and 2–6-lobed stigmata that are usually included in the corolla tubes or slightly exerted, moniliform internal trichomes, and large perforation in seed exotesta cells in contrast to completely exerted anthers and truncated stigmata, flat internal trichomes and small perforation in seed exotesta cells of *Virectaria*.

**2.3 Phylogenetic relationships within Sabiceae s.l.** — In the most parsimonious ITS-*rpoC1-trnT-F* tree (Chapter 6.2, Fig. 1), Sabiceae sensu Khan & al. (Chapter 6.1, Fig. 3) is strongly resolved as a monophyletic group, inconsistent with Dessein & al. (2001a) and Robbrecht & Manen (2006). Within the Sabiceae s.l. clade, two *Hekistocarpa* accessions are constantly resolved as sister to the weakly to moderately supported *Tamridaea-Virectaria-Sabicea* clade, which suggest the sister-group relationship of *Hekistocarpa* to the group of *Tamridaea*, *Virectaria*, and *Sabicea* s.l., consistent with Khan & al. (2007, Chapter 6.1, Fig. 3) but inconsistent with the result of *rbcL* analysis of Dessein & al. (2001a), showing that *Hekistocarpa* forms a moderately supported clade with *Tamridaea* and *Virectaria*. Within the *Tamridaea-Virectaria-Sabicea* clade, the *Tamridaea-Virectaria* clade and *Sabicea* s.l. clade have unstable positions, due to which the separate relationship between *Hekistocarpa* and *Tamridaea-Virectaria* or *Sabicea* s.l. is unsettled, although *Hekistocarpa* is confirmed as sister to the *Tamridaea-Virectaria-Sabicea* clade.

Within the *Tamridaea-Virectaria-Sabicea* clade, all *Virectaria* accessions form a weakly to strongly supported clade with *Tamridaea* (Chapter 6.2, Fig. 1), which support the sister-group relationship between *Virectaria* and *Tamridaea*, consistent with the combined ITS-*trnT-F* analysis of Khan & al. (2007). These result are also consistent with Bremer & Thulin (1998),



and Robbrecht & Manen (2006), but inconsistent with the result of the *rbcl* analysis of Dessein & al. (2001a). On the other hand, *Sabicea* never forms a clade with any of the genera of Sabiceae s.l. except a weakly supported clade with *Tamridaea* in a *trnT-F* tree, which seems to indicate the close relationship of *Sabicea* s.l. to *Tamridaea*, i.e. an unsettled relationships between *Tamridaea*, *Virectaria*, and *Sabicea*, but its consistency could not be confirmed. None of the relationships between the genera of Sabiceae s.l. is supported by any morphological synapomorphy. They contain some autapomorphic characters or share mostly homoplasious characters (Chapter 6.2, Table 3 & 4, Figs. 3A–H; Chapter 6.1, Table 4; Appendix 2 & 3, Dessein & al. 2001a). This study additionally shows that *Sabicea* s.l. (Khan & al. 2007) is supported, as all sampled species of *Sabicea* s.l. are strongly resolved as a monophyletic group (Chapter 6.2, Fig. 1).

**2.4 Monophyly, infrageneric relationships and phylogeographical origins of *Virectaria*.** — The African herbaceous to semi-woody genus *Virectaria* have established its position in the subfamily Ixoroideae (Rubiaceae; Bremekamp, 1934, 1966; Verdcourt, 1953, 1958; Dessein & al., 2001b), as well as in the tribe Sabiceae s.l. (Bremer & Thulin, 1998; Robbrecht & Manen, 2006; Khan & al., 2007) by its morphological and molecular characteristics. It has been thoroughly revised by Verdcourt (1953) and Dessein & al. (2001b). However, neither the monophyly of the genus, nor the relationships between its species have ever been examined using molecular data sets. Likewise, its biogeographical or phylogeographical origins have never been investigated based on a molecular phylogeny. Khan & al. (2007) showed for the first time that two *Virectaria* species (*V. multiflora*, *V. procumbens*) are strongly resolved as a monophyletic group. In all analyses of this study including molecular and morphological data sets (Chapter 6.2, Fig. 1–2), all *Virectaria* accessions are constantly resolved as strongly supported monophyletic group, consistent with Khan & al. (2007). The morphological synapomorphies of the genus such as splitting of its capsules into one persistent and one deciduous valve, absence of raphides, indistinct calyx tubes, completely exerted anthers (Chapter 6.2, Fig. 3A) truncated stigmata, flat internal indument, and elongated floral disc, perforate sexine, and elongated seed exotesta with prominently thickened angles and small perforations etc. strongly support its resolving as a monophyletic group.

In the most parsimonious ETS-ITS-*rpoC1-trnT-F* tree, all *Virectaria* accessions are resolved in to two major clades – Clade A (*V. herbacoursi*-*V. multiflora* clade; Chapter 6.2, Fig. 2: A) and Clade B (*Virectaria* sp.-*V. angustifolia*-*V. procumbens*-*V. major*-*V. belingana* clade; Chapter 6.2, Fig. 2: B) with strong support. Clade A is further resolved as sister to clade B, mostly consistent with Dessein & al. (2001b), indicating that the *Virectaria* species belonging to each of these two clades are closely related. Clade A is supported by three morphological synapomorphies: the easily visible 2–3 distinct lobes of stipules, long and stiff

trichomes on outer surface of calyx lobes, and two lanceolate to narrowly lingulate and usually bilobed parts of floral disc (Chapter 6.2, Figs. 3B, G). Clade B shares two synapomorphic characters – undivided stipules and undivided cylindrical floral disc (Chapter 6.2, Fig. 3A, 3G). In Clade A, two *V. herbacoursi* accessions, (Chapter 6.2, Subclade I, Fig. 2: I), resolved as sister to all *V. multiflora* (Subclade II, Chapter 6.2, Fig. 2: II), are distinct only by their 1–2 trichomes of outer calyx lobe surface of in contrast to few to many trichomes of *V. multiflora* calyx lobes. Although the sampled members of *V. multiflora* are well resolved in ETS-ITS-*rpoC1-trnT-F* tree, any categorization within this species is morphologically unsupported, consistent with Dessein & al. (2001b).

Subclade III (*Virectaria* spp.-*V. angustifolia*-*V. procumbens*) of clade B is supported by two synapomorphies – short corolla tubes and inward folding of valves. Therefore, the close relationships between two *Virectaria* sp., *V. angustifolia*, and *V. procumbens* are tenable from both molecular and morphological indications. Within this subclade, *Virectaria* sp. 1, resolved as sister to the group of *Virectaria* sp. 2, *V. angustifolia*, and *V. procumbens*, is morphologically distinct by its dwarf (15–18 cm long) semi-erect habit, up to 1 mm long trichomes, densely leaved branches, 0.8–1–2 (–2.5) × 0.4–1.1 cm leaves, spatulate calyx lobes, 4–5 mm long corolla tubes, and undivided disc. Morphologically *Virectaria* sp. 1, collected from Nimba range, Liberia, appears to be an intermediate of *V. procumbens* (Guineo-Congolian species; Fig. 70c, Dessein & al., 2001b) and *V. tenella* J. B. Hall (endemic to Ghana). The widely separate distribution of *Virectaria* sp. 1 and *V. tenella* do not support their conspecificity despite their morphological similarities. On the other hand, its locality is covered by the wide distribution range of *V. procumbens*, to which it appears similar except for its growth habit, densely leaved branches, size of leaves, and longer trichomes. Therefore, it cannot be ruled out that *Virectaria* sp. 1 is a variety of *V. procumbens*. On the other hand, *Virectaria* sp. 2 resolved as sister to *V. angustifolia* and *V. procumbens*, sharing the distinguishing characters of both *V. angustifolia* and *V. salicoides*. The resolving of *V. angustifolia* as sister to *V. procumbens* indicates that they are closely related, although the exact position of *V. salicoides*, appearing most closely related to *V. angustifolia*, is unsettled.

Subclade IV (*V. major*-*V. belingana*; Chapter 6.2, Fig. 2: IV) formed in clade B, is not supported by morphological synapomorphies, rather its members share the synapomorphies either with *V. herbacoursi* and *V. multiflora* (Chapter 6.2, Figs. 3C, F, H) or with *V. angustifolia* and *V. procumbens* (Chapter 6.2, Fig. 3G). Therefore, the close relationship between *V. major* and *S. belingana* is based only on molecular ground. The resolving of two *V. major* as sister to *S. belingana* is inconsistent to Verdcourt's (1953) placement of *V. major* at the central line of his scheme and also incompatible with Dessein & al. (2001b) in hypothesizing *V. major* as the basal species within the clade of *V. angustifolia*, *V. procumbens*, *V. major*, and *V. belingana*. *V. major* is distinct from *V. belingana* by its lack of divaricate branching and fairly longer and filiform to spatulate calyx lobes.

The combined ITS-rpoC1-*trnT*-F tree (Chapter 6.2, Fig. 1) suggest the tropical African, possibly Guineo-Congolian, origin for the whole Sabiceae as *Hekistocarpa*, constantly resolved as sister to the clade of *Tamridaea*, *Virectaria* and *Sabicea* s.l., is Lower-Guinean. The high number of both molecular and morphological autapomorphies of *Tamridaea* indicates for its long isolated evolution. This study reveals for the first time that *Virectaria* species of any of three phylogeographical regions, Upper-Guinea, Lower-Guinea, and Congolia (White 1983), are not closely related, as in the parsimonious tree generated from most combined analysis (Chapter 6.2, Fig. 2), neither the Upper-Guinean (e.g., *V. multiflora* 2, *Virectaria* sp. 1), nor the Lower-Guinean (e.g., *V. herbacoursi*, *V. angustifolia*, *V. belingana*), nor the Congolian elements (e.g., *V. multiflora* 3, *V. major* 1) form a monophyletic group. All *Virectaria* species of the Guineo-Congolian and Zambezan Regional Center of Endemism (White, 1993) are closely related, as all sampled *Virectaria* accessions combinedly form a strongly supported monophyletic group. In contrast, the Lower-Guinean (e.g., *V. herbacoursi*) and the Guineo-Congolian (e.g., all *V. multiflora*), the Upper-Guinean and Lower-Guinean (*Virectaria* sp. 1 and *Virectaria* sp. 2-*V. angustifolia*-*V. procumbens*), the Congolian-Zambezan and the Lower-Guinean elements (e.g., *V. major*, *V. belingana*) form monophyletic groups. These results suggest an ongoing floral exchange or a wide range of dispersal of *Virectaria* species within these regions, without a clearly defined direction of migration. Furthermore, these results appear to indicate the presence of three (*V. herbacoursi* and *V. multiflora*, *V. angustifolia*, and *V. procumbens*, *V. major* and *V. belingana*) vicariant couples within the Guineo-Congolian and Zambezan regional center of endemism (White 1993).

The results of most combined analyses (Chapter 6.2, Fig. 2) further appear to indicate that the Upper- and Lower Guinean population of *V. multiflora* might have originated from its Congolian element, because although *V. multiflora* is a Guineo-Congolian species, its Congolian element (*V. multiflora* 3) is resolved as sister to its Upper Guinean (*V. multiflora* 2) and Lower Guinean (*V. multiflora* 1 and *V. multiflora* 4) elements.

**2.5 Taxonomic revision of Neotropical *Sabicea*.** — The Neotropical *Sabicea* (Rubiaceae, subfamily Ixoroideae, tribe Sabiceae) consisting of 54 species of predominantly vines, lianas or shrubs with lianescent branches, occasionally erect herbs to suffruticose or (sub-) shrubs, occur from southeast Brazil to southern Mexico (Chapter 6.3, Fig. 2). After Wernham (1914), this is the first revisionary study on *Sabicea* of the Neotropics based on the morphological characters of 3300 specimens. This study recognizes 37 species out of the previously described 54 species and merged the remaining 17 presumed species with other well-defined species, as no reason was found for their recognition. Six new species, *S. boyacana* Liede, Meve & Khan (from Colombia), *S. chiapensis* Liede, Meve & Khan *S. cochabambensis* Liede, Meve & Khan (from Bolivia and Peru), *S. liedeeae* Liede, Meve & Khan (from Mexico), *S. noelii* Liede, Meve & Khan (from Bolivia), and *S. tayloriae* Liede, Meve & Khan (from Bolivia, Peru, Brazil, and Ecuador) are reported (Chapter 6.3, Figs.11, 18, 22,

29, 34, 40). Finally, this study provides a comprehensive taxonomic treatment of 43 species, 37 of which are from South America, four from Mesoamerica, and four from both South- and Mesoamerica, with distribution maps for all species, and 30 illustrations, of which 13 are completely new (Chapter 6.3). All descriptions are originally generated from DELTA (Dallwitz & al., 1999) based on 620 vegetative and reproductive characters, and finally presented here after manual editing manual. A detailed indented key to all 43 species, mostly based on the characters of indumentum, calyx lobes, inflorescences, and, scantily, on floral parts, is provided. Lectotypes are designated for *S. amazonensis* Wernham, *S. brasiliensis* Wernham, *S. mexicana* Wernham, *S. mollissima* Benth. ex Wernham, *S. trailii* Wernham, *S. villosa* var. *adpressa* Standl., and *S. villosa* var. *sellowii* (Wernham) Steyerem., all of which are accepted and described in this study. In the Neotropics, the plants of *Sabicea* are widely distributed in five floristic regions (Chapter 6.3, Fig. 1) of Takhtajan' (1986). The highest number of species is found in Brazil (17 sp.), followed by Colombia (15 sp.), Venezuela (15 sp.), Bolivia (12 sp.), Peru (11 sp.), and Ecuador (7 sp.). French Guiana, Guyana, and Suriname harbor five species each (Chapter 6.3, Table 2). The Mesoamerican countries do not harbor more than two species, except for Mexico, where four species including two new ones are found. In none of the Caribbean countries more than one species occur, except for Trinidad & Tobago harboring three species (Chapter 6.3, Table, 1). This study reveals that the highest degree of endemism of the genus in the Neotropics comprising four species appears to occur in Brazil, Bolivia, Venezuela, and Colombia. Mexico harbors three endemic species, Peru two and each of Jamaica and Suriname one (Chapter 6.3, Table, 1).

## 2.6 Taxonomically useful characters of Neotropical *Sabicea*. —

Neotropical *Sabicea* appear to show high ranges of variations in the characteristics of vegetative and reproductive parts, however, the taxonomic utility of most of their morphological characters is limited to inter- and infraspecific delimitations.

Habit: The species of Neotropical *Sabicea* are predominantly vines, lianas or (sub-) shrubs with lianescent branches. Only two species, *S. brasiliensis* and *S. humilis*, are known as erect. Few species occasionally display the erect and few a suffruticose growth habit. The habit character is taxonomically barely applicable in recognizing the species of Neotropical *Sabicea*.

Indumentum: In most of Neotropical *Sabicea*, indumentum of branchlets is comprised of two to few types and appears taxonomically useless. However, the exclusively arachnose or lanate to lanuginose indumentum types or their presence-absence in addition to other indument types are taxonomically useful in specific or infraspecific delimitation. The indumentum types of upper and lower surface of leaves, especially the presence-absence of arachnose or lanuginose to lanate indumentum appears stable in most species (Chapter 6.3, Fig. 2A, F, G, I, J, K, Fig. 18A-C, 21A-C, 23A-C, 28A-C). The presence-absence, types and distribution of indumentum at inner surface of stipules (Chapter 6.3, Fig. 5A, 35E), bracts, and

calyces (Chapter 6.3, Fig. 5E, F, J, 21G, J, 25G, 30F, 32G, 34J, 35H, K, 42I), especially at upper part, entire or serrulate to sparsely denticulate margins, and presence-absence of cilia (Chapter 6.3, Fig. 5D, J, 11H, 22G, 28H, 35D, G, K, 37F) appear stable for some species or group of species. The indumentum types of outer surface of corolla tube, especially the erectness and orientation of trichomes (Chapter 6.3, Fig. 5H, 8H, 13G, 21H, 23F, 41F, 44F), are stable in most of the species and have been found applicable in interspecific delimitation. The indumentum characters of upper and lower surface of leaves, inner and external surface of stipules, bracts, and calyces, and external surface of corolla tubes, and ovaries are useful in taxonomic delimitation, usually with and sometimes without the combination of other diagnostic characters. The usefulness of indument characters of stipules bracts and inner surface of calyx lobes is hardly known from previous studies.

The colleters of *Sabicea* are almost unknown from the previous studies except those of Steyermark (1967, 1974). In this study, the position of colleters has been found as an important source of taxonomic characters. The number and location of colleters inside the base or basal part of bracts and at or near the sinus or near the middle inside the calyx tubes (Chapter 6.3, Fig. 5F, J, 26G, 32G, 34J, 42I) have been found as discrete and consistent which indicate their taxonomic utility in species delimitation.

**Stipules:** The ranges of variation in size (2–20 × 2–15 mm), margins (Chapter 6.3, Fig. 5D), orientation, division, and number of main veins (5–24) per stipule seem stable in some species. The stipule characters of Neotropical *Sabicea* appear useful for some inter- or infraspecific delimitations.

**Leaves:** Although the leaf shape or size hardly have been found constant, the variation in leaf apex and leaf base (Chapter 6.3, Fig. 5A, 23A, 34A, 44A), and thickness, length (2–18 cm) and width (0.5–11 cm) of lamina appear discrete and stable in some species, indicating the limited usefulness of these characters. The variation in number (7–20 pairs) and position of costa and secondary veins at upper leaf surface, and the length (0.2–5 cm) of petioles appear occasionally constant due to which their taxonomic utility is very narrow.

**Inflorescences:** The inflorescences are variable from sessile to (sub-) sessile, (sub-) sessile to shortly (3–8 mm long) pedunculate, and distinctly (1–4.5 cm long) pedunculate. Accordingly, the inflorescence are comprised of verticillate to glomerulate, verticillate (Chapter 6.3, Fig. 36A, D, Fig. 17A, E, 46A, E.), capitate (Chapter 6.3, Fig. 40A, F), capitate to compact fasciculate (Chapter 6.3, 15A, F, 34A, F), compact fasciculate (Chapter 6.3, Fig. 5A, E, 32A, D42E), verticillate to umbellate, umbellate (Chapter 6.3, Fig. 26D, 31E, 35F), or paniculate (Chapter 6.3, Fig. 37E), and lax paniculate or thyrsoid (Chapter 6.3, Fig. 22A, 41A) types. This variation in inflorescence structures is not always discrete and constant, however, mostly found as important taxonomic character for species delimitation, in addition to other characters. The range of variation in inflorescence size (1–8 × 0.7–7.5 cm, excluding peduncles), lengths of primary axis (0.1–6.5 cm) and flower numbers (1–88) per inflorescence appear as constant for few groups of species. The division of bracts, length and diameter of

involucre, length and width of exinvolucrate bracts, and apex and margins of bracts appear as the source of some important characters that can be useful for interspecific delimitation.

Flowers: Many Neotropical *Sabicea* species produce usually pedicellate flowers, 16 species sessile to subsessile flowers, and only four species strictly sessile flowers. The ranges of variation in pedicel lengths (0.5–15 mm) are mostly coinciding but distinct only in a few species. The types of calyces (Chapter 6.3, Fig. 5H, J, 8E, H, J, 29E, H, 32E, G, 42G, I), lengths and diameters of calyx tubes (0.3–11 mm and 0.8–6.5 mm respectively) and lengths and widths (0.2–15 mm and 0.1–7 mm, respectively) of calyx lobes, and the shape (Chapter 6.3, Fig. 5J, H, 8H, J 23F, 28F, H, 33F, 34H, 43F, H), erectness, margins and apex type of calyx lobes in Neotropical *Sabicea* are proved as noteworthy, though sometimes labile. Markedly unequal calyx lobes exist in few species (Chapter 6.3, Fig. 30D, F). Lengths of corolla tubes (2.7 mm to 25 mm) and widths (1.5 to 7 mm), length-width ratios or shape of corolla lobes appear to be species-specific for some species. The insertion points of stamens in corolla tubes (at 1.8–20 mm from the base of tubes) and anther's lengths (0.8–4 mm) show a considerable range of variation that seem consistent for few groups of species. The taxonomic utility of locule number seems unreliable due to its overlapping and unstable variation.

Fruits and Seeds: The ranges of variation in colour (pale to dark red or crimson, pinkish, purplish, violet), size of fruits (5–18 × 5–18 mm) and size of seeds (0.3–1 × 0.2–0.8) appear as narrow and unstable for most of the species due to which these characters appear taxonomically inapplicable for inter- and infraspecific delimitation.

It has not yet been investigated in detail whether the sharing of characters by two or more species of Neotropical *Sabicea* is due to homoplasy or synapomorphy. In this study it appeared impossible to recognize all Neotropical *Sabicea* from African *Sabicea* based on any consistent character. Apart from African *Sabicea*, the Neotropical species of *Sabicea* do not share also any synapomorphic character. Therefore, the characteristics of Neotropical *Sabicea* found in this revisionary study are inconsistent to their emerging as a monophyletic group in Khan & al. (2007), but consistent to their close relationships with African *Sabicea*. It has been shown in other families that geography is sometimes a better indication of relationship than character similarity, which might have evolved due to similar environmental pressures (e.g., Liede-Schumann & al., 2005). In this study, it has been revealed that it is impossible to characterize most of the Neotropical species *Sabicea* based on any single or unique character. Finally, this study forecasts the prospects of further comprehensive studies for the reclassification within the tribe Sabiceae, especially within the genera *Sabicea* s.l. and *Virectaria*, continuing the exploration of the genus *Sabicea* in the Neotropics, and the revisionary work on African *Sabicea*. Based on the formidability and restrictions experienced during the revisionary work, this study evokes the urgency of collaborative scientific involvements to accomplish the revision of the genus of tropical Africa.

### 3. SUMMARY

The pantropical tribe Sabiceae (Ixoroideae s.l., Rubiaceae) has been variously circumscribed previously, resulting in strong conflicts in its tribal and generic limits. The monophyly of Sabiceae including its all established genera or the monophyly of any non-monotypic genus traditionally included in this tribe has never been examined using molecular data sets. Neither the relationships within this tribe, nor the relationships within any of its genera have ever been explored using molecular data. *Sabicea*, the type and most species rich genus of the tribe and the single genus of Rubiaceae showing African-Asian-American disjunction, has not been revised to any extent after its first monographic treatment (Wernham, 1914), mostly based on typological concept, although the second major genus *Virectaria* has been revised recently (Dessein & al., 2001b). These lacunae in phylogenetic and descriptive knowledge on the tribe Sabiceae and its genera have evoked the need of the present study. This study has focused on the tribal circumscription of Sabiceae and Virectarieae, monophyly and biogeography of *Sabicea*, phylogenetic relationships within the tribe Sabiceae, monophyly of the genus *Virectaria* and relationships between its species, phylogeography of *Virectaria*, taxonomic revision of Neotropical *Sabicea*, and taxonomical utility of morphological characters for the classification of Neotropical *Sabicea*.

The present study reveals for the first time that neither the tribe Virectarieae, currently established as the associated tribe of Sabiceae, nor the subtribe Virectariinae, recently proposed to accommodate the genera of Virectarieae, is monophyletic; rather, the tribe Sabiceae including the genera of Virectarieae or Virectariinae is strongly resolved as a monophyletic group in *trnT-F* (Chapter 6.1, Fig. 1) and combined ITS-*trnT-F* trees (Chapter 6.1, Fig. 3). Consequently, this study suggests the broad circumscription of the tribe Sabiceae (Sabiceae s.l.) consisting of eight genera: *Ecpoma*, *Hekistocarpa*, *Pseudosabicea*, *Sabicea*, *Schizostigma*, *Stipularia*, *Tamridaea*, and *Virectaria* based on the robust phylogeny inferred from the analysis of ITS and *trnT-F* data (Chapter 6.1, Fig. 3). Additionally, this study suggests the placement of both *Pentaloncha* and *Temnopteryx*, previously included in Sabiceae, in subfamily Rubioideae. There is no potential morphological synapomorphy to diagnose this newly delimited Sabiceae, nor to distinguish Virectarieae or Virectariinae. Therefore, the monophyly of the newly delimited Sabiceae s.l. is entirely based on molecular data.

This study further reveals that the genera *Ecpoma*, *Pseudosabicea*, *Sabicea*, *Schizostigma*, and *Stipularia*, traditionally associated with the tribe Sabiceae, together form a monophyletic group and their morphological distinctions are not clear-cut. Therefore, all of these genera are merged under *Sabicea* s.l., and as result, finally the tribe Sabiceae s.l. is recognized with four genera: *Hekistocarpa*, *Sabicea* s.l., *Tamridaea*, and *Virectaria*. The resolved clades of combined ITS-*trnT-F* tree (Chapter 6.1, Fig. 3) indicate that the São

Tomean, Malagasy, and all Neotropical *Sabicea* presumably originated from African ancestors. They reached São Tomé & Príncipe, Madagascar, and the Neotropics independently via three single long-distance dispersal events. Two hypotheses are postulated here for explaining the means of the major dispersal events- 1) by wind and/or ocean currents or 2) by birds. This study also indicates that most probably the major diversification of *Sabicea* s.l. started in mainland Africa and the second major radiation occurred through starting the colonization of the genus in the Neotropics. The presence of only one species– *Sabicea ceylanica* in Sri Lanka indicates the unsuccessful diversification of the genus in Asia.

The results of combined ITS-*rpoC1-trnT-F* analysis (Chapter 6.2, Fig. 1) suggest that the monotypic genus *Hekistocarpa*, restricted to Cameroon and Nigeria, is closely related with the group of the Guineo-Congolian wide genus *Virectaria*, the monotypic *Tamridaea*, confined to Socotra of Yemen, and the Pantropical *Sabicea* s.l., as *Hekistocarpa* is constantly resolved as sister to the *Tamridaea-Virectaria-Sabicea* clade. Within the *Tamridaea-Virectaria-Sabicea* clade, the *Tamridaea-Virectaria* Clade and the *Sabicea* Clade change their positions depending on the data set. Supporting morphological synapomorphies are absent here as well as in the whole tribe Sabiceae s.l. The clade of all *Virectaria* accessions strongly resolved in the ITS-*rpoC1-trnT-F* tree supports the monophyly of the genus *Virectaria*, consistent with its ample morphological synapomorphies. The combined ETS-ITS-*rpoC-trnT-F* tree (Chapter 6.2, Fig. 2) exhibits the close relationships within the genus under two highly resolved groups, and the monophyly of the six sampled species of *Virectaria* in correspondence to their morphological characters.

The resolved clades of the combined ITS-*rpoC1-trnT-F* tree suggest the tropical African, possibly Guineo-Congolian, origin for the whole Sabiceae as *Hekistocarpa*, constantly resolved as sister to the clade of *Tamridaea*, *Virectaria* and *Sabicea* s.l., is Lower-Guinean. The high number of both molecular and morphological autapomorphies of *Tamridaea* testifies only for a long isolated evolution. The species of *Virectaria* are distributed over the four phylogeographical regions, Lower- and Upper-Guinean, Guineo-Congolian and Zambezi region, but the species of these regions are not closely related. The resolved clades of *Virectaria* (Chapter 6.2, Fig. 2) also indicate the floral exchange between these regions. The ETS-ITS-*rpoC-trnT-F* tree indicates the presence of at least three (*V. herbacoursi* and *V. multiflora*, *V. angustifolia*, and *V. procumbens*, *V. major* and *V. belingana*) vicariant couples within the Guineo-Congolian and Zambezi regional center of endemism.

The taxonomic revision of Neotropical *Sabicea*, based on a large bulk of specimens, recognizes 37 species from the previously described 54 species and merges the remaining 17 with other well-defined species of the genus, as no reason was found for their recognition. Additionally six new species (*S. boyacana*, *S. chiapensis*, *S. cochabambensis*, *S. liedae*, *S. noelii*, and *S. tayloriae*; Chapter 6.3, Figs.11, 18, 22, 29, 34, 40) are reported. Finally, this revisionary study provides a comprehensive taxonomic treatment of 43 species, 37 from South America and five from Mesoamerica, with distribution maps and 30 illustrations



(Chapter 6.3). All descriptions are originally generated from DELTA (Dallwitz & al., 1999) using 620 vegetative and reproductive characters. A detailed indented key to all of 43 species is provided. Lectotypes are designated for six species. This study reveals that the highest degree of endemism of the genus in the Neotropics occurs in Brazil, Bolivia, Venezuela, and Colombia with four species each. Mexico harbors three endemic species, Peru two and Jamaica and Surinam one each.

The studies on morphological characters of Neotropical *Sabicea* prove that the taxonomic utility of most of the characters is limited for inter- and infraspecific delimitations and it is barely possible to define a Neotropical species based on a single character. Types and composition of indumenta, especially of leaves and flowers, types of inflorescences, lengths of calyx tubes, and shape, size and orientation of calyx lobes are the main sources of taxonomically useful characters for the classification of Neotropical *Sabicea*. Taxonomical utility of habit types, characters of stipules, leaves, and bracts, and position of colleters in calyces, however, is very limited.

Lastly, this study is an excellent base for the completion of the reclassification within the tribe Sabiceae, especially within the genera *Virectaria* and *Sabicea* s.l. in Africa.

## 4. ZUSAMMENFASSUNG

Die pantropische Tribus Sabiceae (Ixoroideae s. l., Rubiaceae) ist in der Vergangenheit mehrfach umschrieben worden, wobei sich große Konflikte sowohl bei der Umschreibung als auch bei der Gattungsabgrenzung innerhalb der Tribus ergaben. Die Monophylie der Tribus ist bislang in keiner ihrer Umschreibungen mit Hilfe molekularer Datensätze bestätigt worden. *Sabicea*, die Typusgattung, die zugleich auch die artenreichste Gattung der Tribus darstellt, und die einzige Gattung der Rubiaceae mit afrikanisch-asiatisch-amerikanischer Disjunktion, ist seit ihrer ersten monographischen Untersuchung durch Wernham (1914), die überwiegend ein typologisches Artkonzept vertritt, nicht mehr revidiert worden. Die zweitgrößte Gattung, *Virectaria*, wurde dagegen vor einigen Jahren revidiert (Dessein & al., 2001b). Diese Lücken, sowohl in der Kenntnis der Phylogenie als auch des taxonomischen Merkmalsbestandes der Tribus Sabiceae, haben die vorliegende Studie angeregt. Zunächst wurde die Umschreibung der Tribus Sabiceae und Virectarieae geklärt, dann die phylogenetischen Zusammenhänge innerhalb der Sabiceae untersucht. Weiterhin wurde die Monophylie der Gattung *Virectaria* sowie die Verwandtschaftsverhältnisse zwischen ihren Arten und ihre Biogeographie geklärt. Schließlich wurde eine taxonomische Revision der Neuweltarten der Gattung *Sabicea* sowie eine Analyse taxonomischer wichtiger morphologischer Merkmale in dieser Gruppe vorgenommen.

Die vorliegende Studie zeigt zum ersten Mal, daß weder die Tribus Virectarieae, die derzeit als eine den Sabiceae nahestehende Tribus gilt, noch die Subtribus Virectariinae, die vor kurzem für die Gattungen der Virectarieae vorgeschlagen wurde, monophyletisch sind, vielmehr stellt die Tribus Sabiceae zusammen mit den Virectarieae (oder Virectariinae) eine sehr gut unterstützte Gruppe in den molekularen Analysen von *trnT-F* (Kapitel 6.1, Abbildung 1) und einer Kombination von ITS und *trnT-F* dar (Kapitel 6.1, Abbildung 3). Entsprechend wird eine weite Umschreibung der Tribus Sabiceae (Sabiceae s.l.) mit acht Gattungen, *Ecpoma*, *Hekistocarpa*, *Pseudosabicea*, *Sabicea*, *Schizostigma*, *Stipularia*, *Tamridaea* und *Virectaria*, vorgeschlagen. Außerdem wird die Überführung der Gattungen *Pentaloncha* und *Temnopteryx*, die bisher als Mitglieder der Sabiceae angesehen wurden, in die Unterfamilie Rubioideae unterstützt. Eine morphologische Synapomorphie, die diese Umschreibung der Tribus unterstützt, wurde nicht gefunden, auch keine, die es erlauben würde, Virectarieae oder Virectariinae abzutrennen. Folglich basiert die neue Umschreibung von Sabiceae ausschließlich auf molekularen Daten.

Es konnte gezeigt werden, daß die Gattungen *Ecpoma*, *Pseudosabicea*, *Sabicea*, *Schizostigma* und *Stipularia*, die auch traditionell mit der Tribus Sabiceae in Verbindung gebracht wurden, eine monophyletische Gruppe bilden, wenngleich auch ihre morphologische Differenzierung keinesfalls eindeutig ist. Daher wurden diese Gattungen unter *Sabicea* s.l.

zusammengefaßt, womit die neue Tribus Sabiceae nunmehr die vier Gattungen *Hekistocarpa*, *Sabicea* s. l., *Tamridaea* und *Virectaria* enthält. Die aufgelösten Clades der kombinierten ITS-*trnT-F* Analyse (Kapitel 6.1, Abbildung 3) lassen darauf schließen, daß die *Sabicea*-Arten der Neotropis, Madagaskars und São Tomés mit großer Wahrscheinlichkeit jeweils von afrikanischen Vorfahren abstammen. Sie sollten unabhängig voneinander mittels dreier einzelner Fernausbreitungsereignisse in ihre neuen Areale gelangt sein. Es werden zwei Hypothesen für den Mechanismus der Fernausbreitung diskutiert – 1) durch Wind oder Ozeanströmungen oder 2) durch Vögel. Die stärkste Differenzierung innerhalb von *Sabicea* hat auf dem afrikanischen Festland stattgefunden. Eine weitere Differenzierung ist nach der Kolonisierung der Neotropen durch die Gattung erfolgt. Das Vorkommen von lediglich einer einzigen Art, *Sabicea ceylanica*, auf Sri Lanka läßt auf eine ausgebliebene Radiation der Gattung in Asien schließen.

Aus der kombinierten ITS-*rpoC1-trnT-F*-Analyse (Kapitel 6.2, Abbildung 1) läßt sich ablesen, daß die auf Kamerun und Nigeria beschränkte monotypische Gattung *Hekistocarpa* nahe mit der im Guinea-Congo-Gebiet verbreiteten Gruppe um *Virectaria*, der monotypischen, yemenitischen *Tamridaea* sowie der pantropischen *Sabicea* s.l. verwandt ist. Während jedoch *Hekistocarpa* stets als Schwestergattung zu den restlichen drei Gattungen identifiziert wird, wechseln die Positionen der zwei Clades (Der *Tamridaea-Virectaria* Clade und *Sabicea* Clade) auf dem *Tamridaea-Virectaria-Sabicea* Clade. Für keine der Kombinationsmöglichkeiten finden sich morphologische Synapomorphien. Der Clade aller untersuchten *Virectaria*-Aufsammlungen ist im ITS-*rpoC1-trnT-F* Cladogram statistisch gut abgesichert und unterstützt damit die Monophylie der Gattung *Virectaria*, für die auch etliche morphologische Synapomorphien bestehen. Das kombinierte ETS-ITS-*rpoC1-trnT-F* Cladogram (Kapitel 6.2, Abbildung 2) zeigt die engen Beziehungen innerhalb der Gattung und ihren zwei stark unterstützten Gruppen, und es bestätigt die Monophylie der sechs *Virectaria*-Arten in Übereinstimmung mit deren morphologischen Merkmalen.

Das konstante Verhältnis von *Hekistocarpa* als Schwester zu *Tamridaea*, *Virectaria* und *Sabicea* s.l. im ITS-*rpoC1-trnT-F* Cladogram läßt auf einen Ursprung der Tribus im tropischen Afrika, möglicherweise in Guinea-Kongo, schließen. Die große Zahl an molekularen und morphologischen Autapomorphien bei *Tamridaea* weist auf ihre lang andauernde unabhängige Evolution hin. Die *Virectaria*-Arten sind über die vier Phylogeographische Regionen Unterguinea, Oberguinea und Guinea-Kongo und der Zambesi-Region verbreitet, jedoch innerhalb der einzelnen Regionen nicht nahe miteinander verwandt. Die erhaltenen Clades in *Virectaria* (Kapitel 6.2, Abbildung 2) deuten auf lebhaften floristischen Austausch zwischen den Regionen Unterguinea, Oberguinea und Guinea-Kongo hin. Die wenigstens drei vikarianten Artenpaare (*V. herbacoursi* and *V. multiflora*, *V. angustifolia*, and *V. procumbens*, *V. major* and *V. belingana*) deuten auf einen erheblichen genetischen

Austausch besonders innerhalb den Endemismuszentren Guinea-Kongo und der Zambesi-Region hin.

Die Revision der Neotropischen *Sabicea*-Arten, die auf einer großen Zahl von Herbarbögen beruht, anerkennt 37 der bisher beschriebenen 54 Arten und subsummiert die verbleibenden 17 unter andere, gut definierte Arten der Gattung. Zusätzlich werden sechs neue Arten beschrieben (*S. boyacana*, *S. chiapensis*, *S. cochabambensis*, *S. liedeeae*, *S. noelii* und *S. tayloriae*; Kapitel 6.3, Abbildung 11, 18, 22, 29, 34, 40). Diese Revision umfaßt eine umfassende taxonomische Beschreibung der 35 südamerikanischen, 4 mittelamerikanischen und 4 süd- und mittelamerikanischen Arten werden hier umfassend neu beschrieben, inkl. Verbreitungskarten und 30 Illustrationen. Alle Beschreibungen wurden ursprünglich aus DELTA (Dallwitz & al., 1999) generiert, wobei die Merkmalsliste 620 vegetative und generative Merkmale umfaßt. Ein dichotomer Schlüssel zu allen 43 Arten wurde erstellt (Kapitel 6.3). Lektotypen werden für sechs Arten ausgewählt. Diese Analyse zeigt, daß der höchste Endemismusgrad in den Neotropen in Brasilien, Bolivien, Venezuela und Kolumbien mit je vier Arten erreicht wird, während Mexiko nur drei, Peru zwei und Jamaika und Surinam jeweils eine endemische Art aufweisen.

Der taxonomische Nutzen der meisten der untersuchten morphologischen Merkmale ist für die inter- und infraspezifische Abgrenzung sehr beschränkt. Es ist fast unmöglich, eine Neuweltart anhand eines einzigen Merkmals zu umgrenzen. Es konnte aber gezeigt werden, daß die Behaarungstypen, insbesondere der Blätter und Blüten, die Blütenstandstypen, die Länge der Kelchröhren sowie die Form, Größe und Orientierung der Kelchzipfel taxonomisch verwertbarer Merkmale für die Klassifikation der neotropischen *Sabicea*-Arten darstellen. Der taxonomische Nutzen der Wuchsformtypen, Nebenblattmerkmale, Blatt- und Brakteenmerkmale sowie die Position der Kolleteren im Kelch ist dagegen beschränkt.

Die vorliegende Arbeit ist eine hervorragende Basis für die Vollendung der Reklassifikation der Sabiceeae, insbesondere innerhalb von *Virectaria* und *Sabicea* s.l. in Afrika.

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## Sabiceae and Virectarieae (Rubiaceae): One or two tribes? – New tribal and generic limits of Sabiceae and biogeography of *Sabicea* s.l.

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The results of two phylogenetic studies led to the reinstatement of the tribe Sabiceae, currently classified in the subfamily Ixoroideae s.l. (Rubiaceae), but with two conflicting circumscriptions. In the present study, phylogenetic analyses based on both the ITS and *trnT-F* sequence data of 78 taxa are performed to: (1) test the monophyly of the competing circumscriptions of Sabiceae and *Sabicea*; (2) assess the phylogenetic relationships within Sabiceae; and (3) infer the biogeographical origin of *Sabicea*. The genera *Pentaloncha* and *Temnopteryx*, previously included Sabiceae sensu Andersson, are shown not to belong to Ixoroideae s.l. but to the subfamily Rubioideae. Our results favour a broad circumscription of Sabiceae that includes *Ecpoma*, *Hekistocarpa*, *Pseudosabicea*, *Sabicea*, *Schizostigma*, *Stipularia*, *Tamridaea*, and *Virectaria*. *Sabicea* sensu Wernham is not monophyletic, unless *Ecpoma*, *Pseudosabicea*, *Schizostigma*, and *Stipularia* are included. We find no support for the monophyly of *Stipularia* and *Sabicea* and *Pseudosabicea* both sensu Hallé. Our newly circumscribed Sabiceae contains only *Hekistocarpa*, *Sabicea* s.l. (*Ecpoma*, *Pseudosabicea*, *Schizostigma*, and *Stipularia*), *Tamridaea*, and *Virectaria*. Finally, our analyses indicate continental African origins of the Malagasy, São Tomean, Asian, and Neotropical *Sabicea* s.l. most likely via independent single long dispersal events.

KEYWORDS: biogeography, ITS, Rubiaceae, *Sabicea*, Sabiceae, *trnT-F*, Virectarieae.

### INTRODUCTION

The pantropical group Sabiceae was described for the first time by Grisebach (1864) as the fourth of eight subtribes of his tribe Cinchonaceae based on its valvate corolla lobes. Grisebach's (1864) subtribe Sabiceae included two genera (*Sabicea* Aubl. and

*Coccocypselum* P. Br.). Bremekamp (1934) described Sabiceae, originally spelled as Sabiceae, for the first time as a monogeneric tribe due to its axillary inflorescences. No rubiacean taxonomist, except Bremekamp (1934, 1966), accepted the tribal status of Sabiceae between 1934 and 1996 (see Table 1). The type genus *Sabicea* was classified either in the Isertieae (Verdcourt, 1958; Hallé, 1961; Hallé, 1966; Steyermark, 1962, 1972, 1974; Kirkbride, 1979, 1982; Robbrecht, 1988, 1993), the tribal name having priority over Mussaendeae.

Bremekamp (1966) made the last attempt to re-establish his Sabiceae based on its simple stipules, axillary inflorescences, and very narrow testa cells rather than bifid stipules, terminal inflorescences, and large testa cells in his Mussaendeae. Hallé (1961) classified *Sabicea* and its four paleotropical and traditionally or currently associated genera [*Ecpoma* K. Schum. (Schumann, 1896), *Pentaloncha* Hook. f. (Hooker, 1873a), *Stipularia* P. Beauv. (Beauvois, 1807), and *Temnopteryx* Hook. f. (Hooker, 1873a)] in Mussaendeae, Hallé (1966) placed the genera like *Ecpoma* and *Pseudosabicea*, in the subtribe Mussaendenae, whereas, *Pentaloncha* in the subtribe Urophyllinae of Mussaendeae.

Steyermark (1962) classified the Neotropical *Isertia* Schreb., *Pittierothamnus* Steyerm. (Steyermark, 1962), and *Sabicea* in Mussaendeae but later merged *Pittierothamnus* with *Amphidasya* Standl. (Steyermark, 1972, 1974). Kirkbride (1979, 1982), endorsed by Robbrecht (1988), placed *Amphidasya* (including *Pittierothamnus*) and *Sabicea* in Isertieae. Robbrecht (1988) also transferred the Indo-Malesian genus *Acranthera* Arn. ex Meisn. (Meisner, 1838), previously placed by Bremekamp (1966) in its own tribe, and the above four paleotropical genera there (Table 1).

Sabiceae was resurrected as a result of the morphological-based phylogeny of Isertieae sensu Robbrecht (1988) conducted by Andersson (1996). Sabiceae sensu Andersson (1996) contained nine genera: *Acranthera*, *Amphidasya*, *Ecpoma*, *Pentaloncha*, *Pittierothamnus*, *Pseudosabicea*, *Sabicea*, *Schizostigma* Arn. ex Meisn. (Meisner, 1838), and *Temnopteryx*. *Stipularia* was deeply nested within Sabiceae sensu Andersson (1996: Fig. 5) but was not among the nine genera he recognized in his Sabiceae. Based on a *rbcl* phylogeny Bremer and Thulin (1998) strongly showed that Sabiceae sensu Andersson (1996) was highly polyphyletic, as *Amphidasya* was resolved with high support (BS = 97) as sister to *Pauridiantha* Hook. f. (Hooker, 1873a) in the subfamily Rubioideae. They additionally questioned the placement of *Acranthera* in Sabiceae and postulated that the genus might perhaps belong to Rubioideae. Their hypothesis was consistent with Alejandro & al.'s (2005: Fig. 1) *trnT-F*-based phylogeny. Bremer and Thulin (1998) showed for the first time that the African genus *Virectaria* Bremek., previously placed by Verdcourt (1958) in its own tribe Virectarieae, is closely related to *Pseudosabicea* and *Sabicea*. Accordingly, they tentatively proposed another broad circumscription of Sabiceae including *Pseudosabicea*, *Sabicea*, *Virectaria*, and their new genus *Tamridaea* Thulin & B. Bremer (Bremer and Thulin, 1998). They considered *Stipularia* to be closely related to *Pseudosabicea* and *Sabicea* based on

morphological ground (e.g., seed exotesta with narrow cells, distinct thickenings on the radial walls, with large pits and knobs). In their morphological and anatomical studies of *Virectaria*, Dessein & al. (2001a: 22) supported the placement of *Tamridaea* in Sabiceae sensu Bremer and Thulin (1998) but considered *Virectaria* to be an isolated genus within the tribe based on some morphological characters (e.g., internal indument and seed anatomy). Dessein & al.'s (2001b) *rbcL* evidence confirmed the close relationships between *Tamridaea* and *Virectaria*. Both their *rbcL* and *rps16* jackknife trees showed for the first time that the African monotypic genus *Hekistocarpa* Hook. f. (Hooker, 1873b), previously placed in the tribe Hedyotideae (e.g., Robbrecht, 1988), is closely related to *Virectaria* and *Tamridaea*. Surprisingly, they argued against the placement of *Tamridaea* in Sabiceae sensu Thulin (1998) and placed, instead, *Tamridaea*, *Hekistocarpa*, and *Virectaria* in their emended tribe Virectarieae. In addition, they restricted Sabiceae to include *Ecpoma*, *Pentaloncha*, *Pseudosabicea*, *Sabicea*, and *Stipularia*. Dessein & al. (2001b: 75) stressed that they “fail to find any morphological characteristics that are common to the five genera (*Hekistocarpa*, *Pseudosabicea*, *Sabicea*, *Tamridaea*, and *Virectaria*) of Sabiceae in a broad sense” but also admitted that their emended Virectarieae was difficult to diagnose morphologically. More recently, Robbrecht and Manen (2006) adopted another broader circumscription of Sabiceae including the following eight genera: *Ecpoma*, *Hekistocarpa*, *Pseudosabicea*, *Sabicea*, *Schizostigma*, *Stipularia*, *Tamridaea*, and *Virectaria*; plus, they recognized two subtribes, Sabiceinae (Bremek.) Robbr. & Manen (including *Ecpoma*, *Pseudosabicea*, *Sabicea*, *Schizostigma*, and *Stipularia*) and Virectariinae (Verdc.) Robbr. & Manen corresponding to Virectarieae sensu Dessein & al. (2001b) (including *Hekistocarpa*, *Tamridaea*, and *Virectaria*). The above conflicting circumscriptions of Sabiceae (see also Table 1) drew our attention to further investigations.

Within Sabiceae sensu Bremer & Thulin (1998) or sensu Dessein & al. (2001b), *Sabicea* is the most species-rich genus with ca. 145 species of scandent shrubs, woody climbers and scramblers or twiners. With two centres of diversity, mainland Africa (ca. 82 species) and the Neotropics (ca. 54 species), *Sabicea* shows a trans-Atlantic distribution shared with few other Rubiaceae genera. Six species are endemic to Madagascar (Razafimandimbison and Miller, 1999), three to São Tomé and Príncipe (Joffroy, 2001), and one, *S. ceylanica* Puff. (Puff & al., 1998), originally described as *Schizostigma hirsutum* Arn. ex Meisn. (Meisner, 1838), to Sri Lanka. Aublet (1775) originally described *Sabicea* from South America including two species, *S. aspera* Aubl. and *S. cinerea* Aubl., with twining habits and 3–5-locular ovaries. Wernham (1914) proposed a broad circumscription of *Sabicea* including 105 species from Africa and South America with usually shrubby, climbing or prostrate to scrambling habits, isophyllous or anisophyllous leaves, entire to fimbriate or lacinate stipules, axillary inflorescences, (sub-) free bracts, valvate corolla lobes, and (2) 4–5-locular ovaries. Wernham (1914), endorsed by Hiern (1877), Hallé (1961), Hallé (1963, 1966), Andersson (1996), Bremer and Thulin (1998), and Dessein & al. (2001b), recognized

the African *Stipularia* as a distinct genus because of its large stipules and well-developed campanulate involucre bracts completely surrounding the entire inflorescence (Beauvois, 1807). On the other hand, Hepper's (1958) herbarium studies on the involucre bracts of some African *Sabicea* species (e.g., *S. venosa* Benth., *S. capitellata* Benth, *S. dewevrei* De Wild. & T. Durand, *S. cordata* Hutchinson & Dalziel, and *S. urceolata* Hepper) and *Stipularia africana* P. Beauv. (type species of *Stipularia*) revealed that involucre bracts also occurred in these *Sabicea* species with the degree of fusion varying from inconspicuous bracts (e.g., *S. venosa*), to free bracts forming a distinct involucre (e.g., *S. capitellata*) to bracts basally fused to fused up to half length (e.g., *S. dewevrei*), or fused into a close-fitting campanulate cup around the calyx of the solitary flower (e.g., *S. cordata*) or completely fused into a campanulate cup with several flowers (e.g., *S. urceolata*). In addition, Hepper (1958) noticed that *Stipularia* species (e.g., *S. elliptica* Schweinf. ex Hiern) have also small stipules. As a result, he merged the five described species of *Stipularia* (*S. africana*, *S. efulenensis* Hutchinson, *S. elliptica*, *S. gabonica* Hiern and *S. mollis* Wernham) with *Sabicea*. Both Hallé (1961) and Hallé (1963, 1966) rejected Hepper's (1958) circumscription of *Sabicea* and reinstated *Stipularia* as a distinct genus. Hallé (1963) viewed *Sabicea* sensu Wernham (1914) as morphologically heterogeneous and accordingly restricted the genus to include only species with usually lianescent, slender and twining habit, long corollas, (4)–5-locular ovaries, fleshy juicy fruits with often-red carmine pulp, accrescent fleshy axis of ovary, and narrow, thin and sessile placentae. He then described the genus *Pseudosabicea* to accommodate all the previously described African *Sabicea* species with creeping or climbing but non-twining habit, small corolla, 2–(3)-locular ovaries, scanty fleshy fruits with colourless pulp, non-fleshy centre and oblong, peltate and fleshy placentae. In addition, Hallé (1963) transferred five African *Sabicea* species (*E. bicarpellata* K. Schum., *E. cauliflora* Hiern, *E. geantha* Hiern, *E. gigantostipula* K. Schum., and *E. hierniana* (Wernham) N. Hallé & F. Hallé) to the African genus *Ecpoma*. Arnott (1839) viewed *Schizostigma* as closely related to *Sabicea* and more recently, Puff & al. (1998) merged *Schizostigma* in *Sabicea*, which they considered to be closely related to *Ecpoma*, *Pseudosabicea*, *Stipularia*, and *Temnopteryx*. Finally, Hiern (1877) attempted to merge both *Pentaloncha* and *Temnopteryx* with *Schizostigma*, but this was totally rejected by Hallé (1961), Hallé (1966) and Puff & al. (1998). Although most Rubiaceae systematists seem to accept *Sabicea* sensu Hallé (1963, 1966), the monophyly of the above conflicting circumscriptions of *Sabicea* or its close allies have never been tested before.

Finally, Wernham (1914) recognized two subgenera (*Sabicea* subgenus *Stipulariopsis* Wernham with nine species and *Sabicea* subgen. *Eusabicea* Wernham with 96 species) for his *Sabicea* based on the combination of habit and leaf and stipule sizes. To the former subgenus belong erect shrubs, often subherbaceous, with leaves at least 20 cm long (when mature), whereas the latter subgenus is usually comprised of scandent shrubs with leaves up to 15 cm long (Wernham, 1914). *Sabicea* subgen. *Stipulariopsis* included five of the six

*Ecpoma* species (Hallé, 1963) [*E. bicarpellata* (K. Schum.) N. Hallé, *E. cauliflora* (Hiern) N. Hallé, *E. geantha* (Hiern) N. Hallé, *E. gigantostipula* (K. Schum.) N. Hallé, and *E. hierniana*].

Previous phylogenetic studies in some Rubiaceae groups based on the ITS region of rDNA (e.g., Andreasen & al., 1999; Razafimandimbison & al., 2004; Motley & al., 2005) and the *trnT-F* region of chloroplast DNA (e.g., Razafimandimbison and Bremer, 2002; Alejandro & al., 2005) have demonstrated that both markers are useful for inferring phylogenetic relationships at tribal and generic levels in the family. The main objective of this study is to reconstruct phylogenies of *Sabicea* and its closely related genera using both ITS and *trnT-F* sequence data. The resulting phylogenies will be used to: 1) test the monophyly of the conflicting circumscriptions of both Sabiceae and *Sabicea*, 2) assess the phylogenetic relationship within Sabiceae, and 3) make inference on the biogeographical origin of *Sabicea*.

## MATERIALS AND METHODS

**Taxon selection.** — A total of 36 species (38 individuals) belonging to *Sabicea* and nine genera (*Ecpoma*, *Hekistocarpa*, *Pentaloncha*, *Pseudosabicea*, *Schizostigma*, *Stipularia*, *Tamridaea*, *Temnopteryx*, and *Virectaria*) currently or traditionally associated with Sabiceae and 19 genera presently placed in Cinchonoideae s.s., Ixoroideae sensu lato (s.l.), and Rubioideae were included in the *trnT-F* analyses to test the monophyly of the competing circumscriptions of Sabiceae. Both *Acranthera* and *Amphidasya* were not included in our analyses, as they have recently been shown by Alejandro & al. (2005) and Bremer and Thulin (1998), respectively, to be related to Rubioideae. No material was available for *Pittierothamnus*. The genus *Luculia* Sweet (*L. grandifolia* Ghose) was used as the outgroup taxon, in agreement with its basal position in Rubiaceae (Bremer & al., 1999; Rova & al., 2002). For both the ITS and combined ITS-*trnT-F* analyses a total of 40 species of *Sabicea* (41 individuals), eight species of *Pseudosabicea*, one species each of *Ecpoma* and *Stipularia*, one individual each of the monotypic *Hekistocarpa*, *Schizostigma*, and *Tamridaea* and two species of *Virectaria* were included. One species each of *Heinsia* DC. (Mussaendeae sensu Bremer and Thulin, 1998), *Canthium* Lam. (Vanguerieae), *Ixora* L. (Ixoreae sensu Andreasen and Bremer, 2000), and *Warszewiczia* Klotzsch (Condamineae sensu Rova & al., 2002), all currently classified in Ixoroideae s.l., were selected to root the ITS and combined analyses (see Appendix 1).

**DNA isolation, amplification, and sequencing.** — DNA isolation, amplification and sequencing of the ITS region were accomplished following the protocols described in Alejandro & al. (2005). The amplification and sequencing of the *trnT-F* region were performed following the protocols described in Razafimandimbison and Bremer (2002). For each 25 µL PCR reaction we added 15.8 µL dH<sub>2</sub>O, 2 µL MgCl<sub>2</sub> (25mM), 1.5 µL dNTP (2 mM), 1.0 µL each of forward (P17F, 5'-CTA CCG ATT GAA TGG TCC GGT GAA-3') and reverse (26S-

82R, 5'-TCC CGG TTC GCT CGC CGT TAC TA-3') primer (10 pmol/ $\mu$ L), 2.5  $\mu$ L PCR buffer (10 $\times$ ), 0.2  $\mu$ L TAQ DNA polymerase, and 1.0  $\mu$ L DNA sample.

**Sequence alignment and coding of indels.** — Forward and reverse sequences generated for both the ITS and *trnT-F* regions were assembled using the Perkin Elmer Sequence Navigator, version 1.0.1 and Sequencer 3.1.1, aligned with the CLUSTAL-W (Thompson & al., 1994) to obtain preliminary alignments, which were subsequently edited manually. We coded all informative indels using the simple gap coding method (Simmons and Ochoterena, 2000) and assessed their effects on the results.

**Phylogenetic analyses.** — Maximum parsimony analyses (hereafter MPA) of both the ITS and ITS-*trnT-F* data were performed with PAUP, version 4.0b (Swofford, 2000) on a Power Macintosh G3 computer using the heuristic search settings: MULTREES option on, tree-bisection-reconnection (TBR) branch swapping, swap on best only in effect, and 5,000 random addition sequences. We performed MPA of the *trnT-F* matrix using the same settings, but the searches were frequently terminated prematurely due to the limitation of computer memory. As a result, we analysed the *trnT-F* data with MULTREES option off, TBR branch swapping, swap on best only in effect, and 10,000 random addition sequences. To estimate homoplasy the consistency index (CI, Kluge and Farris, 1969) and retention index (RI, Farris, 1989) were calculated. To assess the support of the retained clades the bootstrap values (Felsenstein, 1985) were computed using 10,000 replicates, MULTREES option off, TBR branch swapping and five random addition sequences. Bootstrap values of 50–69%, 70–85%, and 86–100% were considered as weak, moderate, and strong support, respectively. We performed parsimony and bootstrap analyses of each of the three data sets with and without indels to assess the effects of indel coding. In all analyses, characters were of equal weight, gaps were treated as missing data, and only parsimony-informative characters were included. Visual comparisons between the *trnT-F* and ITS trees from the preliminary parsimony analyses revealed the topological conflicts regarding the position of *Tamridaea* (Figs.1–2). Therefore, we assessed the combinability of the ITS and *trnT-F* data partitions by the ILD test (Farris & al., 1995) using partition-homogeneity test, implemented in PAUP\*. We performed Bayesian analyses (hereafter BA) in MrBayes, version 3.1.2 (Huelsenbeck and Ronquist, 2001) using the substitution model parameters: Prset statefreqpr = dirichlet (1,1,1,1); Lset nst = 6 rates = equal; selected as best fit under Akaike Information Criterion (AIC) by MrModeltest, version 2.2 (Nylander, 2004) for the uncoded *trnT-F*, ITS and combined ITS-*trnT-F* data sets. In all searches, we used the default settings (MrBayes, version 3.1.2) for all active parameters for the corresponding substitution models, as well as, for the heating scheme. Eight chains under two simultaneous runs, with 100 sample frequencies were executed and monitored up to  $3.4\text{--}3.6 \times 10^6$  Markov Chain Monte Carlo (mcmc) generations for arriving at the stationary phase (with average standard deviation of split frequencies < 0.01 and PSRF = about 1.0). Examining the output file identified the burn-in of generated trees for each analysis. After discarding 25% of the



samples as burn-in (MrBayes 3.1 Manual), the graphical presentations of summarized resulting trees were generated in PAUP\* and Tree View (Page, 1996.) program. Internodes with posterior probabilities of more than 95% were considered as reliable support (Hilu & al., 2003).

## RESULTS

**Sequence and alignment characteristics.** — The characteristics of the non-aligned *trnT-F* and ITS sequences of Sabiceae s.l. and the aligned matrices of the *trnT-F*, ITS and *trnT-F* partitions of the combined-data sets are summarized in Table 2. The characteristics of the ITS sequences and alignment were the same in the ITS and combined ITS-*trnT-F* matrices. Both the ranges of lengths and the average lengths of ITS1 and ITS2 of Sabiceae taxa fall within the recorded ranges for other Angiosperms (Baldwin & al., 1995; Noyes, 2006). The records of GC contents in ITS1 and in ITS2 of Sabiceae taxa coincide with the reports for Rubiaceae (Razafimandimbison and Bremer, 2001; Alejandro & al., 2005) and other angiosperms (Tate & al., 2005). The results of the partition-homogeneity test (Table 3) showed that the ITS and *trnT-F* data sets were incongruent when their indels were coded and the coded positions were excluded (not all results shown). Accordingly, we used the *trnT-F*, ITS and ITS-*trnT-F* matrices without coding of indels. However, we performed additional parsimony analyses (results not shown) using the *trnT-F*, ITS and combined ITS-*trnT-F* matrices including coded indels only to compare the results.

***TrnT-F* analyses.** — The *trnT-F* analysis included 58 sequences, of which 39 are newly published here. The MPA of the *trnT-F* sequences data resulted in 8067 equally parsimonious trees (each 977 steps long [L], CI = 0.679, and RI = 0.879). All ingroup taxa were resolved in three strongly supported (BS = 100, PP = 100) major clades, corresponding to the subfamilies Rubioideae, Cinchonoideae s.s., and Ixoroideae s.l. (Bremer & al., 1999). The investigated members of Sabiceae sensu Andersson (1996) were resolved in three separate highly supported subclades (Fig. 1): the *Pentaloncha* clade (BS = 100, PP = 100) and the *Temnopteryx* clade (BS = 100, PP = 100) both nested in Rubioideae, and the *Ecpoma-Pseudosabicea-Sabicea-Schizostigma-Stipularia* clade (BS = 82, PP = 100; hereafter called Sabiceae s.s.) nested in Ixoroideae s.l. Within Ixoroideae s.l. Virectarieae sensu Dessein & al. (2001b), represented by *Hekistocarpa minutiflora* Hook. f., *Virectaria multiflora* (Sm.) Bremek. and *V. procumbens* (Sm.) Bremek., and *Tamridaea capsulifera* (Balf. F.) Thulin & B. Bremer, was not resolved as monophyletic. *Virectaria multiflora* and *V. procumbens* formed a strongly supported (BS = 100, PP = 100) monophyletic group, whereas *H. minutiflora* was left unresolved. *Tamridaea capsulifera* was resolved with moderate (BS = 81) and high (PP = 100) support, respectively, in the MPA and BA as sister to Sabiceae s.s. The non-monophyletic Virectarieae sensu Dessein & al. (2001b) and Sabiceae s.s. together (hereafter called Sabiceae s.l.) formed a highly supported (BS = 100, PP = 100) monophyletic group. All studied Neotropical *Sabicea* species, with the

exception of *S. mexicana* Wernham, formed a weakly (BS = 61) or highly (PP = 96) supported clade, respectively, in the MPA and BA.

**ITS analyses.** — A total of 61 ITS sequences were included in our all analyses and 56 are newly published here. A MPA of the ITS data resulted in 210 equally parsimonious trees (L = 542, CI = 0.601, and RI = 0.758). In the strict consensus tree shown in Figure 2, *Hekistocarpa minutiflora* was resolved with high support (BS = 100, PP = 100) as sister to a very large, moderately (BS = 83) and highly supported (PP = 98) clade, respectively, in the MPA and BA, containing all investigated members of *Tamridaea*, *Virectaria*, *Stipularia*, *Pseudosabicea*, *Sabicea*, *Schizostigma*, and *Ecpoma*. *Tamridaea capsulifera* and the two *Virectaria* species formed a moderately (BS = 71) and strongly (PP = 100) supported clade, respectively, in the MPA and BA. This *Tamridaea-Virectaria* clade was in turn resolved as sister to the strongly supported (BS = 100, PP = 100) Sabiceae s.s. clade. Within the latter clade, *Stipularia elliptica* was resolved as sister to a moderately supported (BS = 77) clade containing *Stipularia efulenensis* and all sequenced species of *Ecpoma*, *Pseudosabicea*, *Sabicea*, and *Schizostigma* (hereafter called *Pseudosabicea-Sabicea-Stipularia-Schizostigma-Ecpoma* clade). Within this large clade all *Pseudosabicea* species were resolved in two highly supported clades: one formed by five *Pseudosabicea* species (BS = 99, PP = 100) and the other by three *Pseudosabicea* species, including the type species (Good, 1923; Hallé, 1970) *Pseudosabicea nobilis* (R. Good) N. Hallé, (BS = 98, PP = 100). The former *Pseudosabicea* clade was resolved as sister to a weakly supported (BS = 66) and *Sabicea* dominated clade formed by *S. efulenensis*, all studied species of *Ecpoma*, *Sabicea* and *Schizostigma* and the other *Pseudosabicea* clade (containing *P. segregata* (Hiern) N. Hallé, *P. nobilis*, and *P. proselyta* N. Hallé). Furthermore, *Sabicea* sensu Wernham (1914), which included five of the six *Ecpoma* species (*E. bicarpellata*, *E. cauliflora*, *E. geantha*, *E. gigantostipula*, and *E. hierniana*) and six *Pseudosabicea* species [*P. batesii* (Wernham) N. Hallé, *P. floribunda* (K. Schum.) N. Hallé, *P. medusula* (K. Schum. ex Wernham) N. Hallé, *P. mildbraedii* (Wernham) N. Hallé, *P. pedicellata* (Wernham) N. Hallé, and *P. segregata* (Hiern) N. Hallé] as the species of *Sabicea*, was shown to be paraphyletic, as both *Schizostigma hirsutum* and *Stipularia efulenensis* were nested. Both *Pseudosabicea* and *Sabicea* sensu Hallé (1963, 1966) appeared highly polyphyletic. We found no support for the monophyly of Wernham's (1914) subgeneric classification, as the two sequenced species of *Sabicea* subgen. *Stipulariopsis*, *Sabicea xanthotricha* Wernham and *S. hierniana* Wernham (= *Ecpoma hierniana*), did not form a clade and were nested in the large *Pseudosabicea-Sabicea-Stipularia-Schizostigma-Ecpoma* clade. Plus, *Sabicea* subgen. *Eusabicea* appeared polyphyletic, as *Schizostigma* and both *S. xanthotricha* and *E. hierniana* were nested within it. Finally, two investigated Malagasy (*S. diversifolia* Pers. and *S. seua* Wernham) and two São Tomean *Sabicea* (*S. exellii* G. Taylor and *S. thomensis* Joffroy) species formed strongly supported (BS = 100, PP = 100) groups, respectively. Similarly, all sequenced Neotropical *Sabicea* formed a weakly supported (BS = 64) clade in the MPA.

These three clades were all nested within the largely African *Pseudosabicea-Sabicea-Stipularia-Schizostigma-Ecpoma* clade.

**Combined ITS-trnT-F analyses.** — Based on the results of the *trnT-F* analysis we initially selected *Alberta magna* E. Mey., *Canthium coromandelicum* Vahl, *Heinsia zanzibarica* (Boj.) Verdc., *Ixora coccinea* L., and *Warszewiczia coccinea* Klotzsch as the outgroup taxa to root both the ITS and combined ITS-*trnT-F* analyses. However, the results of the ILD tests (see Table 3) revealed that the ITS and *trnT-F* data partitions were congruent when the informative indels were left uncoded and *A. magna* was excluded. Accordingly, we combined the *trnT-F* and ITS data partitions without coding their indels and used *C. coromandelicum*, *H. zanzibarica*, *I. coccinea*, and *W. coccinea* as the outgroup taxa for both the ITS and combined ITS-*trnT-F* analyses.

Both the ITS and *trnT-F* partitions used in the combined analyses each contained 56 new sequences. Of the 56 *trnT-F* sequences, 33 were only used in the *trnT-F* analyses. A MPA of the combined ITS-*trnT-F* matrix, composed of a total of 2,598 positions and 349 (13.43%) parsimony-informative characters (Table 2), generated 104442 equally parsimonious trees (L = 757, CI = 0.651 and RI = 0.782). The overall tree topologies and support values of the resolved nodes in the strict consensus tree (Fig. 3) were largely similar to those of the strict consensus ITS tree (Fig. 2). The support values in the combined tree were higher for some nodes (e.g., the Neotropical *Sabicea* clade; the *Sabicea speciosa-Schizostigma hirsutum* clade) but decreased for the *Tamridaeae-Virectaria* clade due to the conflicting positions of *T. capsulifera* in the *trnT-F* and ITS trees (Figs. 1–2). Plus, the poorly supported sister-group relationships between the Malagasy *Sabicea* clade (*S. diversifolia* and *S. seua*) and the *Pseudosabicea* clade formed by *P. segregata*, *P. nobilis* and *P. proselyta* (Fig. 2) collapsed in the combined tree (Fig. 3).

## DISCUSSION

Firstly, we compare the sequence characteristics between the ITS and *trnT-F* sequences of Sabiceae and those of the some other rubiaceous tribes (e.g., Naucleae s.l., Cinchonoideae s.s. and Mussaendeae and Vanguerieae, both Ixoroideae s.l.). Secondly, we discuss the conflicting tribal circumscriptions of Sabiceae that have been proposed in the light of our results and the phylogenetic relationships between the genera. Accordingly, we propose new generic circumscriptions for the tribe. Thirdly, we make inference on the biogeographical origins of our newly delimited *Sabicea* s.l. and finally provide updated descriptions for *Sabicea* s.l. and make six new combinations.

**Sequence characteristics.** — The total lengths of the ITS region of Sabiceae (566–599 bp) are similar to those of Mussaendeae (570–596 bp) sensu Bremer & Thulin (1998) (Alejandro & al., 2005), shorter than those reported for the tribe Vanguerieae (611–671 bp) (Lantz and Bremer, 2004), all Ixoroideae s.l., and fall within the known range for other Ixoroideae (565–654 bp) (Andreasen & al., 1999). The parsimony informative characters

(PIC) for the ITS region of Sabiceae (202) are higher than those reported from other Ixoroideae tribes [e.g., 103 for Mussaendeae (Alejandro & al., 2005); 121 for the *Alibertia* group of the tribe Gardenieae (Persson, 2000); 188 for Vanguerieae (Lantz and Bremer, 2004)]. On the other hand, they are lower than the PIC (210) recorded for the tribe Naucleae s.l. (Razafimandimbison and Bremer, 2002). So, there is a great variation of the lengths of ITS regions and eventually the number of parsimony informative characters between the different rubiaceae tribes.

The range of the lengths of the *trnT-F* region of Sabiceae (1574–1688 bp) coincides with the records for Mussaendeae (1662–1793 bp) sensu Bremer & Thulin (1998) (Alejandro & al. 2005) and Vanguerieae (1559–1785 bp, Lantz and Bremer, 2004) but is shorter than that of Naucleae s.l. (1707–1785 bp, Razafimandimbison and Bremer, 2002). The lengths of the *trnT-F* region of the studied Sabiceae are 2.8 times longer than those of their ITS region. In contrast, the *trnT-F* region of the sequenced Sabiceae is relatively less informative (21.08%) than their ITS region (30.15%), concurring with Liede and Kunze (2002), Razafimandimbison and Bremer (2002), and Alejandro & al. (2005). In the *trnT-F* matrix, the *trnT-L* spacer (684–788 bp) is more variable than *trnL-F* spacer (268–324 bp), also consistent with Razafimandimbison and Bremer (2002), but our record of the *trnL* intron as more variable than the *trnL-F* spacer is inconsistent with their reports. The variations shown by the ITS, *trnT-L*, *trnL* and *trnL-F* regions further indicate their usefulness for assessing the phylogenetic relationships in Rubiaceae and other families in the order Gentianales (e.g., Meve and Liede, 2002).

**Tribal circumscriptions of Sabiceae.** — Sabiceae sensu Andersson (1996), which includes *Amphidasya*, currently classified by Bremer and Manen (2000) and Robbrecht and Manen (2006) in the tribe Urophylleae (Rubioidae), and *Acranthera*, recently shown by Alejandro & al. (2005) to be associated with Rubioidae, is further revealed as unsupported (Fig. 1) in including the genera *Pentaloncha* and *Temnopteryx*, as both of these genera are resolved with high support (BS = 100, PP = 100) in Rubioidae. This is the first molecular phylogenetic study to include these African rubiaceae monotypic genera. We find no support either for the close relationships of *Temnopteryx* and *Pentaloncha* with *Ecpoma*, *Pseudosabicea*, *Sabicea*, and *Stipularia* postulated, respectively, by Puff & al. (1998) and Dessein & al. (2001b) or Hiern's (1877) attempt to merge both *Pentaloncha* and *Temnopteryx* with *Schizostigma* (= *Sabicea*, Puff & al., 1998). The combined ITS-*trnT-F* tree (Fig. 3) shows that Sabiceae sensu Bremer & Thulin (1998) is not monophyletic, unless *Ecpoma*, *Hekistocarpa*, and *Schizostigma* are also included. Dessein & al. (2001b) restricted the Sabiceae to *Sabicea* and *Pseudosabicea* due to morphological indications, but suggested to include *Pentaloncha* with Sabiceae, which is strongly unsupported our results.

Our results clearly favour a broad circumscription of Sabiceae, which should include the following eight genera: *Ecpoma*, *Hekistocarpa*, *Pseudosabicea*, *Sabicea*, *Schizostigma*, *Stipularia*, *Tamridaea*, and *Virectaria* (Figs. 1–3), consistent with Robbrecht and Manen

(2006). In all our parsimony and Bayesian analyses, we perceive no support for the monophyly of Virectarieae sensu Dessein & al. (2001b), as *Hekistocarpa*, *Virectaria*, and *Tamridaea* never form a clade (Figs. 1–3). Plus, we do not find any potential morphological characters that can be used to diagnose Virectarieae sensu Dessein & al. (2001b). For the same reason our results do not support the new subtribal classification of Sabiceae (Sabiceinae and Virectariinae) by Robbrecht and Manen (2006). We were unable to include the Neotropical genus *Pittierothamnus* (Steyermark, 1962) due to lack of material. Therefore, its phylogenetic position in Sabiceae postulated by Andersson (1996) has yet to be tested with molecular-based phylogenies. We have not been able to find any potential morphological synapomorphy to diagnose our newly delimited Sabiceae s.l. Therefore; the monophyly of the tribe is entirely based on molecular data.

**Phylogenetic relationships and generic circumscriptions in Sabiceae s.l.** — Our newly circumscribed Sabiceae contains the following four genera: *Hekistocarpa*, *Sabicea* s.l. (including *Ecpoma*, *Pseudosabicea*, *Schizostigma*, and *Stipularia*), *Tamridaea*, and *Virectaria*.

*Hekistocarpa* is an African monotypic genus restricted to Cameroon and Nigeria (Dessein & al 2001b; Fig. 37). This genus can be characterized by the following characters: herbaceous growth habit, entire stipules, lateral scorpioid cymes, laterally compressed fruits, exotesta cells with strongly thickened walls, tuberculate surface and one perforation, and tricolpate pollen (Dessein & al., 2001b). *Hekistocarpa* was classified for a long time in the tribe Hedyotideae (Rubioideae) because of its herbaceous habit, scorpioid inflorescences and many seeded fruits (Hooker, 1873b). The study of Dessein & al. (2001b) was the first to place *Hekistocarpa* in Virectarieae (Figs. 1–3). All the *trnT-F*, ITS and combined ITS-*trnT-F* trees (Figs. 1–3) strongly (BS = 100, PP = 100) favour its placement in Sabiceae s.l. Furthermore, *Hekistocarpa* is resolved as sister to the rest of Sabiceae s.l. (Figs. 2–3) and therefore, its current generic status should be maintained.

All ITS and combined analyses (Figs. 2–3) indicate that *Sabicea* sensu Wernham (1914) is only monophyletic if *Pseudosabicea proselyta*, *Schizostigma*, and *Stipularia efulenensis* are also included. The circumscription of the genus *Stipularia* appears polyphyletic, as the two sequenced species, *S. elliptica* and *S. efulenensis*, are resolved in two separate clades (Figs. 2–3). The type species *S. africana* is not included in the present study, so the generic status of *Stipularia* could still be maintained if it turns out that *S. africana* forms a clade with *S. elliptica*. On the other hand, our results indicate that the generic concept of *Stipularia* based mainly on the presence of the large campanulate involucre bracts subtending the entire inflorescence is untenable, as the two sequenced *Stipularia* species bearing the same type of the involucre bracts (Hepper, 1958) do not form a clade. Plus, Hepper (1958: 289–291) convincingly explained that the involucre bracts of some African *Sabicea* species show a great range of the degree of fusion (from inconspicuous to distinct and totally free to partly or completely fused bracts). Also, Hallé (1966) showed that many African *Sabicea* species

(e.g., *Sabicea duparquetiana* H. Baillon ex Wernham, *S. najatrix* N. Hallé) have large and partly fused campanulate involucre bracts. Based on the above evidence presented we concur with Hepper's (1958) decision to merge *Stipularia* with *Sabicea*.

Our analyses further reveal the polyphyly of *Sabicea* sensu Hallé (1963), as *Ecpoma*, represented by *E. hierniana*, *Pseudosabicea*, represented by *P. segregata*, *P. nobilis*, and *P. proselyta*, and *Schizostigma* are all resolved in the largely *Sabicea* clade with weak and high support (e.g., BS = 65, PP = 100; Fig. 3), respectively, in the MPA and BA. Similarly, *Pseudosabicea* sensu Hallé (1963) is also shown to be para- or polyphyletic, as the sequenced *Pseudosabicea* species group in two separate clades (Figs. 2–3). Accordingly, we merge *Pseudosabicea* with *Sabicea*. The range of variation in the characters of *Sabicea* includes the diagnostic characters of *Pseudosabicea* sensu Hallé. One could recognize the strongly supported clade of five *Pseudosabicea* species at generic level but we find no distinctive character for diagnosing this clade, three members of which (*P. batesii*, *P. medusula*, and *P. mildbraedi*) were once included in *Sabicea* (Wernham, 1914).

The African genus *Ecpoma* (Schumann, 1896) is comprised of six species and characterized by its shrubby habit, isophylly, colourless pulp of small fruits, bilocular ovaries, non-acrescent septa, rounded or twisted to peltate placentae (Hallé, 1963). *Ecpoma* was traditionally classified in Isertieae (Hallé, 1961; Hallé, 1966; Robbrecht, 1988) or in Sabiceae (Andersson, 1996; Robbrecht and Manen, 2006). In Andersson's (1996) study, *Ecpoma* did not form a monophyletic group with *Pseudosabicea-Sabicea-Schizostigma*. In the ITS and ITS-*trnT-F* trees (Figs. 2–3), *Ecpoma*, represented by *E. hierniana*, however, is consistently and deeply nested within the moderately supported *Pseudosabicea-Sabicea-Stipularia-Schizostigma-Ecpoma* clade, inconsistent with Hallé (1963) and Andersson (1996). Accordingly, we merge *Ecpoma* with *Sabicea* even if the type species is not included in our analyses because its character states clearly fall within the range of variation in *Sabicea* s.l.

Adopting the broadened circumscription of *Sabicea* including *Ecpoma*, *Pseudosabicea*, *Schizostigma*, and *Stipularia* requires only a maximum of six new combinations, as five of the six *Ecpoma* species (Hallé, 1963) and eight of the 13 *Pseudosabicea* species (Hallé, 1963, 1966) were originally described as *Sabicea* (see Wernham, 1914; Good, 1923). Plus, all five *Stipularia* species and *Schizostigma* have already been merged, respectively, by Hepper (1958) and Puff & al. (1998) in *Sabicea*. *Sabicea* s.l. is very distinct from the other three genera (*Hekistocarpa*, *Tamridaea*, and *Virectaria*) of Sabiceae in many aspects (see Table 4).

All our ITS and combined ITS-*trnT-F* analyses find no support for the monophyly of Wernham's (1914) two subgenera of *Sabicea* based on habit and leaf and stipule sizes. New molecular phylogenetic investigations based on multiple markers and using a much broader sampling of *Ecpoma*, *Pseudosabicea*, *Stipularia*, and *Sabicea* will be performed in attempt to establish, if possible, new infrageneric classifications for our newly delimited *Sabicea* with ca. 183 species and also address some evolutionary questions.

The monotypic genus *Tamridaea*, endemic to Socotra (Yemen), is characterized by its shrubby habit, reduplicate-valvate aestivation, terminal cymes, calyces without any petaloid lobes, flat,  $\pm$  obcordate corolla lobes with emarginate-mucronate apices, bilobed stigma, bilocular ovaries (Bremer and Thulin, 1998), exotesta cells with verrucose thickenings, and 4-colporate pollens (Dessein & al. 2001b). *Tamridaea* was originally described by Bremer and Thulin (1998) to accommodate *Pseudomussaenda capsulifera* (Balf. F.) Wernham, previously classified in Isertieae sensu Robbrecht (1988), and was placed in their Sabiceae s.l. Dessein & al. (2001a) accept the generic status of *Tamridaea* and its placement in Sabiceae sensu Bremer and Thulin (1998) but later place the genus in their emended Virectarieae (Dessein & al. 2001b). In our *trnT-F* tree (Fig. 1), *Tamridaea* is moderately (BS = 81) and highly (PP = 100) resolved, respectively, as sister to Sabiceae s.s. in the MPA and BA analyses. In the MPA of the ITS and combined ITS-*trnT-F* data, the genus and *Virectaria* form a moderately to highly (BS = 71, PP = 100; Fig. 2) and poorly (BS = 58; Fig. 3) supported clade, consistent with Bremer and Thulin (1998) and Dessein & al. (2001b). However, our results do not support the placement of *Tamridaea* in Virectarieae sensu Dessein & al. (2001b), which appears non-monophyletic.

The tropical African genus *Virectaria* is comprised of eight species, of which three species (*V. major* K. Schum., *V. multiflora* and *V. procumbens*) are Guineo-Congolian wide (Dessein & al., 2001a), while the others are endemic to the Domains of Guineo-Congolian region (*V. herbacoursi* N. Hallé, *V. belingana* N. Hallé, *V. salicoides* (C. H. Wright) Bremek. and *V. angustifolia* (Hiern) Bremek. to Lower Guinea, *V. tenella* J. B. Hall to Upper Guinea)

The genus can be characterized by its herbaceous to semi-woody habit, terminal compound determinate inflorescences, truncated stigma, dehiscent fruits, flat trichomes of the corolla orifice or inside the corolla tubes, exotesta cells of seeds with elongated verrucose thickenings and many small perforations, and 3-colporate pollen grains (Dessein & al., 2001b). Our results support the placement of *Virectaria* in Ixoroideae s.l., also consistent with Bremer and Thulin (1998) and Dessein & al. (2001a, 2001b) but inconsistent with Bremekamp (1952, 1966) who classified the genus in the tribe Ophiorrhizeae of his Cinchonoideae, and Verdcourt (1975) who placed it in Cinchonoideae as a monogeneric tribe Virectarieae. In both ITS and combined ITS-*trnT-F* trees (Figs. 2–3), *Virectaria* is strongly (BS = 100, PP = 100) resolved as a monophyletic group, which is sister to *Tamridaea*, consistent with Dessein & al. (2001a) and Robbrecht and Manen (2006), but inconsistent with their placement in a separate tribe Virectarieae (Dessein & al., 2001a) or subtribe Virectariinae (Robbrecht and Manen, 2006), both including *Hekistocarpa*. The two sister genera, *Tamridaea* and *Virectaria*, are morphologically distinct and therefore, their generic status can be maintained.

**Biogeographical origin of *Sabicea* s.l.** — The Islands of São Tomé & Príncipe have three endemic *Sabicea* species (Joffroy, 2001). These three São Tomean *Sabicea* species (*S. exellii*, *S. ingrata* K. Schum., and *S. thomensis*) are consistently nested in the almost

African *Sabicea* clade and group together with three continental African *Sabicea*, *S. capitellata*, *S. johnstonii*, and *S. rosea* (Figs. 2–3), indicating that the São Tomean species must have had African ancestors. Similarly, the two sequenced Malagasy species of *Sabicea*, *S. diversifolia* and *S. seua* (Razafimandimbison and Miller, 1999), form a highly supported (BS = 100, PP = 100) clade, which is nested in the African *Sabicea* clade. Madagascar is about 400 km off the southwestern coast of Mozambique, whereas São Tomé & Príncipe are only within 225 to 250 km off of the northwestern coast of Gabon. Plus, all sequenced Neotropical *Sabicea* species form a moderately supported (BS = 74) clade in the MPA and highly supported (PP = 99) clade in the BA (Fig. 3), indicating a single origin of all Neotropical *Sabicea*. The Neotropical *Sabicea* additionally appear to have originated from an African common ancestor. Our analyses indicate that the African common ancestors of the Malagasy, São Tomean, and Neotropical *Sabicea*, respectively, most likely reached Madagascar, São Tomé & Príncipe, and the Neotropics via four independent and single long-distance dispersal events either via wind and/or ocean currents (Hypothesis # 1) or dispersal of seeds across the Mozambique Channel, the Gulf of Guinea and the South Atlantic Ocean by birds (Hypothesis # 2). *Sabicea* s.l. produce fleshy and sub- to globose or obovoid berries bearing many small seeds, which would presumably provide an important source of food for tropical frugivorous birds. This seems to favour the Hypothesis # 2 over the Hypothesis # 1 (but see Renner, 2004). The fact that the Neotropics and São Tomé & Príncipe do not share in common any *Sabicea* species seems to exclude stepping-stone long-distance dispersal (i.e., dispersal from the mainland Africa to the Neotropics via São Tomé & Príncipe) as the mode of dispersal responsible for the present trans-Atlantic distribution of *Sabicea* s.l. No record of *Sabicea* s.l. is known from the neighbouring Islands of Madagascar. In addition, our results (Fig. 3) further suggest that three African *Sabicea* species (*S. angolensis* Wernham, *S. orientalis* Wernham, and *S. venosa*), appear to be most closely related to the Neotropical *Sabicea* s.l., also consistent with morphological ground. Furthermore, *Sabicea* s.l. seems to have started to diversify in mainland Africa, where at least 107 species are presently known. A second major radiation of *Sabicea* appears to have occurred after the group began to colonize the Neotropics. The occurrence of the single Asian species *Sabicea ceylanica* (restricted to Sri Lanka) indicates *Sabicea* to have failed to diversify in Asia to disperse to the rest of Asia. A similar with regard to origin alone biogeographic pattern has recently been discovered in the rubiaceous genus *Mussaenda* s.s., which also appears to have had an African origin (Alejandro & al., 2005) but currently has its centre of diversity in Southeast Asia and is totally absent in the Neotropics.

## CONCLUSION

The present phylogenetic analyses favour a broad circumscription of Sabiceae, which includes the following four genera: *Hekistocarpa*, *Sabicea* s.l. (including *Ecpoma*, *Pseudosabicea*, *Schizostigma*, and *Stipularia*), *Tamridaea*, and *Virectaria*. Both *Pentaloncha*



and *Temnopteryx* are for the first time shown to belong to Rubioideae. Furthermore, Sabiceae sensu Bremer & Thulin (1998) is not monophyletic, unless *Ecpoma*, *Hekistocarpa*, and *Schizostigma* are also included. Virectarieae sensu Dessein & al. (2001b) appears para- or polyphyletic. Dessein & al.'s (2001b) Sabiceae and Robbrecht and Manen's (2006) subtribal classification of Sabiceae are not supported by our results. In addition, *Sabicea* sensu Wernham (1914) is monophyletic only if *Pseudosabicea proselyta*, *Stipularia efulenensis*, *Schizostigma* are included. We perceive no support for the monophyly of *Sabicea* and *Pseudosabicea* both sensu Hallé (1963, 1966) and *Stipularia*. Finally, our analyses support the monophyly of the Malagasy and Neotropical *Sabicea*. The São Tomean, Malagasy and Neotropical *Sabicea*, all appear to have had African origins.

**Taxonomic implication.** — *Sabicea* Aubl., Hist. Pl. Guiane Française, 1: 192. t, 75. Jun.-

Dec. 1775. – Lectotype: *S. cinerea* Aubl. designated by P. C. Standley, N. Amer. Fl. 32: 148. 10 May 1921. PHAN.-RUBIACEAE (75/104).

= *Schwenkfelda* Schreb., Gen. Pl. 123 (1789) – Type: not designated.

= *Schwenkfeldia* Willd., Sp. Pl. i. 982 (1797) – Type: not designated.

= *Paiva* Vell., Fl. Flumin. 104 (1825) – Type: not designated.

= *Stipularia* P. Beauv., Fl. Oware 2: 26 (1807) – Type: *Stipularia africana* P. Beauv. – Holotype: South Nigeria, P. de Beauvois (G!), Isotype (P, not seen).

= *Ecpoma* K. Schum. syn. nov., Bot. Jahrb. 23: 430 (1896) – Type: *Ecpoma apocynaceum* K. Schum. – Holotype: Cameroon, near Lolodorf, *Staudt 204* (B, presumably destroyed; K, photo!).

= *Pseudosabicea* N. Hallé syn. nov., Adansonia ser. 2 III (1963) – Type: *Pseudosabicea nobilis* (R. Good) N. Hallé – Holotype: Gabon, piste de Bouéni, 20 km SE de Makokou, *N. Hallé 1129* (P, photo!, K, photo!).

Scandent shrubs, lianas or woody vines, climbing or scrambling to erect herbs or shrubs, rarely small tree, stems rounded to shallowly quadrangular. Stipules interpetiolar, free, persistent, minute to vigorous, usually entire, sometimes fimbriate to deeply lacinate, usually with few to many colleters inside the base. Leaves isophyllous or anisophyllous, membranaceous to subcoriaceous. Inflorescence axillary, sessile to pedunculate, solitary to compactly capitate to lax thyrsoid and few to many flowered cymes, subtended by inconspicuous to distinct and free to completely united and variously lobed bracts with usually 2–many colleters inside the base, with or without forming spreaded to enclosed or deeply campanulate involucre, rarely followed by prophylls. Calyces shallowly to deeply campanulate to funnel-shaped, 3–5-lobed, lobes filiform to elliptic or obovate, antrorse to abruptly reflex, usually with 1–2 colleters in or below each sinus. Corollas hypocrateriform or broadly infundibuliform, usually white, occasionally pinkish, usually 5-lobed, lobes valvate, narrowly to widely ovate, margins entire, glabrous or papillate inside, (sub-) acute at apex. Stamens included to slightly exerted just beyond the corolla tubes, anthers linear to

narrowly oblong, acute to rounded at base and apex, dehiscent by longitudinal slits, dorsifixed near the middle by the very short free part of filiform filaments, attached to the upper part of corolla tubes. Pollens colporate to pororate, apertures 3 or 4, exine surface minutely reticulate, released as monads. Styles filiform, usually glabrous and included to slightly exerted just beyond the corolla tubes, stigmatic lobes 2–5, filiform to oblong or very narrowly elliptic or oblanceolate to widely spatulate or dilated. Ovaries usually (sub-) globose, 2–7-locular with axile placentation and numerous ovules per locule. Fruits (sub-) globose, indehiscent berries. Seeds minute, usually numerous, variously angular, exotesta cells narrow and elongated, with few to many rounded pits, radial wall with verrucose thickenings. Indument of stem, branches, leaves, stipules, inflorescences, bracts, hypanthia and corolla tubes isolatedly to densely puberulous to hirsute or pilose, strigose or sericeous to villous, velutinous or arachnose and indument of corolla orifice or inside the corolla tubes usually moniliform. The karyologically reported taxa are tetraploid with basic chromosome numbers  $x = 9$  or  $11$  (Kiehn, 1995). Number of species: ca. 170 species (116 confined to the African mainland, 54 restricted to the Neotropics, 6 endemic to Madagascar and 3 to São Tomé and Príncipe).

*Sabicea* s.l. can easily be distinguished from the other three genera of Sabiceae s.l. by the combination of the following characters: axillary inflorescences usually composed of few to many flowered fascicles or densely capitulate to laxly paniculate cymes or solitary flowers, hypocrateriform or broadly infundibuliform corollas with ovate, (sub-) acute lobes, anthers and 2–6-lobed stigmata usually included in the corolla tubes, moniliform trichomes of corolla orifice or inside the corolla tubes, and narrow to elongated exotesta cells of seeds, with few to many rounded pits and verrucose thickenings on the radial wall (see also Table 4).

**New combinations.** — Here, we present six new combinations: five for the African *Pseudosabicea* species and one for the type species of *Ecpoma*.

1. ***Sabicea apocynaceum*** (K. Schum.) Razafim., B. Bremer, Liede-Schum. & Khan, comb. nova.  $\equiv$  *Ecpoma apocynaceum* K. Schum., Bot. Jahrb. 23: 430. 1897 – Type: CAMEROON, Lolodorf, February (fl.), *Staudt 208* (B, presumably destroyed; K, photo!).

2. ***Sabicea becquetii*** (N. Hallé) Razafim., B. Bremer, Liede-Schum. & Khan, comb. nova.  $\equiv$  *Pseudosabicea becquetii* N. Hallé, Bull. Jard. Bot. État 34: 400. 1964 – Type: BURUNDI, Bururi chefferi Arawe-territoire, alt. 1600 m, *Becquet 115* (holotype, P; isotype, K).

3. ***Sabicea aurifodinae*** (N. Hallé) Razafim., B. Bremer, Liede-Schum. & Khan, comb. nova.  $\equiv$  *Pseudosabicea aurifodinae* H. N. Hallé, Fl. Gabon 12: 201. 1966 – Type: GABON, Moubigou-2, au bout de la route de Massima vers Moumba, région d'Etéké, *N. Hallé et G. Cours 6137* (holotype, P).

4. *Sabicea proselyta* (N. Hallé) Razafim., B. Bremer, Liede-Schum. & Khan, comb. nova.  $\equiv$  *Pseudosabicea proselyta* N. Hallé, *Adansonia* ser. 2, 3: 172–173. 1963 – Type: GABON, la Nkoulounga, 11 July 1959, *N. Hallé 748* (holotype, P).

5. *Sabicea sanguinosa* (N. Hallé) Razafim., B. Bremer, Liede-Schum. & Khan, comb. nova.  $\equiv$  *Pseudosabicea sanguinosa* N. Hallé, *Adansonia* ser. 2, 11: 313–315. 1971 – Type: GABON, environs de la Station forestière du Petit Bam-Bam, 50 km SW de la base rivière Ramboué, au sud de l'Estuaire, pays de savanes, 21 August 1966 (fl.), *N. Hallé & A. Le Thomas 573* (holotype, P).

6. *Sabicea sthenula* (N. Hallé) Razafim., B. Bremer, Liede-Schum. & Khan, comb. nov.  $\equiv$  *Pseudosabicea sthenula* N. Hallé, *Fl. Gabon* 12: 208. 1966 – Type: GABON, Makokou, 27 February 1961, *N. Hallé 1339* (holotype, P!).

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Table 1. Previous and new tribal positions of *Sabicea* and its traditionally and presently allied genera. Acr = tribe Acranthereae, Hed = Hedyotideae, Ins = Incertae sedis, Ise = Isertieae, Mus = Mussaendeae, Oph = Ophiorrhizeae, Pau = Pauridiantheae, Rubi = Rubioideae, Sab(S) = Sabiceae(Sabiceinae), and Vir = Virectarieae or SabV (Sabiceae-Virectariinae), Uro = Urophylleae s.l. (including *Pauridiantheae*) - = not mentioned.\*\*\* as here presented, loss of information

Genera	Breme- kamp (1934)	Verdc -ourt (1958)	Hallé (1961)	Breme- kamp (1966)	Hallé (1966)	Steyer -mark (1962)	Steyer -mark (1972)	Robbr- echt (1988)	Ander -sson (1996)	Bremer & Thulin (1998)	Dessein & al. (2001b)	Robbrecht & Manen (2006) ***	This study
<i>Acranthera</i> Arn.	-	-	-	Acr	-	-	-	Ise	Sab	Rubi	-	-	Rubi
<i>Amphidasya</i> Standl.	-	-	-	-	-	-	Mus	Ise	Sab	Rubi	-	Uro	Rubi
<i>Ecpoma</i> K. Schum.	-	-	Mus	-	Mus	-	-	Ise	Sab	-	Sab	SabS	Sab
<i>Hekistocarpa</i> Hook. f.	-	-	-	-	-	-	-	Hed	-	-	Vir	SabV	Sab
<i>Pentaloncha</i> Hook. f.	-	-	Mus	Pau	Mus	-	-	Ins	Sab	-	Sab	-	Rubi
<i>Pittierothamnus</i> Steyerl.	-	-	-	-	-	Mus	-	-	Sab	-	-	-	-
<i>Pseudosabicea</i> N. Hallé	-	-	-	-	Mus	-	-	Ise	Sab	Sab	Sab	SabS	Sab
<i>Sabicea</i> Aubl.	Sab	Mus	Mus	Sab	Mus	Mus	Mus	Ise	Sab	Sab	Sab	SabS	Sab
<i>Schizostigma</i> Arn.	-	-	-	-	-	-	-	Ise	Sab	-	-	SabS	Sab
<i>Stipularia</i> P. Beauv.	-	-	Mus	-	Mus	-	-	Ise	Sab	Sab	Sab	SabS	Sab
<i>Tamridaea</i> Thulin & B. Bremer	-	-	-	-	-	-	-	-	-	Sab	Vir	SabV	Sab
<i>Temnopteryx</i> Hook. f.	-	-	Mus	Pau	Mus	-	-	Ise	Sab	-	-	-	Rubi
<i>Virectaria</i> Bremek.	-	Vir	-	Oph	Hed	-	-	Hed	-	Sab	Vir	SabV	Sab

Table 2. Characteristics of the sequence alignments and Sabiceae sequences.

Markers	Range of non-aligned sequence lengths in Sabiceae s.l. (bp)	Range of GC contents in the non-aligned sequences of Sabiceae s.l. (%)	Number of characters	Uninformative characters	Informative characters	Uninformative characters in Sabiceae s.l.	Informative characters in Sabiceae s.l.
<i>trnT-F</i>	1574–1688	28.9–32.5	2348	389	495 (21.08%)	138	273 (11.63%)
<i>trnT-L</i> spacer	684–788	21.2–27.6	1165	204	291 (12.39%)	89	165 (07.03%)
<i>trnL</i> intron	544–616	36.7–38.5	761	97	108 (04.60%)	27	62 (02.64%)
<i>trnL-F</i> spacer	268–324	32.1–36.2	422	88	96 (04.09%)	22	46 (01.96%)
ITS	566–599	53.7–65.5	670	118	202 (30.15%)	19	157 (23.28%)
ITS1	196–221	52.7–68.7	268	66	109 (16.27%)	34	78 (11.49%)
S5.8	165	54.5–53.3	165	06	06 (00.90%)	01	06 (00.90%)
ITS2	207–216	54.2–70.9	237	46	87 (12.98%)	30	73 (10.90%)
<i>trnT-F</i> (ITS- <i>trnT-F</i> )	1295–1673	37.2–38.7	1928	241	147 (07.63%)	123	66 (03.42%)
<i>trnT-L</i> spacer	699–766	24.3–26.5	949	147	82 (04.25%)	75	48 (02.49%)
<i>trnL</i> gene	523–616	36.5–38.6	642	67	30 (01.56%)	48	18 (00.93%)
<i>trnL-F</i> spacer	185–324	35.4–37.3	337	27	35 (01.82%)	11	11 (00.57%)

Table 3. Scores of Incongruency Length Difference (ILD) test for the combinability of ITS and *trnT-F* data partitions (\* $P < 0.05$ ).

Excluded taxa	ITS and <i>trnT-F</i> data	<i>P</i> values	Significance
No exclusion	Matrix with uncoded indels	0.008000	Incongruent
<i>Hekistocarpa</i> excluded	“	0.014000	Incongruent
<i>Tamridaea capsulifera</i> excluded	“	0.018000	Incongruent
<i>Canthium coromandelicum</i> excluded	“	0.004000	Incongruent
<i>Heinsia zanzibarica</i> excluded	“	0.006000	Incongruent
<i>Ixora coccinea</i> excluded	“	0.002000	Incongruent
<i>Alberta magna</i> excluded	“	0.308000	Congruent*
No exclusion	Matrix with coded indels (excluding the coded positions)	0.002000	Incongruent
<i>Tamridaea capsulifera</i> excluded	“	0.014000	Incongruent
<i>Canthium coromandelicum</i> excluded	“	0.002000	Incongruent
<i>Heinsia zanzibarica</i> excluded	“	0.004000	Incongruent
<i>Ixora coccinea</i> excluded	“	0.002000	Incongruent
<i>Alberta magna</i> excluded	“	0.008000	Incongruent

Table 4. Morphological distinctive characters of *Hekistocarpa*, *Sabicea* s.l., *Tamridaea*, and *Virectaria*.

Characters	<i>Hekistocarpa</i>	<i>Sabicea</i> s.l.	<i>Tamridaea</i>	<i>Virectaria</i>
<b>Habit</b>	Herbaceous	Lianas, erect woody herbs, straggling herbs, shrubs or erect shrubs (up to 4 m tall), woody climbers	Shrub (ca. 1 m tall)	Herbaceous
<b>Inflorescence position and types</b>	Axillary, scorpioid cymes	Axillary, fascicle or densely capitulate to paniculate or thyrsoid, simple to compound dichasial cymes or solitary flowers	Terminal, usually dichasial corymbose cymes.	Terminal, dichasial thyrsoid to monochasial or simple cymes
<b>Flower types</b>	Homostylous	Hetero- and homostylous	Heterostylous	Homostylous
<b>Corolla aestivation</b>	Reduplicate valvate	True valvate	Reduplicate valvate	True valvate
<b>Corolla lobes</b>	Ovate to deltoid with (sub-) acute apices	Ovate with (sub-) acute apices	obcordate corolla lobes with emarginate-mucronate apices	Lanceolate to deltoid with (sub-) acute apices
<b>Anther fixation and position</b>	Dorsimedifixed, inserted	Dorsimedifixed, included (short-styled flowers) and slightly exerted (long-styled flowers)	Dorsifixed, included (short-styled flowers) and slightly exerted (long-styled flowers)	Dorsimedifixed, exerted
<b>Stigma branches</b>	2, filiform	2–5(6), filiform to oblong or very narrowly elliptic or oblanceolate to widely spatulate or dilated	2, filiform-oblong	Initially 2, eventually truncated, spherical
<b>No. of locules per ovary</b>	ca. 10	2–5(7)	2	2
<b>Fruit types</b>	Dry indehiscent fruits	Berries	Dry capsular	Dry capsular
<b>Pollen type</b>	3-colporate	3–4-colporate	4-colporate	3-colporate

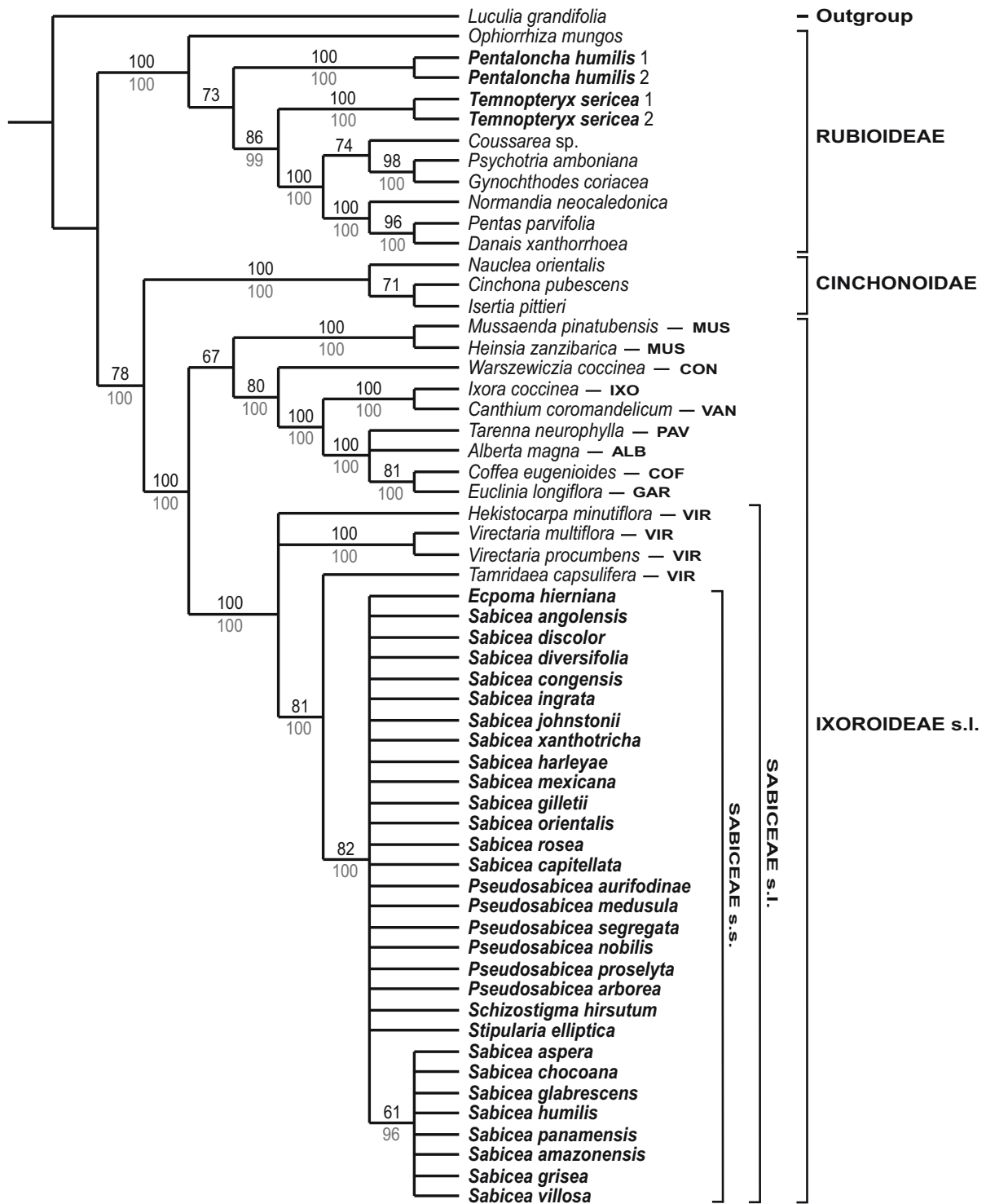


Fig. 1. Strict consensus tree generated from 8067 equally parsimonious trees based on the phylogenetic analysis of the *trnT-F* data. The numbers above the branches are bootstrap support values (> 50%) and those below the branches are Bayesian posterior probabilities (> 95%). MUS = Mussaendeae, CON = Condamineae, IXO = Ixoreae, VAN = Vanguerieae, PAV = Pavetteae, ALB = Alberteae, COF = Coffeae, GAR = Gardenieae, and VIR = Virectarieae. Brackets delimit the three subfamilies (sensu Bremer & al., 1999), Sabiceae s.l., and Sabiceae s.s. The genera shown in boldface belong to Sabiceae sensu Andersson (1996).

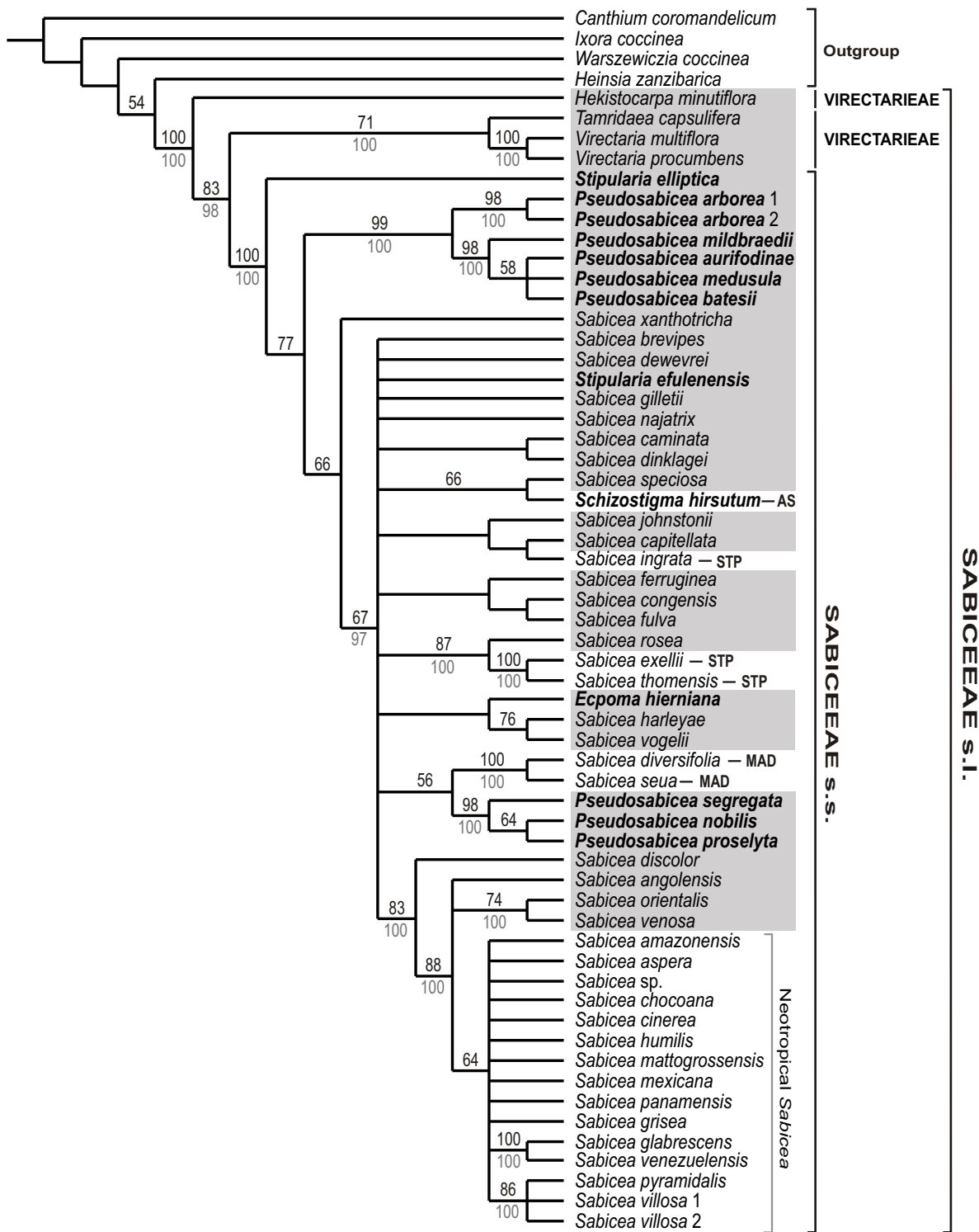


Fig. 2. Strict consensus tree generated from 210 equally parsimonious trees based on the phylogenetic analysis of the ITS data. The numbers above the branches are bootstrap support values (> 50%) and those below the branches are Bayesian posterior probabilities (> 95%). Brackets delimit the outgroup taxa, Sabiceae s.l., Sabiceae s.s., and the Neotropical *Sabicea*. The vertical bars delimit the genera of Virectarieae sensu Dessein & al. (2001b). AS = Asia, MAD = Madagascar, and STP = São Tomé and Príncipe. See my suggestion in text to add differentiating biogeographical categories next to the names of the continental African taxa. The taxa shown in boldface are the sequenced species of *Ecpoma*, *Pseudosabicea*, *Schizostigma*, and *Stipularia*. All shadowed taxa are continental African.

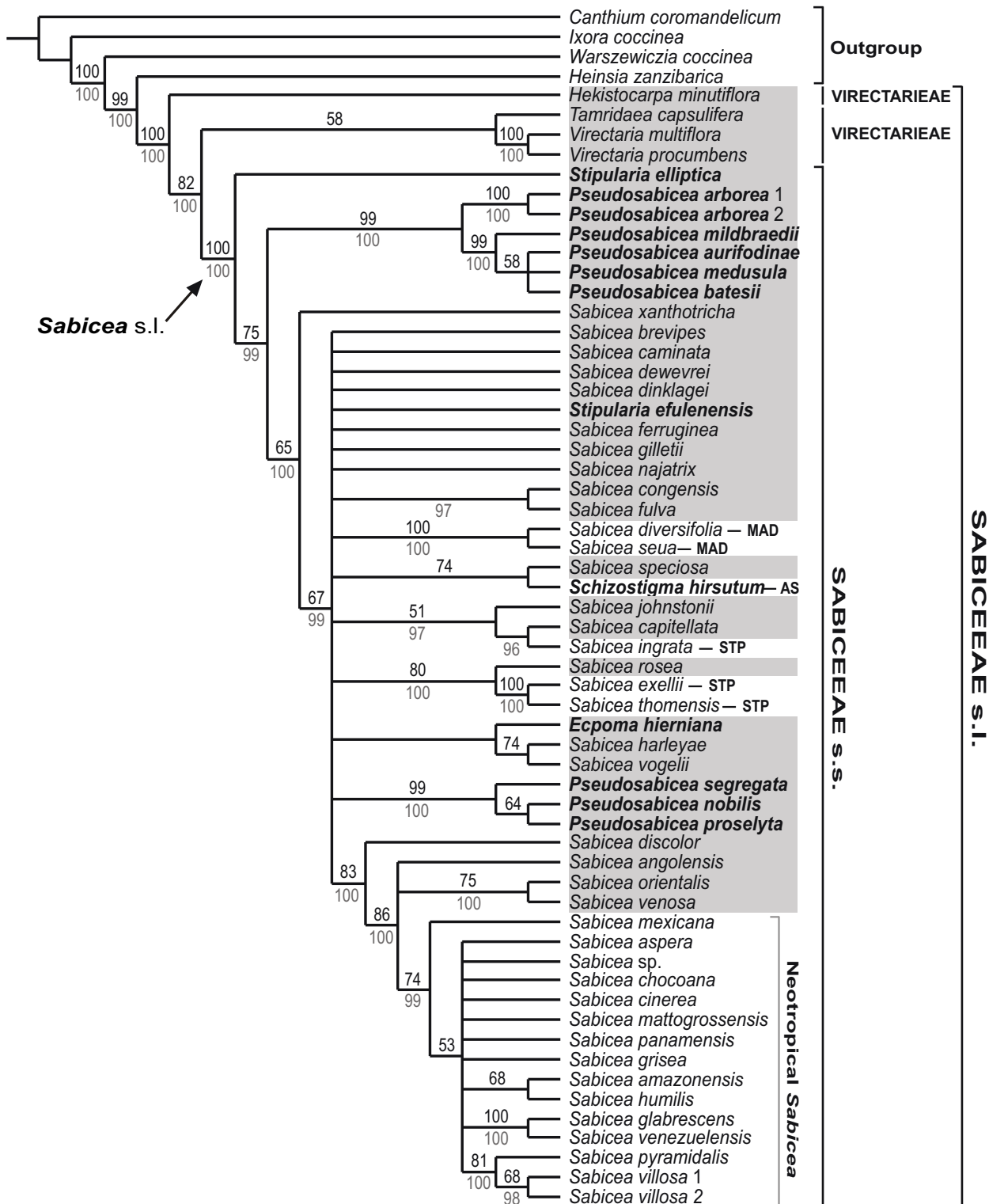


Fig. 3. Strict consensus tree generated from 104442 equally parsimonious trees based on the phylogenetic analysis of the ITS-*trnT-F* data. The numbers above the branches are bootstrap support values (> 50%) and those below the branches are Bayesian posterior probabilities (> 95%). Brackets delimit the outgroup taxa, Sabiceae s.l., Sabiceae s.s., and the Neotropical *Sabicea*. The vertical bars indicate the position of the genera of Virectarieae sensu Dessein & al. (2001b). AS = Asia, MAD = Madagascar, and STP = São Tomé and Príncipe. See my suggestion in text to add differentiating biogeographical categories next to the names of the continental African taxa. The taxa shown in boldface are the sequenced species of *Ecpoma*, *Pseudosabicea*, *Schizostigma*, and *Stipularia*. All shadowed taxa are continental African.

## Appendix 1. Voucher information and accession numbers for all species included in this study.

**Species, Country origins, Voucher, *trnT-F* acc. no, ITS acc. no.**

*Alberta magna* E. Mey., GenBank, AJ620118, -; *A. magna*, GenBank, -, AJ224842; *Canthium coromandelicum* (Burm. f.) Alston, GenBank, AJ847401, -; *C. coromandelicum*, GenBank, -, AJ315081; *Cinchona pubescens* Vahl, GenBank, AJ346963, -; *Coffea eugenoides* S. Moore, GenBank, AJ847402, -; *Coussarea* sp., GenBank, AF152612, -; *Danais xanthorrhoea* (K. Schum.) Bremek., GenBank, AM409329, -; *Ecpoma hierniana* (Wernham) N. Hallé & F. Hallé, *Thompson 1803* (K), AM409140, AM409055; *Euclina longiflora* Salisb., GenBank, AJ847399, -; *Gynochthodes coriacea* Blume, GenBank, AJ847407, -; *Heinsia zanzibarica* (Boj.) Verdc., GenBank, AJ847377, AJ846880; *Hekistocarpa minutiflora* Hook. f., Cameroon, *Sonké & al. 2708* (BR), AM409141, AM409056; *Isertia pittieri* (Standl.) Standl., GenBank, AJ847404, -; *Ixora coccinea* L., GenBank, AJ620117, -; *I. coccinea*, GenBank, -, AJ224826; *Luculia grandifolia* Ghose, GenBank, AJ346929, -; *Mussaenda pinatubensis* Elmer, GenBank, AJ847365, -; *Nauclea orientalis* (L.) L., GenBank, AJ346958, -; *Normandia neocaledonica* Hook. f., New Caledonia, *Munzinger 532* (MO), AM409177, -; *Ophiorrhiza mungos* L., GenBank, AF152610, -; *Pentaloncha humilis* Hook. f. (2), Gabon, *Wilde & al. 10235* (WAG), AM409173, -; *P. humilis* (1), Gabon, *Breteler & al. 10985* (WAG), AM409174, -; *Pentas parvifolia* Hiern, GenBank, AJ847406, -; *Pseudosabicea arborea* (K. Schum.) N. Hallé (1), Burundi, *Reekmans 11116* (K), AM409167, AM409049; *P. arborea* (2), Burundi, *Reekmans 11116* (WAG), AM409138, AM409050; *P. aurifodinae* N. Hallé, Gabon, *Wieringa & al. 5026* (WAG), AM409162, AM409046; *P. batesii* (Wernham) N. Hallé, Gabon, *Valkenburg & al. 2569* (WAG), AM409139, AM409048; *P. medusula* (K. Schum. ex Wernham) N. Hallé, Cameroon, *Andel & al. 3555* (WAG), AM409163, AM409047; *P. mildbraedii* (Wernham) N. Hallé, Gabon, *Wieringa & al. 5032* (WAG), AM409137, AM409051; *P. nobilis* (R. Good) N. Hallé, Gabon, *Valkenburg & al. 2604* (WAG), AM409165, AM409052; *P. proselyta* N. Hallé, Gabon, *Valkenburg & al. 2646* (WAG), AM409166, AM409053; *P. segregata* (Hiern) N. Hallé, Gabon, *Wieringa & al. 5025* (WAG), AM409164, AM409054; *Psychotria amboniana* K. Schum., GenBank, AJ847409, -; *Sabicea amazonensis* Wernham, Brazil, *Campbell & al. P22037* (MO), AM409157, AM409007; *S. angolensis* Wernham, Republic of the Congo, *Lisowski B-7136* (BR), AM409142, AM409006; *S. aspera* Aubl., French Guiana, *Andersson & al. 2003* (NY), AM409143, AM409008; *S. brevipes* Wernham, Ghana, *Jongkind & Nieuwenhuis 2793* (WAG), AM409178, AM409009; *S. caminata* N. Hallé, Gabon, *Wilde & Sosef 10311* (WAG), AM409118, AM409010; *S. capitellata* Benth., Equatorial Guinea, *Sonké & Esono 2533* (BR), AM409161, AM409012; *S. chocoana* C. M. Taylor, Colombia, *Delprete 6342* (NY), AM409144, AM409013; *S. cinerea* Aubl., French Guiana, *Andersson & al. 1903* (NY), AM409120, AM409014; *S. congensis* Wernham, Gabon, *Breteler 12428* (WAG), AM409146, AM409015; *S. dewevrei* De Wild. & T. Durand, Republic of the Congo, *Lemaire 1393* (BR), AM409121, AM409016; *S. dinklagei* K. Schum., Malawi, *Pawek 6510* (UPS), AM409122, AM409017; *S. discolor* Stapf, Ivory Coast, *Jongkind & al. 4880* (WAG), AM409145, AM409018; *S. diversifolia* Pers., GenBank, AJ847396, AJ846883; *S. exellii* G. Taylor, São Tomé and Príncipe, *Joffroy 188* (BRLU), AM409124, AM409020; *S. ferruginea* Benth., Liberia, *Jongkind & al. 5683* (WAG), AM409125, AM409021; *S. fulva* Wernham, Gabon, *Wieringa & al. 4094* (WAG), AM409126, AM409022; *S. gillettii* De Wild., Dem. Rep. of the Congo (Zaire), *Lejoly 82/903* (BR), AM409154, AM409023; *S. glabrescens* Benth., Guyana, *Gillespie & Tiwari 825* (NY), AM409147, AM409024; *S. grisea* Cham. & Schltld., Brazil, *Arbo & al. 7191* (NY), AM409159, AM409040; *S. harleyae* Hepper, Ivory Coast, *Jongkind & al. 4867* (WAG), AM409152,



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AM409025; *S. humilis* S. Moore, Brazil, *Malme 2684* (S), AM409148, AM409026; *S. ingrata* K. Schum., São Tomé and Príncipe, *Ogonnovsky 10* (BRLU), AM409149, AM409027; *S. johnstonii* K. Schum. ex Wernham, Gabon, *Wieringa & al. 4652* (WAG), AM409150, AM409028; *S. mattogrossensis* Wernham, Bolivia, *Beck & Haase 9986* (NY), AM409127, AM409029; *S. mexicana* Wernham, Mexico, *Hahn 639* (NY), AM409153, AM409030; *S. najatrix* N. Hallé, Gabon, *Wieringa & al. 4653* (WAG), AM409128, AM409031; *S. orientalis* Wernham, Tanzania, *Mhoro 443* (UPS), AM409155, AM409032; *S. panamensis* Wernham, Ecuador, *Harling & Ståhl 26896* (S), AM409156, AM409033; *S. pyramidalis* L. Andersson, Ecuador, *Burnham 1455* (F), AM409129, AM409034; *S. rosea* Hoyle, Ivory Coast, *Jongkind 4550* (WAG), AM409158, AM409035; *S. seua* Wernham, Madagascar, *Malcomber & al. 1085* (WAG), AM409130, AM409036; *S. speciosa* K. Schum., Nigeria, *Meer 1623* (WAG), AM409131, AM409037; *S. thomensis* Joffroy, São Tomé and Príncipe, *Ogonnovsky 18* (BRLU), AM409132, AM409038; *S. venezuelensis* Steyerm., Venezuela, *Huber 4201* (NY), AM409133, AM409039; *S. venosa* Benth., Central Africa Republic, *Sonké & Beina 2797* (WAG), AM409134, AM409041; *S. villosa* Willd. ex Roem. & Schult. (1), Costa Rica, *Delprete 5102* (NY), AM409160, AM409042; *S. villosa* (2), Ecuador, *Delprete & Verduga 6396* (NY), AM409135, AM409043; *S. vogelii* Benth., Ivory Coast, *Jongkind & al. 4859* (WAG), AM409136, AM409044; *S. xanthotricha* Wernham, Cameroon, *Sonké 1082* (BR), AM409151, AM409045; *Sabicea* sp., Bolivia, *Nee 46014* (NY), AM409119, AM409011; *Schizostigma hirsutum* Arn.(= *S. ceylanica* Puff.), Sri Lanka, *Iwarsson 576* (UPS), AM409168, AM409057; *Stipularia efulenensis* Hutch., Cameroon, *Andel 3417* (WAG), AM409123, AM409019; *S. elliptica* Schweinf. ex Hiern, Dem. Rep. of the Congo (Zaire), *Lisowski 56663* (BR), AM409169, AM409058; *Tamridaea capsulifera* (Balf. f.) Thulin & B. Bremer, Yemen, *Miller & al. 10087* (UPS), AM409170, AM409059; *Tarenna neurophylla* (S. Moore) Bremek., GenBank, AJ847403, -; *Temnopteryx sericea* Hook. f. (1), Equatorial Guinea, *Wieringa & Haegens 2266* (WAG), AM409175, -; *T. sericea* (2), Gabon, *Tabak 99* (WAG), AM409176, -; *Virectaria multiflora* (Sm.) Bremek., Ivory Coast, *Leeuwenberg 2295* (UPS), AM409171, AM409060; *V. procumbens* (Sm.) Bremek., Liberia, *Adams 453* (UPS), AM409172, AM409061; *Warszewiczia coccinea* Klotzsch, GenBank, AJ847397, AJ846884.

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## Phylogenetic relationships within Sabiceae s.l. (Ixoroideae, Rubiaceae) - phylogeography of *Virectaria* Bremek.

(Submitted: Plant Systematics and Evolution)

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**Abstract.** The phylogenetic relationships within the pantropical tribe Sabiceae s. l. (Ixoroideae, Rubiaceae) were inferred from the combined analysis of nuclear ITS and chloroplast *rpoC1* and *trnT-F* nucleotide sequence data. Phylogenetic relationships within *Virectaria* were investigated using combined analyses of ETS (nrDNA), ITS, *rpoC1* and *trnT-F*. The present analyses further show that *Hekistocarpa* is sister to the *Tamridaea-Virectaria-Sabicea* clade, *Tamridaea* and *Virectaria* are sister genera, and *Sabicea* s.l. is sister to *Tamridaea-Virectaria* clade. Our results strongly support the monophyly of *Virectaria* and the sister-group relationships between *V. multiflora* and *V. herbacoursi*, *V. angustifolia* and *V. procumbens*, and *V. major* and *V. belingana*. Our analyses indicate a tropical African origin for Sabiceae s.l., a long isolated evolution for *Tamridaea* and a wide range of dispersal of *Virectaria* species in the Lower-, Upper-, and Congolian regions, without a clearly defined direction of migration.

**Keywords:** ETS, ITS, Morphology, Phylogeny, Phylogeography, *rpoC1*, Rubiaceae, Sabiceae, *trnT-F*, *Virectaria*.

When it was established by Bremekamp (1966), the pantropical tribe Sabiceae, presently classified in the subfamily Ixoroideae of the coffee family (Rubiaceae), was monogeneric and characterized by simple stipules, axillary inflorescences, and very narrow testa cells. Since then, conflicting circumscriptions of Sabiceae have been proposed (e.g. Andersson, 1996, Bremer and Thulin 1998, Dessein et al. 2001b, Robbrecht and Manen 2006). More recently, Khan et al. (accepted) performed phylogenetic analyses based on sequence data from the chloroplast *trnT-F* region and the nuclear ribosomal internal transcribed spacers. The results of that study has led to the establishment of new tribal and generic circumscriptions of Sabiceae, which comprises four genera: the monospecific *Hekistocarpa* Hook.f., restricted to Cameroon and Nigeria, the most species rich (170 species) pantropical *Sabicea* s. l.

(including *Ecpoma* K. Schum., *Pseudosabicea* N. Hallé, *Schizostigma* Arn. ex Meisn., and *Stipularia* P. Beauv.), the monospecific *Tamridaea* Thulin & B. Bremer, confined to Socotra of Yemen, and the tropical African *Virectaria* Bremek. (8 species, Dessein et al. 2001a). The intergeneric relationships within this newly delimited Sabiceae, entirely based on molecular data, were not addressed in Khan et al. (accepted) mainly due to lack of enough resolution and a limited sampling of *Virectaria*.

The mostly Guineo-Congolian wide (Robbrecht 1996) genus *Virectaria* Bremek., the second largest genus of the tribe with eight species, is characterized by its herbaceous or subshrubby habit, lack of raphides, truncate stigmata, flat internal indument, elongated floral disc, and one persistent and one deciduous valve during fruit dehiscence. The word *Virecta* is derived from “*vireo*”, to be verdant, alluding to the verdure of the plant (Smith 1819). All proposed species circumscriptions of *Virectaria* are summarized in Table 1 (see Dessein et al. 2001a for more information on the taxonomic history of the genus). For this study we adopted the circumscription of Dessein et al. (2001a), who presented a morphology-based analysis of *Virectaria*, in which the seven of the eight *Virectaria* species were resolved in two major clades.

This is the first phylogenetic study of the genus based on combined morphological and molecular (ETS, ITS, *rpoC1*, and *trnT-F*) data. This study was undertaken with four goals: 1) to assess rigorously the phylogenetic relationships between *Virectaria* and the other genera of Sabiceae sensu Khan et al. (Khan et al. accepted); 2) to test the monophyly of the genus *Virectaria*; 3) to test the interspecific relationships within *Virectaria* postulated by Dessein et al. (2001a), and 4) to infer the phylogeography of *Virectaria*.

## Materials and Methods

**Plant sampling.** Twenty-one species representing *Virectaria* and its allied genera were included in this study for the combined analyses of ITS, *rpoC1* and *trnT-F* sequence data including morphological data to examine the relationships within Sabiceae and to test the monophyly of *Virectaria*. Ten additional sequences of six *Virectaria* species were included for the separate analysis of each of the ITS, *rpoC1* and *trnT-F* data sets, as well as their combined analysis to compare the results. Two species of subfamily Ixoroideae s. l., *Mussaenda pinatubensis* Elmer (tribe Mussaendeae) and *Warszewiczia coccinea* Klotzsch (tribe Condamineae) were used as outgroup taxa. Eleven species including sixteen individuals of *Virectaria* representing six species were included in the combined analyses of molecular and morphological data to assess the phylogenetic relationships within the genus. Five species, *Hekistocarpa minutiflora* Hook. f., *Tamridaea capsulifera* (Balf. f.) Thulin & B. Bremer, *Sabicea becquetii* (N. Hallé) Razafim., B. Bremer, Liede & Khan, *Sabicea elliptica* (Schweinf. ex Hiern) Hepper, and *Sabicea xanthotricha* Wernham were used as outgroup

taxa. Material for *Virectaria salicoides* (C. H. Wright) Bremek., known only from the type and *Virectaria tenella* J. B. Hall was not available.

**DNA isolation, amplification, and sequencing.** DNA isolation, amplification and sequencing of the ITS region were accomplished following the protocols described in Alejandro et al. (2005) and Hassan et al. (2005), except the concentration of dH<sub>2</sub>O (15.8- $\mu$ L) and DNA samples (1.0  $\mu$ L) following Khan et al. (accepted). The amplification and sequencing of the *trnT*-F region were performed following the protocols outlined in Razafimandimbison and Bremer (2002). The amplification and sequencing of the ETS region were accomplished according to the protocols described in Razafimandimbison et al. (2005). The *rpoC1* exon 1 including *rpoC1* intron (partial) was amplified using the two DNA barcoding primers *rpoC1.2f* (5' GGC AAA GAG GGA AGA TTT CG 3') and *rpoC1.4r* (5' CCA TAA GCA TAT CTT GAG TTG G 3'). For each 25- $\mu$ L PCR reaction we added 16.3- $\mu$ L dH<sub>2</sub>O, 1- $\mu$ L MgCl<sub>2</sub> (25mM), 2- $\mu$ L dNTP (2mM), 1.0  $\mu$ L each of forward (*rpoC1.2f*) and reverse (*rpoC1.4r*) primer, (10 pmol/ $\mu$ L), 2.5- $\mu$ L PCR buffer (10X), 0.2  $\mu$ L TAQ (QUIAGEN) DNA polymerase, and 1.0  $\mu$ L DNA sample. PCR reaction was done with initial denaturation for 3 min. at 94°C, followed by 30 cycles for 1 min. at 93°C, 1 min. at 55°C, and finishing with 72°C for 2 min. Using the same primers, the sequencing reactions were conducted with ABI PRISM Big Dye Terminator Cycle sequencing kit (Applied Biosystems, Bayreuth, Germany). ABI Prism Model 310, version 3.0, sequencer was used for sequencing.

**Morphological data.** Morphological characters were recorded from 180 herbarium specimens of different herbaria that belong to the species listed in Table 2. The reproductive parts were studied after boiling in hot water for better pliability. Twenty-six characters (Table 3) were coded for the morphological matrix (Table 4) that was included in the combined ETS-ITS-*rpoC1*-*trnT*-F-morphological analyses for the infraspecific structure of the genus. The autapomorphic characters or fully or partially overlapping characters were excluded from the analysis. A somewhat different morphological matrix (available from the corresponding author) comprising 28 coded characters, mostly of Table 3, was also used in the combined ITS-*rpoC1*-*trnT*-F-morphological analyses for comparing the results of the combined ITS-*rpoC1*-*trnT*-F analyses to test the monophyly of the genus and its relationship with its allied genera. Before selecting the final characters for the study, a morphological matrix of 51 coded characters (not shown) including some seed and palynological characters used by Dessein et al. (2001a) was included in the preliminary analyses to assess their influence on the resolution of the phylogenetic analyses. The characters of seed exotesta of the species of *Sabicea* were studied by SEM (Philips XL-30) following the procedure outlined in Alejandro et al. (2005) and those of other genera (excluding *M. pinatubensis* and *W. coccinea*) were based on Dessein et al. (2001a).

**Data analyses.** The forward and reverse sequences of the ETS, ITS, *rpoC1*, and *trnT*-F were assembled in Perkin Elmer Sequence Navigator, version 1.0.1 and Sequencher 3.1.1. The consensus sequences were aligned and modified manually. Potentially informative indels

were coded using the simple gap coding method (Simmons and Ochoterena 2000). Maximum parsimony analyses (MPA) of the combined ITS-*rpoC1-trnT-F* and ETS-ITS-*rpoC1-trnT-F* matrices, including and excluding the morphological matrix, were performed in PAUP, version 4.0b (Swofford 2000). All data matrices were analyzed using the following heuristic search settings: MULTREES option on, tree-bisection-reconnection (TBR) branch swapping, swap on best only in effect, and 5,000 random addition sequences. Consistency index (CI, Kluge and Farris 1969) and retention index (RI, Farris 1989) were calculated to estimate homoplasy. Bootstrap analyses were performed using 10,000 replicates, MULTREES option on, TBR branch swapping and five random addition sequences to assess the support of the resolved clades. In all analyses, we finally used the baseline matrices avoiding the coding of indels. However, to compare the results, we performed additional parsimony analyses including the coded indels, but excluding the coded positions and the results are mentioned only when these differed from those based on baseline matrices. In final analyses, all characters were given equal weight, gaps were treated as missing data, and only parsimony-informative characters were included. To explore the combinability of all data sets included in the ITS-*rpoC1-trnT-F* and ETS-ITS-*rpoC1-trnT-F* matrices, we conducted the ILD test as implemented in PAUP\*, and compared the tree topologies generated from separate analyses of each data set.

To evaluate the statistically potential monophyletic groups, Bayesian analyses (BA) were performed in MrBayes, version 3.1.2 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003) using the substitution model parameters: Prset statefreqpr=dirichlet (1,1,1,1); Lset nst=6 rates=equal; selected for the best fit model (GTR+I+G) by both Hierarchical Likelihood Ratio Tests (hLRT) and Akaike Information Criterion (AIC) in MrModeltest, version 2.2 (Nylander 2004) for the uncoded and combined ITS-*rpoC1-trnT-F* and ETS-ITS-*rpoC1-trnT-F* data sets. In the combined analyses including morphological matrix, the morphological character partition was treated as standard and the model parameters lset applyto=(1/DNA) nst=6 rates=invgamma; unlink shape=(all) pinvar=(all) statefreq=(all) revmat=(all); prset ratepr=variable; were applied. In all searches, the default settings (MrBayes, version 3.1.2) were used for all active parameters for the corresponding substitution models, as well as for the heating scheme. Eight chains under two simultaneous runs, with 100 sample frequencies were executed and monitored up to  $3.5\text{--}4.5 \times 10^6$  Markov Chain Monte Carlo (mcmc) generations for arriving at the stationary phase. 25% of the samples were discarded as burn-in. The graphical presentations of summarized resulting trees were generated in PAUP\* and Tree View (Page 1996). Internodes with posterior probabilities of more than 95 % were considered as strongly supported.

## Results

**Phylogenetic analyses.** Description of all MPA of the combined data sets and resulting trees are summarized in Table 7.

Separate analysis of ITS, *rpoC1* and *trnT-F* data: The results of the ILD test supported the combinability of the ITS, *rpoC1*, and *trnT-F* data sets of the 23 taxa used in evaluating the relationships between the genera of Sabiceae and testing the monophyly of *Virectaria* (Table 5). However, the tree topologies of the strict consensus trees resulted from the separate analyses of ITS, *rpoC1*, and *trnT-F* data (results not shown) appeared conflicting regarding the positions of *Hekistocarpa* and *Tamridaea*. But neither of the positions was supported by more than 50% BS. In both ITS and *trnT-F* analyses (results not shown), *Hekistocarpa* was resolved as sister (BS = 100) to the clade of *Tamridaea*, *Sabicea* and *Virectaria* (BS = 57, ITS, BS = 54, *trnT-F*). In *rpoC1* analysis, *Tamridaea*, instead of *Hekistocarpa* (ITS or *trnT-F* tree), was resolved as sister (BS = 98) to an unsupported *Hekistocarpa-Virectaria-Sabicea* clade (BS = < 50). In one *trnT-F* analysis (results not shown) *Tamridaea* and *Sabicea* s. l. were resolved as a weakly supported monophyletic group (BS = 60) in the unsupported *Tamridaea-Sabicea-Virectaria* clade (BS = < 50). Based on the results of the ILD test and lack of support for the topological conflicts, we combined the ITS, *rpoC1*, and *trnT-F* data sets.

Combined ITS-*rpoC1-trnT-F* analyses: The most parsimonious tree generated from the combined analyses of the ITS, *rpoC1* and *trnT-F* data of 23 taxa (Fig. 1) exhibited strong support to the clade of Sabiceae sensu Khan et al., in which two *Hekistocarpa* accessions were shown to be sister to a weakly to moderately supported clade comprising *Tamridaea*, six species of *Virectaria* and twelve species of *Sabicea* s. l. This *Tamridaea-Virectaria-Sabicea* clade was further resolved into two major clades, the moderately to strongly supported *Tamridaea-Virectaria* clade, which was resolved with weak to moderate support as sister to the *Sabicea* clade. Within the *Tamridaea-Virectaria* clade, *Tamridaea* was consistently shown to be sister to the strongly supported monophyletic group comprising all *Virectaria* species (hereafter *Virectaria* clade). Within the *Virectaria* clade, *V. herbacoursi* and *V. multiflora* formed a strongly supported clade (hereafter *V. herbacoursi-V. multiflora* clade), which was further resolved as sister to the strongly supported clade formed by *V. angustifolia*, *V. procumbens*, *V. belingana*, and *V. major* (hereafter *V. angustifolia-V. procumbens-V. belingana-V. major* clade). This clade of four *Virectaria* was resolved into two subclades, the strongly supported *V. angustifolia-V. procumbens* subclade and the moderately supported *V. belingana-V. major* subclade. Within the *Sabicea* clade, *S. elliptica* was appeared to be sister to a moderately to strongly supported clade consisting of all other sampled species of *Sabicea* s. l. The *Tamridaea-Virectaria* clade or resolving of *Tamridaea* as sister to *Virectaria* was weakly supported when 28 morphological characters (not shown) were included in the analyses. The topology of the most parsimonious tree generated from the combined ITS-*rpoC1-trnT-F* analysis was mostly similar to that resulting from the separate analysis of the

ITS or *trnT*-F data sets (not shown). The strict consensus tree generated from a separate analysis of *rpoC1* data (not shown) was mostly unresolved.

Separate analysis of the ETS, ITS, *rpoC1* and *trnT*-F data: The results of the ILD test did not support the combinability of ETS, ITS, *rpoC1*, and *trnT*-F data sets to assess the infraspecific relationships and phylogeography within the genus. But the combinability of either the ETS, ITS, and *rpoC1* or the ITS, *rpoC1*, and *trnT*-F data sets were supported (Table 5). On the other hand, the separate analyses of each of the ETS, ITS, and *trnT*-F data sets (*rpoC1* data resulted in an unresolved tree), and the ETS-ITS-*rpoC1*, ITS-*rpoC1*-*trnT*-F, and ETS-ITS-*rpoC1*-*trnT*-F matrices (results not shown) imparted the unsupported topological conflicts in resolving the two *V. herbacoursi* accessions as sister group to the subclade of *V. multiflora* accessions (e.g. ITS, *trnT*-F, ITS-*rpoC1*-*trnT*-F, ETS-ITS-*rpoC1*-*trnT*-F trees) versus the clade of all *Virectaria* accessions (e.g. ETS tree). Based on the lack of clear-cut evidence to the reason of incongruence of ETS, ITS, *rpoC1*, and *trnT*-F data sets or the topological conflicts, we combined these four data sets. Finally, to describe the infraspecific relationships within the genus, we present our results based on the combined ETS-ITS-*rpoC1*-*trnT*-F analyses.

Combined ETS-ITS-*rpoC1*-*trnT*-F analyses: In the most parsimonious ETS-ITS-*rpoC1*-*trnT*-F tree (Fig. 2), the sampled *Virectaria* formed a strongly supported monophyletic group, in which all individuals were resolved in two major clades: the moderately to strongly supported *Virectaria herbacoursi*-*Virectaria multiflora* clade (hereafter Clade A, Fig. 2), and the strongly supported *Virectaria* sp.-*Virectaria angustifolia*-*Virectaria procumbens*-*Virectaria major*-*Virectaria belingana* clade (hereafter Clade B, Fig. 2). The Clade A is further resolved as sister to the Clade B. Within the Clade A, two accessions of *V. herbacoursi* were resolved as sister (hereafter subclade I, Fig. 2) to the strongly supported subclade comprising all sampled *V. multiflora* accessions (hereafter subclade II, Fig. 2).

Within the Clade B, the two *Virectaria* sp., one *V. angustifolia*, and two *V. procumbens* formed a strongly supported subclade (hereafter subclade III, Fig. 2) which was further resolved as sister to another moderately supported subclade consisting of two subspecies of *V. major* (*V. major* 1 = *V. major* subsp. *spathulata*, *V. major* 2 = *V. major* subsp. *major*) and three accessions of *V. belingana* (hereafter subclade IV, Fig. 2). In the subclade III, *Virectaria* sp. 1 was resolved as sister to the moderately supported group of *Virectaria* sp. 2, *V. angustifolia* and two *V. procumbens*. Within this group, *Virectaria* sp.2 was resolved with weak to moderate support as sister to the well-supported group of one *V. angustifolia* and two *V. procumbens*, while *V. angustifolia* was further resolved with moderate to strong support as sister to the moderately to strongly supported monophyletic group of two *V. procumbens*. Within the subclade IV, the two sampled subspecies of *V. major*, forming a strongly supported monophyletic group, were resolved as sister to the strongly supported monophyletic group of three *V. belingana* (Fig. 2). The topology of the combined ITS-*rpoC1*-*trnT*-F or the ETS-ITS-*rpoC1*-*trnT*-F tree was mostly similar to the most parsimonious tree

resulting from the separate analyses of the ITS or *trnT-F* data sets. The topology of the combined ETS-ITS-*rpoC1* tree was mostly similar to that of the strict consensus tree generated from the separate ETS analysis. The strict consensus tree generated from a separate analysis of *rpoC1* data was mostly unresolved. The resolution of each species exhibited in the most parsimonious tree generated from the combined analysis of molecular data sets was mostly compatible with its morphological characters but the resolutions within the species were uncongenial with their morphological distinctiveness.

## Discussion

Here, we focus mainly on the relationship of *Virectaria* with its associated genera of Sabiceae sensu Khan et al. (accepted), the monophyly of *Virectaria* and interspecific relationships between its species, and phylogeography of the genus as inferred by our results.

**Sequence characteristics.** ETS and *rpoC1* data are here used for the first time for the Sabiceae, while the ITS and *trnT-F* data were used in our earlier study (Khan et al. accepted). Consequently the sequence characteristics of the ITS and *trnT-F* (Table 6) correspond closely to those in Khan et al. The range of variation in the ETS lengths and the percentage of GC contents (Table 6) appear close to the record for other Rubiaceae (469 bp, Nepokroff et al. 2003, 51 %, Negrón-Ortiz and Watson 2002). The non-coding sequences from the *rpoC1* region have been frequently used in Angiosperms, in intrafamilial (e.g. Apiaceae, Downie et al. 1996a, Fabaceae, Liston and Wheeler 1994) or infrageneric (e.g. *Lathyrus* L., Asmussen and Liston 1998, *Trifolium*, Watson et al. 2000) phylogeny studies. However, in Rubiaceae only Samson et al. (2007) explored the implication of the *rpoC1* region of *Coffea arabica* L. for phylogenetic relationships in angiosperms. Using the DNA barcoding primers (*rpoC1.2f* and *rpoC1.4r*), we could amplify only exon 1 and a tiny part of intron from *rpoC1* region. The lack of *rpoC1* intron in some angiosperms is reported (Downie et al. 1996b, Wallace and Cota 1996, Hansen et al. 2006). However, we are unable to conclude here, whether or not the *rpoC1* intron or *rpoC1* exon 2 is missing in the genera included in this study. The low variation of lengths and potentially informative characters of the aligned *rpoC1* matrix (484 bp and 13 informative characters) appears close to the report for the *rpoC* spacer of the flowering plant genus *Styrax* (Styracaceae, Ebenales, Fritsch 2001). The mostly unresolved to moderately resolved trees resulting from the separate analysis of the *rpoC1* data corresponds to its very low variation. However, it generates moderate to strong supports to the resolved clades (not shown), which indicates its potential phylogenetic implication at generic level in Rubiaceae.

**Relationships between *Virectaria* and its associated genera of Sabiceae s. l.** While the position of *Hekistocarpa* as sister to the *Tamridaea-Virectaria-Sabicea* clade is only weakly to moderately supported in the combined ITS-*rpoC-trnT-F* tree (Fig. 1), this sister-



group relationship is consistently retained in the parsimonious trees from the combined analyses conducted in this study. Plus, it is highly supported (BS = 82, PP = 100) by the combined ITS-*trnT*-F analysis of Khan et al. (accepted). However, this result is inconsistent with that of the *rbcL* analysis of Dessein et al. (2001b, Fig. 38), in which *Sabicea* is resolved with weak support (JK = 66) as sister to a clade containing *Hekistocarpa*, *Tamridaea*, and *Virectaria*. The poorly supported (BS = 58) sister-group relationships between *Tamridaea* and *Virectaria* shown in Khan et al. (accepted, Fig. 3) is further corroborated by our results (Fig. 1). Both of *Tamridaea* and *Virectaria* appear to share a sister-group relationship with *Sabicea* s.l., as the moderately to strongly supported *Tamridaea-Virectaria* clade was resolved as sister to the *Sabicea* clade with weak to moderate support. In sum, the present analyses have confirmed that *Hekistocarpa* is sister to the *Tamridaea-Virectaria-Sabicea* clade and *Tamridaea* and *Virectaria* are sister genera. It is important to stress that these relationships are only supported by molecular data. *Virectaria* and its associated genera contain some autapomorphic characters and share mostly homoplasious characters (Table 3–4, Figs. 3A-H; Table 4, Khan et al. accepted; Appendix 2–3, Dessein et al. 2001a).

**Monophyly of *Virectaria*.** The morphological characteristics (Verdcourt 1953, Table 4, Dessein et al. 2001a) of the herbaceous to semi-woody genus *Virectaria* support its position in Rubiaceae and Sabiceae, which is confirmed by molecular data (Bremer and Thulin 1998, Khan et al. accepted). However, the monophyly of the genus has never been tested using molecular phylogenetic analysis. In Khan et al. (accepted), two *Virectaria* species (*V. multiflora*, *V. procumbens*) form a monophyletic group. In all analyses of the present study including morphological data (Figs. 1–2), all sampled *Virectaria* are constantly resolved as one strongly supported monophyletic group. There are several morphological synapomorphies supporting the genus *Virectaria*, such as, indistinct calyx tubes, completely exerted anthers (Fig. 3A), truncated stigmata, flat internal indument, elongated floral disc, splitting of capsules into one persistent and one deciduous valve, perforate sexine, and elongated seed exotesta with prominently thickened angles and small perforations (Dessein et al. 2001a). Therefore, the monophyly of the genus *Virectaria* is strongly supported by both molecular and morphological analyses and easily identified by the several distinct morphological characters. On the other hand, the constant resolving of all sampled species of *Sabicea* as a monophyletic group conform to *Sabicea* s.l. (Khan et al. accepted).

**Relationships within *Virectaria*.** The previous studies discussing the relationships within the genus *Virectaria* (e.g. Verdcourt 1953, Dessein et al. 2001a) were exclusively based on morphological data. The overall tree topology of our most parsimonious ETS-ITS-*rpoC1-trnT*-F tree or ETS-ITS-*rpoC1-trnT*-F-morphology tree (Fig. 2) is mostly consistent to that of Dessein et al. (2001a), however, *V. tenella*, included in the study by Dessein et al. (2001a), is missing from our analyses. The groups of *Virectaria* species resolved in two major clades (Clade A and Clade B) are strongly supported by both molecular and morphological data.

However, we avoid any new circumscription within *Virectaria*, as it is a small genus and we could not include two of the species (*V. salicoides* and *V. tenella*) in our analyses.

*Virectaria herbacoursi*-*Virectaria multiflora* clade (Clade A). Within the Clade A (Fig. 2), *V. herbacoursi* is well resolved as sister (Fig. 2: I) to *V. multiflora* (Fig. 2: II), consistent with Dessein et al. (2001a). This clade shares three morphological synapomorphies: 2–3 distinct lobes of stipules, long and stiff trichomes on outer surface of calyx lobes, and two lanceolate to narrowly lingulate and bilobed parts of floral disc (Figs. 3B, G). The additional synapomorphy of this group includes broad exotesta cells and smaller pollen (Dessein et al. 2001a). Therefore, the close relationship of *V. herbacoursi* with *V. multiflora* is strongly supported by both molecular and morphological data. *V. herbacoursi* can easily be distinguished from *V. multiflora* by its constantly 1–2 trichomes of outer calyx lobe surface in contrast to more than two, usually few to many trichomes of *V. multiflora* calyx lobes. All four accessions of *V. multiflora* from Gabon, Congo, and Liberia form a strongly supported subclade (Fig. 2: II). The resolving of four *V. multiflora* accessions within this subclade i.e. the resolving of *V. multiflora* 3 as sister to other three accessions (*V. multiflora* 2, *V. multiflora* 1, and *V. multiflora* 4) or *V. multiflora* 2 as sister to *V. multiflora* 1 and *V. multiflora* 4, is unsupported by their morphological characters, consistent with Dessein et al. (2001a).

A close relationship between *V. herbacoursi* and *V. tenella* based on the characters of floral disc and trichomes of calyces was postulated in the study of Dessein et al. 2001a. These two species contain notable autapomorphies, such as, creeping habit, erect branches, narrowly elliptic or lingulate, long (> 20 mm) leaves, and linear calyx lobes of *V. herbacoursi* in contrast to prostrate habit without erect branches, widely ovate and shorter (< 15 mm) leaves, deltoid, foliaceous or spatulate calyx lobes of *V. tenella*. On the other hand, *V. tenella* appears close also to *V. belingana* due to their relatively small leaves and short trichomes.

*Virectaria* sp.-*Virectaria angustifolia*-*Virectaria procumbens*-*Virectaria major*-*Virectaria belingana* clade (Clade B). Within the Clade B (Fig. 2), the subclade III (*Virectaria* spp., *V. angustifolia*, *V. procumbens*) is supported by two synapomorphies– smaller corolla tubes, inward folding of valves, and presumably the presence of a sexine and <1.2 P/E of pollen (Dessein et al. 2001a). *Virectaria* sp. 1, resolved here with low support as sister to the group of *Virectaria* sp. 2, *V. angustifolia*, and two accessions of *V. procumbens*, is morphologically distinct from all other members of this subclade, by its dwarf (15–18 cm long) semi-erect habit, up to 1 mm long trichomes, densely leafy branches, 0.8–1–2 (–2.5) × 0.4–1.1 cm leaves, spatulate calyx lobes, 4–5 mm long corolla tubes, and undivided disc. Morphologically, *Virectaria* sp. 1 seems an intermediate between *V. procumbens* and *V. tenella*, as its habit, shape and size of leaves and structure of inflorescence appear similar to those of *V. tenella*, whereas, flower characters seem similar to those of *V. procumbens*. Although *Virectaria* sp. 1 (Nimba range, Liberia) and *V. tenella* (endemic to Ghana) have widely separate distribution, morphologically they appear close. On the other hand, excluding its growth habit, densely leaved branches, size of leaves, and longer trichomes, *Virectaria* sp.

1 is similar to *V. procumbens*. It is unclear whether *Virectaria* sp. 1 is a variety of *V. procumbens*, widely distributed in Guineo-Congolian Region (Fig. 70c, Dessein et al. 2001a), or it is a hybrid between *V. procumbens* and *V. tenella*. *Virectaria* sp. 2, resolved as sister to the group of *V. angustifolia* and two accessions of *V. procumbens*, appears as close to both *V. angustifolia* and *V. salicoides*. The duplicate of its voucher specimen (*Nemba & Thomas 321*, BR) is included under *V. angustifolia* by Dessein et al. (2001a). We disagree with this placement, because *Virectaria* sp. 2 is an erect, 33 cm long herb with very narrowly elliptic, apically (sub-) acute to obtuse, and (5-) 2–5.5 × 0.2–0.8 cm leaves, narrowly spatulate calyx lobes, 4.5–5 mm long and externally sparsely strigulose corolla tubes with ciliolate lobes, and almost included stamens and styles, which indicate that it is close to both *V. angustifolia* and *V. salicoides*. The analysis adding morphological data set with molecular data does not support the resolving of *Virectaria* sp. 2 as sister to *V. angustifolia*, rather their resolution as a monophyletic group, because *V. salicoides* is not included in the analysis. *V. angustifolia* and *V. salicoides* morphologically appear closely related by their similar length-breadth ratios of leaves and the length ratios of corolla lobes and tubes, narrowly elliptic to lingulate or oblanceolate leaves, and short trichomes etc. On the other hand, *V. angustifolia* is distinct from *V. salicoides* by its short (usually 4–4.5 mm long, “less than 0.5 mm long” in Dessein et al. is a typological error) corolla tubes and the entire stipules, externally glabrous corolla [Hiern 1877, PL. 12 (2 & 3), Hallé 1966], narrowly lingulate to triangular calyx lobes, and almost included stamens and styles [PL. 12 (3), Hallé 1966]. The recognition of two varieties [*V. angustifolia* (Hiern) Bremek. var. *angustifolia* Bremek., *V. angustifolia* (Hiern) Bremek. var. *schlechteri* Verdc.] within *V. angustifolia* based on leaf shape and size as described by Verdcourt (1953) appears irrational, as the variation in leaf length (0.8–5 cm), leaf width (0.2–1 cm) or length-breadth ratio of leaves is continuous within this species. The variation in leaf shape or apices is also overlapping. Hiern (1877) and Hallé (1966) avoided any infraspecific categorization within this species, a view supported here. Within the subclade III (*Virectaria* spp., *V. angustifolia*, *V. procumbens*), the strongly supported group of *V. angustifolia* and *V. procumbens* appears to share only two synapomorphic characters: exerted part of style longer than corolla lobes and margins of valves folded inwards (Figs. 3F, H). Their notable autapomorphic characters include—narrowly elliptic to lingulate or oblanceolate leaves, lanceolate to triangular calyx lobes, and glabrous to glabrescent upper surface of leaves (*V. angustifolia*) in contrast to ovate to widely lanceolate leaves, spatulate calyx lobes, and sparsely strigulose upper surface of leaves (*V. procumbens*). However, here *V. angustifolia* is resolved as sister to *V. procumbens* which indicates that they are closely related, although the exact position of another ally, *V. salicoides*, is unsettled.

In the subclade IV (*V. major*, *V. belingana*, Fig. 2: IV), the formation of two *V. major* as sister to *V. belingana* is not consistent to Verdcourt's (1953) placement of *V. major* in the central line of his scheme and between *V. angustifolia* and *V. procumbens*. This result is also not compatible with Dessein et al. (2001a) in hypothesizing *V. major* as the basal species

within the clade of *V. angustifolia*, *V. procumbens*, *V. major*, and *V. belingana*, but in consideration of *V. major* and *V. belingana* as a closely related species, as they form a moderately supported monophyletic group (Fig. 2: IV). The close relationship between *V. major* and *V. belingana* appears unsupported by their morphological synapomorphies. On the other hand, this group shares the morphological synapomorphies— much exerted part of style, higher length-breadth ratios (1–4) of corolla lobes, and unfolded margins of valves with *V. herbacoursi* and *V. multiflora* (Figs. 3C, F, H), whereas, undivided and cylindrical floral disc with *V. angustifolia* and *V. procumbens* (Fig. 3G). On the other hand, these species are substantially distinct. *V. major* manifestly differs from *V. belingana* by its lack of divaricate branching and fairly longer and filiform to spatulate calyx lobes. Therefore, the close relationship between *V. major* and *V. belingana* is supported only by molecular data. The recognition of two subspecies *V. major* subsp. *major* (= *V. major* 1) and *V. major* subsp. *spathulata* (= *V. major* 2) seems warranted due to their restricted distribution and dissimilarity in shape of calyx lobes, as described by Dessein et al. (2001a).

**Phylogeography of *Virectaria*.** Khan et al. (accepted, Fig. 3) and all combined analyses performed for this study, including the combined ITS-rpoC1-*trnT*-F analysis (Fig. 1), consistently indicates that *Hekistocarpa* is as sister to the *Tamridaea-Virectaria-Sabicea*. This seems to indicate a tropical African and possibly a Guineo-Congolian origin for the whole tribe, as *Hekistocarpa* is known to restricted to the Lower-Guinea (Dessein et al. 2001b). The fruits of *Hekistocarpa* are dry, small, and crowned with persistent calyx lobes and hairs which might be dispersed by wind or by adhering to the bodies of animals or by sticking to the feathers of birds. *Tamridaea* is restricted to Socotra (Bremer and Thulin, 1998). Socotra is of Gondwanian origin, however, dating of its separation from Africa and Arabia is still debated with estimates ranging from 10 mya (Miller & Morris 2004) to 65–70 mya (Kopp 1999, Mies 2001). Recent geological studies suggest an age between 35–15 mya (Fleitmann et al. 2004, Thiv & Meve 2007). The origin of Rubiaceae is placed in the Danian at 61–64 mya (Wikström et al. 2001) and 78 mya (Bremer et al. 2004), with the earliest fossil evidence dating from 53 mya. However, estimates for differentiation of subfamilies and tribes are not yet available. Thus, it cannot be said with certainty whether *Tamridaea* is the result of vicariance and subsequent evolution in isolation or it arrived in Socotra by a long-distance dispersal event. Its high number of autapomorphies, both molecular and morphological, testifies either for a long isolated evolution or a rapid radiation.

The resolution of the sampled *Virectaria* species in our most parsimonious tree resulting from a combined analysis (Fig. 2) indicates the phylogeography of the genus. In this tree, neither the Upper-Guinean (e.g. *V. multiflora* 2, *Virectaria* sp. 1), nor the Lower-Guinean (e.g. *V. herbacoursi*, *V. angustifolia*, *V. belingana*), nor the Congolian elements (e.g. *V. multiflora* 3, *V. major* 1) form a monophyletic group, indicating that the species of any of these three phylogeographical regions (White 1983, Robbrecht 1996) are not closely related. In contrast, two of the four subclades (Fig. 2: II and IV) contain elements of all three regions, and one

subclade (Fig. 2: III) of two regions. In all three subclades, the Congolian and Upper-Guinean elements are sister to the Lower-Guinean elements. Regarding Clade A (Fig. 2), a Lower-Guinean element (*V. herbacoursi*) is sister to a group with members in all three regions. This pattern suggests an ongoing dispersal of taxa between the three regions, without a clearly defined direction of migration. On the other hand, although *V. multiflora* is a Guineo-Congolian species, however, its Upper-Guinean element (*V. multiflora* 2) is nested within its Congolian and Lower-Guinean elements (*V. multiflora* 3, and *V. multiflora* 1 and *V. multiflora* 4, respectively), which indicates that the Upper-Guinean population of *V. multiflora* might have had radiated from its Congolian or Lower-Guinean population. Similar results are not reflected by Guineo-Congolian species *V. procumbens* or Guineo-Congolian-Zambeian species *V. major*, because their Upper-Guinean elements are not included in the analyses. Dessein et al. (2001a) recognized *Virectaria tenella* and *V. herbacoursi* as a vicariant couple. If this estimate is proved as true then our results appear to indicate the presence of at least three (*V. herbacoursi* and *V. multiflora*, *V. angustifolia*, and *V. procumbens*, *V. major* and *V. belingana*) vicariant couples between the Guineo-Congolian and Zambeian regional center of endemism (White 1993). *V. salicoides* is said to possibly constitute a polyploid of *V. angustifolia* (Dessein et al. 2001), sharing a Lower Guinean distribution with its presumed diploid progenitor.

Our study further establishes Sabiceae sensu Khan et al. as a monophyletic group. Within the clade of Sabiceae sensu Khan et al., *Hekistocarpa* is resolved as sister to the *Tamridaea-Virectaria-Sabicea* clade, in which *Tamridaea* and *Virectaria* are sister genera. The *Tamridaea-Virectaria* clade is also sister to the clade of *Sabicea* s.l., the monophyly of which is further corroborated. Our results provide strong support to the monophyly of *Virectaria*, and the sister-group relationships between *V. multiflora* and *V. herbacoursi*, *V. angustifolia* and *V. procumbens*, and *V. major* and *V. belingana* as well. Our analyses appear to indicate a tropical African, and possibly Guineo-Congolian origin for Sabiceae s.l. It is unclear whether *Tamridaea* is the result of vicariance and subsequent evolution in isolation or it arrived in Socotra by a long-distance dispersal event, however, its long isolated evolution appears supported. Our results reveal the wide dispersal of *Virectaria* species between the Lower-, Upper-, and Congolian regions, without a clearly defined direction of migration. *Virectaria* species of any of these three regions are not closely related. Our study indicates that the Upper-Guinean population of *V. multiflora* might have had radiated from its Congolian or Lower-Guinean population. The close relationships between the species of *Virectaria* appear to indicate the presence of at least three vicariant couples or widely dispersed groups of species of *Virectaria* in the Guineo-Congolian and Zambeian regional center of endemism.

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**Table 1.** Species circumscriptions of *Virectaria*.

Species	Bremekamp (1952)	Verdcourt (1953)	Hallé (1966)	Dessein et al. (2001a)
<i>V. angustifolia</i>	<i>V. angustifolia</i>	<i>V. angustifolia</i>	<i>V. angustifolia</i>	<i>V. angustifolia</i>
<i>V. belingana</i>			<i>V. belingana</i>	<i>V. belingana</i>
<i>V. herbacoursi</i>			<i>V. herbacoursi</i>	<i>V. herbacoursi</i>
<i>V. heteromera</i>	<i>V. heteromera</i>	– <sup>1</sup>		
<i>V. kaessneri</i>	<i>V. kaessneri</i>	– <sup>2</sup>		
<i>V. major</i>		<i>V. major</i>	<i>V. major</i>	<i>V. major</i>
<i>V. multiflora</i>	<i>V. multiflora</i>	<i>V. multiflora</i>	<i>V. multiflora</i>	<i>V. multiflora</i>
<i>V. procumbens</i>	<i>V. procumbens</i>	<i>V. procumbens</i>	<i>V. procumbens</i>	<i>V. procumbens</i>
<i>V. salicoides</i>		<i>V. salicoides</i>	<i>V. salicoides</i>	<i>V. salicoides</i>
<i>V. tenella</i>				<i>V. tenella</i>

<sup>1</sup>Merged in *Virectaria angustifolia*; <sup>2</sup>lumped in *Virectaria major*.

**Table 2.** List of specimens used in this study, voucher information and GenBank accession numbers.

Taxa	Country origins	Voucher information / Reference	ETS	ITS	<i>rpoC1</i>	<i>trnT-F</i>
<i>Hekistocarpa minutiflora</i> Hook. f. (1)	Cameroon	Sonké et al. 2708 (BR)				
<i>Hekistocarpa minutiflora</i> Hook. f. (2)	Cameroon	Etuge & Thomas 143 (WAG)				
<i>Mussaenda pinatubensis</i> Elmer	Philippines	Alejandro 099 (UBT), Alejandro et al. (2005)				
<i>Sabicea aspera</i> Aubl.	French Guiana	Andersson et al. 2003 (NY)				
<i>Sabicea becquetii</i> (N. Hallé) Razafim., B. Bremer, Liede & Khan	Burundi	Reekmans 11116 (WAG)				
<i>Sabicea caminata</i> N. Hallé	Gabon	Wilde 10311 (WAG)				
<i>Sabicea ceylanica</i> Benth.	Ghana	Jongkind et al. 1516 (UPS)				
<i>Sabicea elliptica</i> (Schweinf. ex Hiern) Hepper	Republic Democratic of Congo (former Zaire)	Lisowski 56663 (BR)				
<i>Sabicea hierniana</i> Wernham	Gabon	Wilde 11714 (WAG)				
<i>Sabicea medusula</i> K. Schum. ex Wernh.	Cameroon	Andel et al. 3555 (WAG)				
<i>Sabicea mildbreadii</i> Wernham	Gabon	Wieringa 5032 (WAG)				
<i>Sabicea mexicana</i> Wernham	Mexico	Mendoza et al. 1329 (NY)				
<i>Sabicea nobilis</i> Good	Gabon	Valkenburg 2604 (WAG)				
<i>Sabicea venosa</i> Benth.	Central African Republic	Sonké and Benia 2797 (WAG)				
<i>Tamridea capsulifera</i> (Balf. f.) Thulin & B. Bremer	Yemen	Miller et al. 10087 (UPS)				
<i>Virectaria angustifolia</i> (Hiern) Bremek.	Gabon	Wieringa 4730 (WAG)				
<i>Virectaria belingana</i> N. Hallé (1)	Gabon	Parmentier 2336 (BRLU)				
<i>Virectaria belingana</i> N. Hallé (2)	Equatorial Guinea	Parmentier 3675 (BRLU)				
<i>Virectaria belingana</i> N. Hallé (3)	Equatorial Guinea	Obama & Lejoly 620 (BRLU)				

(continued)

**Table 2.** List of specimens used in this study, voucher information and GenBank accession numbers (continued).

Taxa	Country origins	Voucher information / Reference	ETS	ITS	<i>rpoC1</i>	<i>trnT-F</i>
<i>Virectaria herbacoursi</i> N. Hallé var. <i>petrophila</i> (1)	Equatorial Guinea	Parmentier & Esono 3375 (BRLU)				
<i>Virectaria herbacoursi</i> N. Hallé var. <i>petrophila</i> (2)	Equatorial Guinea	Lejoly & Elad 98/73 (BRLU)				
<i>Virectaria major</i> (K. Schum.) Verdc. subsp. <i>spathulata</i> (Verdc.) Dessein & Robbr. (1)	Republic Democratic of Congo (former Zaire)	Lejoly 2934 (BR)				
<i>Virectaria major</i> (K. Schum.) Verdc. subsp. <i>major</i> (2)	Tanzania	Kayombo 1842 (BR)				
<i>Virectaria multiflora</i> (Sm.) Bremek. (1)	Ivory Coast	Leeuwenberg 2295 (UPS)				
<i>Virectaria multiflora</i> (Sm.) Bremek. (2)	Liberia	Adams 606 (UPS)				
<i>Virectaria multiflora</i> (Sm.) Bremek. (3)	Congo	Champluvier S109 (BR)				
<i>Virectaria multiflora</i> (Sm.) Bremek. (4)	Gabon	Sosef et al. 551(WAG)				
<i>Virectaria procumbens</i> (Sm.) Bremek. (1)	Gabon	Tabak et al. 182/189 (WAG)				
<i>Virectaria procumbens</i> (Sm.) Bremek. (2)	Equatorial Guinea	Obama & Lejoly 538 (BRLU)				
<i>Virectaria</i> sp. 1	Liberia	Adams 453 (UPS)				
<i>Virectaria</i> sp. 2	Cameroon	Nemba & Thomas 321 (WAG)				
<i>Warszewiczia coccinea</i> Klotzsch	South America	Alejandro et al. (2005)				

**Table 3.** Morphological characters and character states used in the phylogenetic analyses.

Char. Nr.	Characters and character states
1.	Plant habit: 0– herb, often woody at the base 1– liana or vine 2– (sub-) shrub 3– tree
2.	Stem: 0– erect 1– climbing 2–straggling
3.	Stipule's shape: 0– oblong to lingulate 1– ovate to deltate 2– triangular 3– lanceolate
4.	Stipule orientation: 0– antrorse and appressed 1– antrorse and spreaded 2– moderately decurved 3– recurved to slightly reflexed
5.	Lobes of stipules: 0– at least 2 lobes present 1– lobes absent
6.	Length-breadth ratios of leaf blade: 0– <3 1– 3–6 2– >6
7.	Shape of leaf blades: 0– elliptic to oblong 1– lanceolate 2– ovate to widely lanceolate 3– very narrowly elliptic to obovate or oblanceolate
8.	Indument of upper surface of leaf blades: 0– covered with indument at least along the veins 1– glabrescent 2– glabrous
9.	Number of flowers: 0– one, sometimes three 1– few 2– many
10.	Calyx: 0– campanulate 1– tubes nearly indistinct 2– infundibuliform
11.	Length-breadth ratios of calyx lobes: 0– < 2 1– 2–5 2– >5
12.	Apex of calyx lobes: 0– acuminate to apiculate 1– obtuse 2– (sub-)acute
13.	Hairiness of calyx lobes margins: 0– eciliate 1– ciliate or ciliolate
14.	Indument of outer surface of calyx lobes: 0– covered with indument 1– glabrescent 2– glabrous
15.	Trichomes of calyx lobes: 0– appressed, ± straight 1– erecto-patent, ± straight, 2– (sub-) appressed to erecto-patent, ± straight or curled
16.	Long, stiff trichomes on outside of calyx lobes: 0– absent 1– present
17.	Length-breadth ratios of corolla lobes: 0– <1 1– >1
18.	Hairiness of corolla lobe margins: 0– eciliate 1– ciliate or ciliolate
19.	Indument cover of outer surface of corolla: 0– covered with indument 1– glabrous 2– glabrescent
20.	Trichomes of outer surface of corolla: 0– appressed, ± straight 1– erecto-patent, ± straight 2–appressed to erecto-patent, ± straight 3– (sub-) appressed to erecto-patent and curled
21.	Protrusion of anthers: 0– Included in corolla tubes, apically with or without protrusion beyond the tubes 1– completely protrusion beyond corolla tubes
22.	Protrusion of style: 0– exerted part is longer than the corolla lobes 1– exerted part is not longer than the corolla lobes 2– included in corolla tube, with or without projecting tip of stigmatic lobes
23.	Flower disc: 0– divided into two bilobed parts 1– undivided and cylindrical 2 – undivided and shallowly campanulate
24.	Fruit dehiscence: 0– fruits dehiscent, margins do not fold inwards 1– fruits dehiscent, margins fold inwards 2– fruits indehiscent
25.	Elongation of exotesta cells: 0– elongated 1– strongly elongated
26.	Trichomes of flowering branchlets and lower surface of leaves: 0– long 1– short

**Table 4.** Morphological matrix for *Virectaria* and outgroup taxa.

Taxa	Character states for characters 1–26																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
<i>Hekistocarpa minutiflora</i> 2	0	1&2	3	1&3	1	1	3	0	2	0	0	2	0	1	2	0	0	0	1	-	0	2	2	0&2	0	1
<i>Sabicea becquetii</i>	1	1	1	1&3	0&1	0	0&1	0&1	1	0	1	0	1	0	2	0	0	0&1	0	3	0	2	2	2	1	0
<i>S. xanthotricha</i>	1	1	1	0&1	1	0	0	0	1&2	0	2	0	1	0	2	0	0	0	1	-	0	2	2	2	1	1
<i>S. elliptica</i>	2	0	1	0	1	0	0	2	1	0	0&1	2	1	0	0	0	0	0	1	-	0	1	2	2	1	0
<i>Tamridaea capsulifera</i>	2&3	0	2	0	1	0	0	2	1	0	1	1	0	1	0	0	0	0	0	0	0	2	2	0	1	1
<i>Virectaria angustifolia</i>	0&2	0	3	0&1	1	1&2	3	2	1	1	1	1&2	1	2	-	0	0	0	1	-	1	1	1	1	1	1
<i>V. belingana</i> 1	0&2	0	3	0&1	1	0	2	0&1	1&2	1	1	0&2	1	1	2	0	1	0	0	0	1	0	1	0&1	1	1
<i>V. belingana</i> 2	0&2	0	3	0&1	1	0	2	0&1	1&2	1	1	0&2	1	1	2	0	1	0	0	0	1	0	1	0&1	1	1
<i>V. belingana</i> 3	0&2	0	3	0&1	1	0	2	0&1	1&2	1	1	0&2	1	1	2	0	1	0	0	0	1	0	1	0&1	1	1
<i>V. herbacoursi</i> 1	0	0	0	2	0	1	3	0&1	2	1	1	2	0	0	1	1	1	0&1	0	1	1	0	0	0	0	0
<i>V. herbacoursi</i> 2	0	0	0	2	0	1	3	0&1	2	1	1	2	0	0	1	1	1	0&1	0	1	1	0	0	0	0	0
<i>V. major</i> 1	1	0&2	3	1	0&1	0&1	0&2	0	2	1	1&2	0&2	1	0	2	0&1	1	1	0	2	1	0	1	0	1	0
<i>V. major</i> 2	2	0&2	3	1	0&1	0&1	0&2	0	2	1	1&2	0&2	1	0	1	0&1	1	1	0	1	1	0	1	0	1	0
<i>V. multiflora</i> 1	0	0	3	1	0	0	2&3	0	2	1	2	2	1	0	1	1	1	1	0	2	1	0	0	0	0	0
<i>V. multiflora</i> 2	0	0	3	1	0	0&1	2&3	0	2	1	2	2	1	0	1	1	1	1	0	2	1	0	0	0	0	0
<i>V. multiflora</i> 3	0	0	3	1	0	1	2&3	0	2	1	2	2	1	0	1	1	1	1	0	2	1	0	0	0	0	0
<i>V. multiflora</i> 4	0	0	3	1	0	1	2&3	0	2	1	2	2	1	0	1	1	1	1	0	2	1	0	0	0	0	0
<i>V. procumbens</i> 1	0	0&2	3	3	1	0	0&2	0	1	1	0&1	1	1	0	0	0	0&1	1	0	2	1	1	1	1	1	1
<i>V. procumbens</i> 2	0	0&2	3	3	1	0	0&2	0	1	1	0&1	1	1	0	0	0	0&1	1	0	2	1	1	1	1	1	1
<i>Virectaria</i> sp. 1	0	0&2	3	3	1	0	0&2	0	1	1	0&1	1	1	0	0	0	0&1	1	0	2	1	1	1	1	1	1
<i>Virectaria</i> sp. 2	0&2	0	3	0&1	1	2	3	0	1	1	1	1&2	1	2	-	0	0	1	1	0	1	1	1	1	1	1

**Table 5.** Scores of Incongruency Length Difference (ILD) test for the combinability of ITS and *trnT*-F data partitions (\* $P < 0.05$ ) without excluding any taxa.

Data partitions	<i>P</i> values	Significance
ITS, <i>rpoC1</i> & <i>trnT</i> -F of 23 taxa	0.916000	Congruent
ETS, ITS, & <i>rpoC1</i> of 21 taxa	0.132000	Congruent
ITS, <i>rpoC1</i> & <i>trnT</i> -F of 21 taxa	0.088000	Congruent
ETS, ITS, <i>rpoC1</i> & <i>trnT</i> -F of 21 taxa	0.004000	Incongruent
ETS, ITS, <i>rpoC1</i> & <i>trnT</i> -F of 17 taxa (excluding <i>T. capsulifera</i> , <i>S. becquetii</i> , <i>S. elliptica</i> , & <i>S. xanthotricha</i> )	0.002000	Incongruent

**Table 6.** Characteristics of the non-aligned sequences and their description in alignments.\*

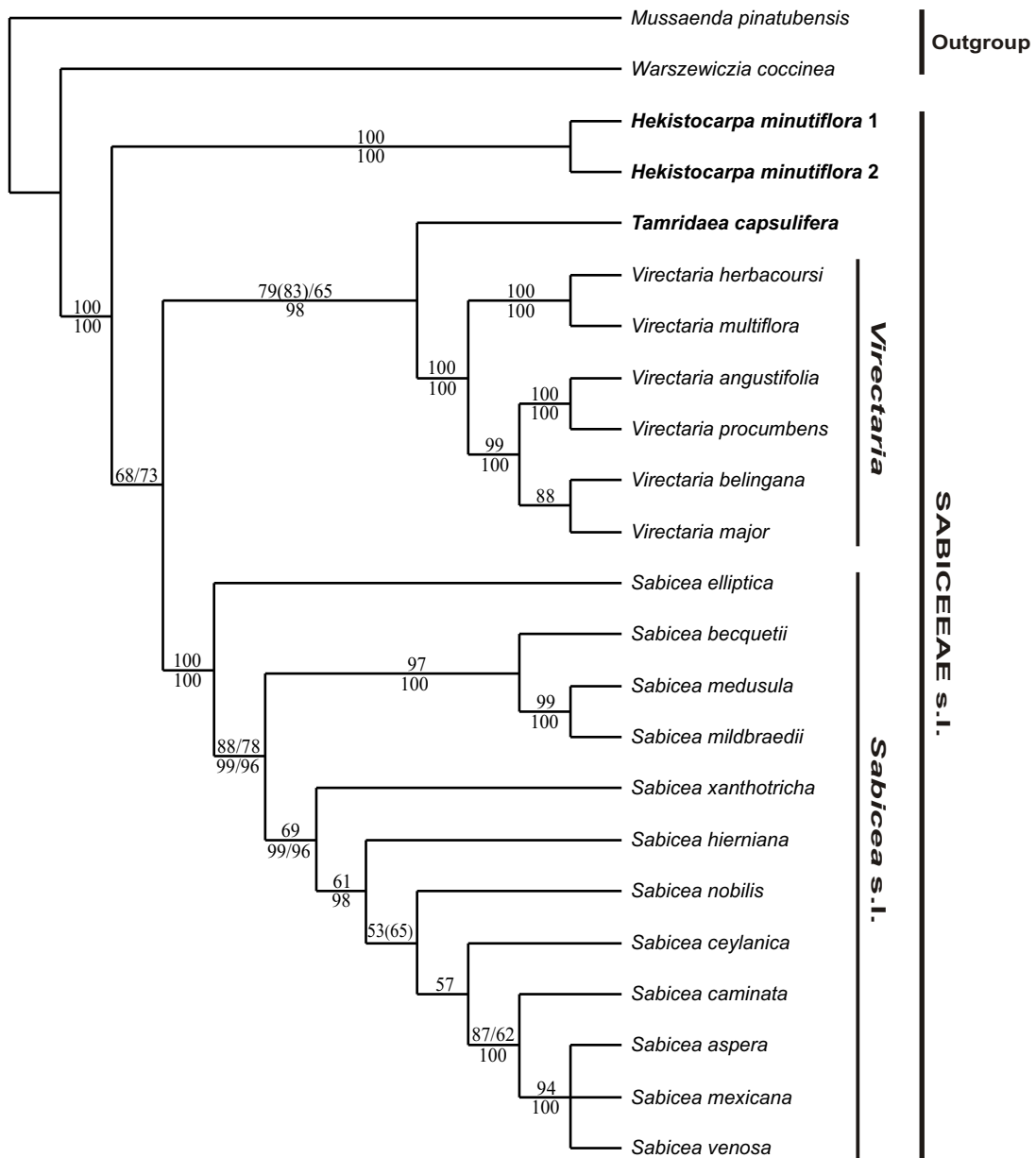
Markers	Length ranges of sequences (bp)	Ranges of GC contents in sequences (%)	Number of positions in Alignments	Parsimony-informative characters in alignments	Parsimony-uninformative variable characters in alignments
ETS region	358 to 449	46.7 to 50.01	--/455	--/54	--/15
ITS region	584 to 713	53.7 to 65.5	638/616	164/140	82/60
ITS1	186 to 294	52.7 to 68.7	245/228	83/75	42/ 28
S5.8	147 to 165	53.3 to 66.1	165/165	05/05	00/00
ITS2	156 to 279	53.6 to 71.6	228/223	76/60	36/32
<i>rpoC1</i> region	493 to 519	41 to 43	484/484	12/06	04/03
<i>rpoC1</i> exon 1	399 to 416	41.3 to 43.3	399/400	12/06	04/03
<i>rpoC1</i> intron (partial)	94 to 103	44.7 to 46.8	85/85	00/00	04/00
<i>trnT</i> -F region	1292 to 1669	28.2 to 36.7	1810/1760	117/93	186/70
<i>trnT</i> -L spacer	388 to 774	24.1 to 32.5	838/826	71/53	110/50
<i>trnL</i> spacer	537 to 615	36.7 to 44.1	641/606	22/13	36/10
<i>trnL</i> intron	455 to 530	35.3 to 42.8	556/521	22/13	32/08
<i>trnL</i> -F spacer	313 to 327	32.1 to 36.1	331/328	24/27	40/10

\* The values before the slash mark corresponds to the combined ITS-*rpoC1*-*trnT*-F matrix and those after the slash mark to the ETS-ITS-*rpoC1*-*trnT*-F matrix.

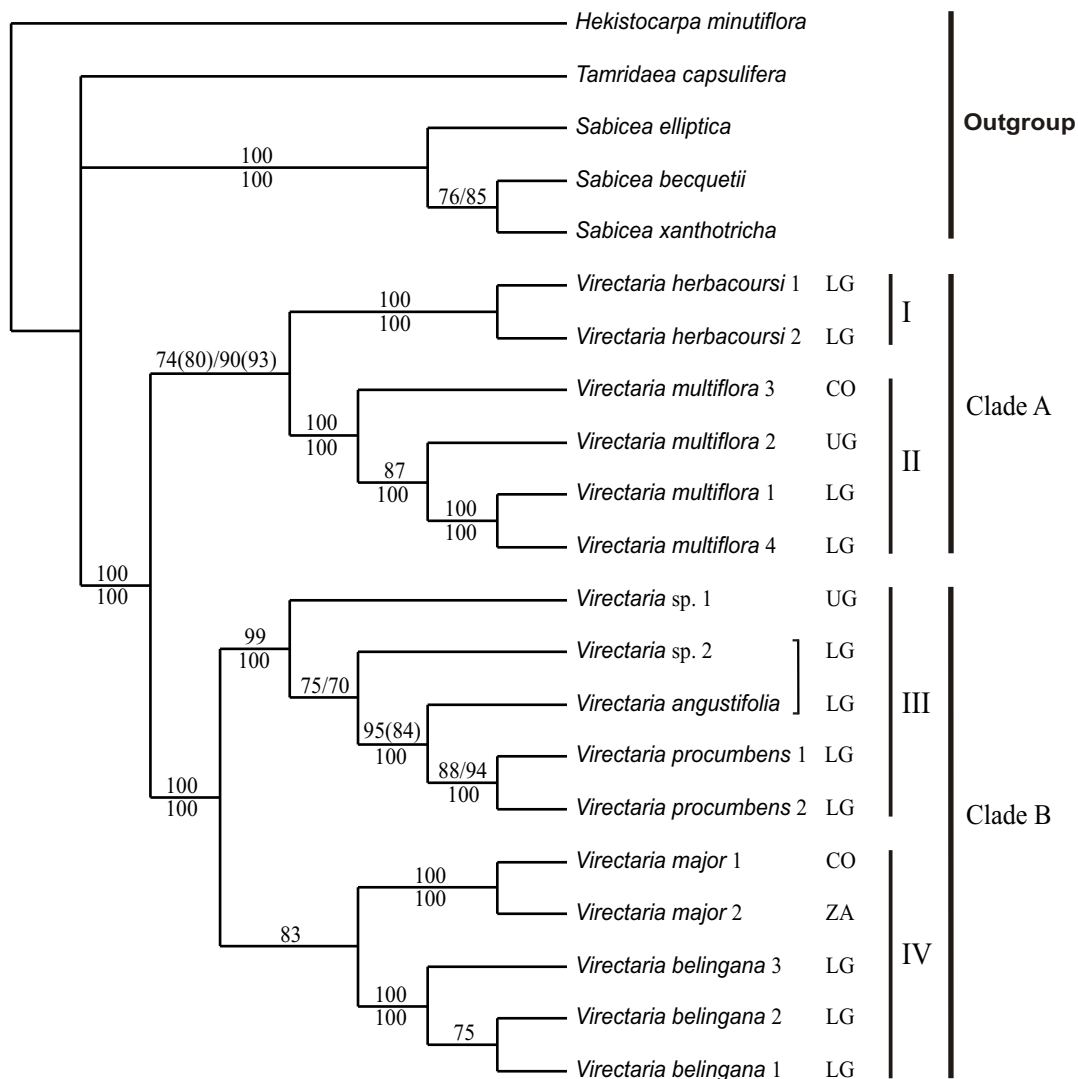
**Table 7.** Descriptions of combined parsimony analyses and resulting trees.

Data partitions and analyses	Outgroup No. /Ingroup taxa	No. informative characters	Length	CI	RI	No. MP trees
ITS + <i>rpoC1</i> + <i>trnT-F</i>	2 / 21	293	546	0.685	0.853	2
ITS + <i>rpoC1</i> + <i>trnT-F</i> + morphology	2 / 21	321	673	0.633	0.814	1
ETS + ITS + <i>rpoC1</i>	5 / 16	200	324	0.750	0.888	1
ETS + ITS + <i>rpoC1</i> + morphology	5 / 16	226	421	0.708	0.863	4
ITS + <i>rpoC1</i> + <i>trnT-F</i>	5 / 16	239	376	0.758	0.883	6
ITS + <i>rpoC1</i> + <i>trnT-F</i> + morphology	5 / 16	265	475	0.726	0.864	6
ETS + ITS + <i>rpoC1</i> + <i>trnT-F</i>	5 / 16	293	462	0.751	0.886	2
ETS + ITS + <i>rpoC1</i> + <i>trnT-F</i> + morphology	5 / 16	319	542	0.720	0.867	1

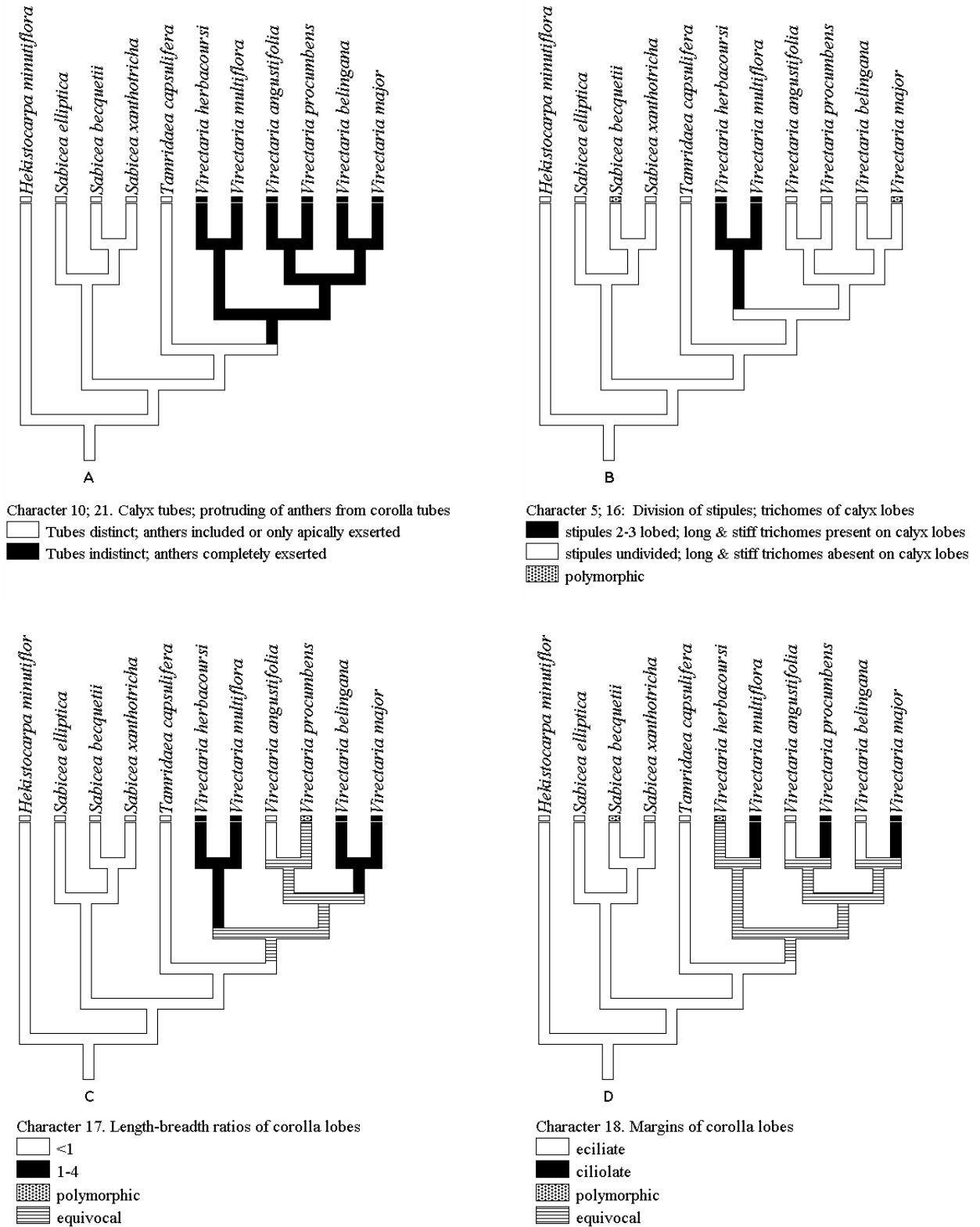




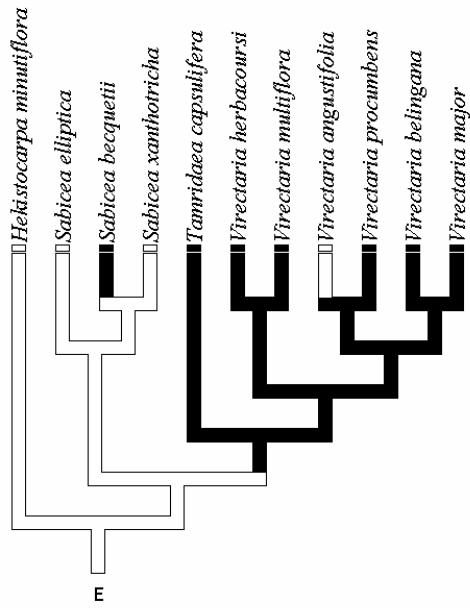
**Fig. 1.** Strict consensus tree based on the combined phylogenetic analysis of the ITS-*rpoC1-trnT-F* data. The numbers above the branches are bootstrap support values (> 50%), those below the branches are Bayesian posterior probabilities (> 95%), those after slash are the support from morphological data, and those in brackets are the supports due to the indels. The taxa shown in boldface are the sequenced individuals of monospecific *Hekistocarpa* and *Tamridaea*.



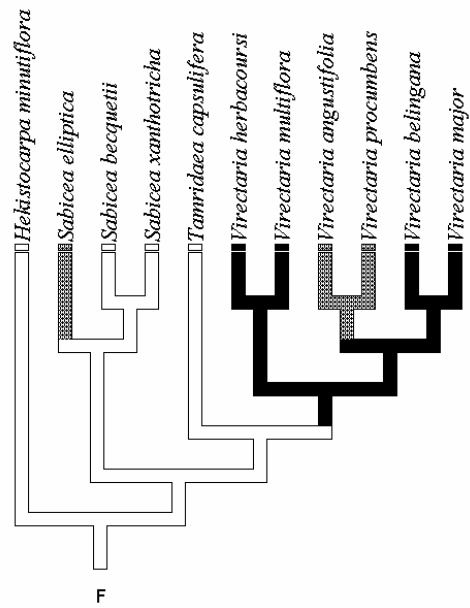
**Fig. 2.** Strict consensus tree based on the combined phylogenetic analysis of the ETS-ITS-*rpoC1-trnT-F* data. The numbers above the branches are bootstrap support values (> 50%), those below the branches are Bayesian posterior probabilities (> 95%), those after slash are the support from morphological data, and those in brackets are the supports due to the indels. *Virectaria sp. 2* and *V. angustifolia*, delimited with bracket, form a subclade when morphological data are included in the analyses. *V. herbacoursi* (= *V. herbacoursi* var. *petrophila*); *V. major 1* (= *V. major* subsp. *spathulata*); *V. major 2* (= *V. major* subsp. *major*). Clade A = *V. herbacoursi-V. multiflora* clade; Clade B = *Virectaria sp.-V. angustifolia-V. procumbens-V. major-V. belingana* clade; I = *V. multiflora* subclade; II = *Virectaria sp.-V. angustifolia-V. procumbens* subclade; III = the *V. major-V. belingana*



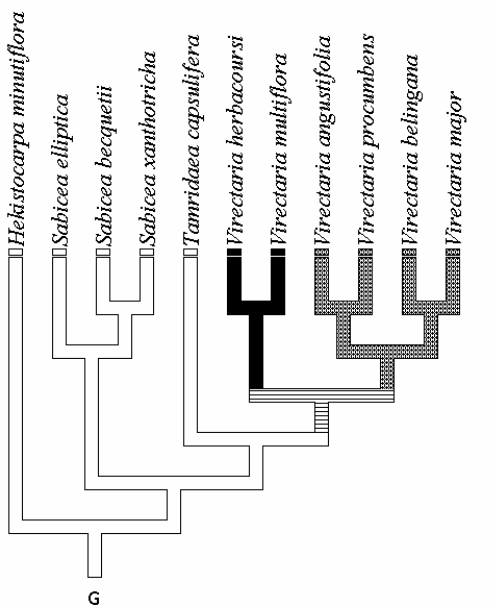
**Fig. 3A-D.** Distribution patterns of some synapomorphic characters on the strict consensus tree generated from the combined analysis of ETS-ITS-*rpoC1-trnT-F* data sets. 3A. Length of calyx tubes and position of anthers (synapomorphies for the genus *Virectaria*). 3B. Division of stipules and long stiff trichomes on calyx lobes (synapomorphies for *V. herbacoursi*, *V. multiflora*). 3C. Length-breadth ratios of corolla lobes (synapomorphy for *V. herbacoursi*, *V. multiflora*, *V. major*, *V. belingana*). 3D. Margins of corolla lobes (synapomorphy for *V. multiflora*, *V. major*, *V. procumbens*).



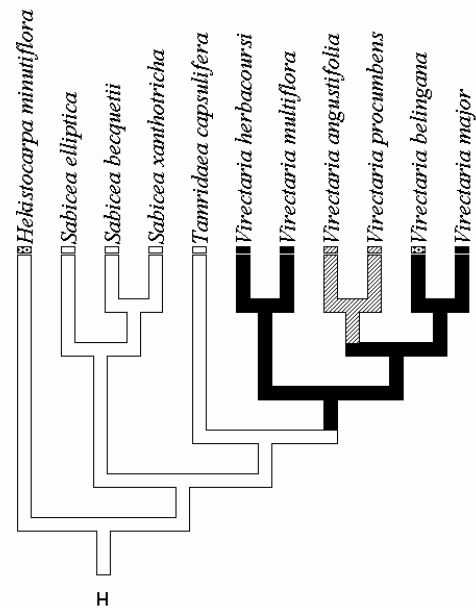
Character 19. External surface of corolla  
 ■ covered with indumentum  
 □ glabrous



Character 22. Protruding of style  
 ■ exserted part is longer than corolla lobes  
 ▨ exserted part is not longer than corolla lobes  
 □ usually included in corolla tube



Character 23. Division and shape of flower disc  
 ■ divided into two lanceolate to lingulate bilobed parts  
 ▨ undivided and cylindrical  
 □ undivided and campanulate  
 ▤ equivocal



Character 24. Fruit dehiscence and folding of valves  
 ■ dehiscent, margins of valve do not fold inwards  
 ▨ dehiscent, margins of valve fold inwards  
 □ indehiscent  
 ▤ polymorphic

**Fig. 3E-H.** External surface of corolla lobes (synapomorphy for *Virectaria* species except *V. angustifolia*, *Tamridaea*, *S. becquetii*). 3F. Protruding of styles (synapomorphy for *V. herbacoursi*, *V. multiflora*, *V. major*, *V. belingana*/ *V. angustifolia*, *V. procumbens*, *S. elliptica*). 3G. Division and shape of floral disc (synapomorphy for *V. herbacoursi*, *V. multiflora*/ *V. angustifolia*, *V. procumbens*, *V. major*, *V. belingana*). 3H. Fruit dehiscence and folding of valves (synapomorphy for *V. angustifolia*, *V. procumbens*/ *V. herbacoursi*, *V. multiflora*, *V. major*, *V. belingana*).

## TAXONOMIC REVISION OF NEOTROPICAL *SABICEA* (RUBIACEAE–IXOROIDEAE)

(Intended for submission to *Monographs in Systematic Botany* from the Missouri Botanical Garden)

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### ABSTRACT

The Neotropical *Sabicea* Aubl. (Rubiaceae, subfamily Ixoroideae, tribe Sabiceae) is comprised of 54 species of vines or lianas, scandent shrubs or herbs, occurring from southern Mexico to southeast Brazil. This study has recognized the previously described 37 species and the newly described six species (*Sabicea boyacana*, *S. chiapensis*, *S. cochabambensis*, *S. liedeeae*, *S. noelii*, and *S. tayloriae*). A complete taxonomic treatment is provided for these 43 species with distribution maps and 30 species-illustrations, of which 13 are new. Lectotypes are designated for *Sabicea amazonensis*, *S. brasiliensis*, *S. mexicana*, *S. mollissima*, *S. traillii*, *S. villosa* var. *adpressa*, and *S. villosa* var. *sellowii*.

**Key words:** Rubiaceae, Ixoroideae, Sabiceae, *Sabicea*, morphology, taxonomy, Neotropics, Belize, Bolivia, Brazil, Colombia, Costa Rica, Dominican Republic, Ecuador, French Guiana, Guatemala, Guyana, Honduras, Jamaica, Mexico, Nicaragua, Panama, Peru, Puerto Rico, Suriname, Trinidad & Tobago, Venezuela.

*Sabicea* Aubl. is the most species-rich genus of the tribe Sabiceae (subfamily Ixoroideae, Rubiaceae) comprised of ca. 145 species. It is distributed throughout the tropics with two main centers of diversity, mainland Africa (ca. 82 species) and the Neotropics (ca. 54 species), and three disjunct assemblages in Madagascar (6 species; Razafimandimbison and Miller, 1999), São Tomé and Príncipe (3 species; Joffroy, 2001), and Sri Lanka (1 species; Puff et al., 1998). In the Neotropics, the diversification of *Sabicea* appears to converge mainly to Takhtajan's (1986) Andean, Amazonian and Guiana Highlands floristic regions.

Aublet (1775) originally coined *Sabicea* for plants with twining habits, ovate to lanceolate and apically acute leaves, appressed indument, 4–5-lobed corolla, and 3–5-locular ovaries, comprising two species, *S. aspera* Aubl. and *S. cinerea* Aubl., from French Guiana. Aublet adopted the name “*Sabicea*” from the common name “sabi-sabi” used by the Galibis of Guiana (Wernham, 1914). Swartz (1788) maintained Aublet's *Sabicea* with 4-fid involucre, infundibuliform corolla, 5 stigmas, 5-locular ovaries, and many seeds. But Schreber (1789)

replaced Aublet's name by "*Schwenkfeldia*" and described the genus with lanceolate and apically acute calyx and corolla lobes, hypocrateriform corolla, 5-lobed calyces, 5 filaments, 5 stigmas, and 5 locular ovaries. Willdenow (1797) adopting the name "*Schwenkfeldia*", whereas Swartz (1797), following Schreber's name *Schwenkfeldia*, described the genus with 4-fided involucre, hypocrateriform corolla, 5 stigmas, 5 locular ovaries, and many seeds. Both of Willdenow's *Schwenkfeldia* and Swartz's *Schwenkfeldia* were apparently based on Schreber (1789). Ruíz & Pavon (1799), Sprengel (1825), Dietrich (1839) maintained *Schwenkfeldia* but others (e.g., Poiret, 1804; Humboldt et al., 1820; Schlechtendal, 1829; Candolle, 1830; Grisebach, 1864; Baillon, 1879) did not accept it because the replacement of Aublet's name was not in conformity to the rules of nomenclature (Wernham, 1914).

After Aublet (1775), 54 species of *Sabicea* were described by different authors until 1913 (see Wernham, 1914), the year when Wernham was influenced to complete the first monographic treatment of the genus after discovering four new species of *Sabicea* investigating only Talbot's collections (Rendle et al., 1913) of Nigerian Rubiaceae. In his monograph, Wernham (1914) described 61 new species and excluded 12 presumed species from the previously published *Sabicea* that raised the species number of the genus up to 105 including 39 Neotropical Species (Table 1). After Wernham 26 new species of *Sabicea* were published from South America and the Caribbean Islands by different authors.

Table 1. Neotropical *Sabicea* species treated by Wernham

Subgenus & Section	Species
<i>Sabicea</i> sect. <i>Laxae</i> ( <i>Sabicea</i> subgen. <i>Eusabicea</i> )	: <i>Sabicea asperula</i> , <i>S. boliviensis</i> , <i>S. colombiana</i> , <i>S. costaricensis</i> , <i>S. cuneata</i> , <i>S. erecta</i> , <i>S. hirta</i> , <i>S. humilis</i> , <i>S. mexicana</i> , <i>S. moorei</i> , <i>S. novo-</i> <i>granatensis</i> , <i>S. panamensis</i> , <i>S. paraensis</i> , <i>S. pearcei</i> , <i>S. setiloba</i> , <i>S. subinvolucrata</i> , <i>S. umbellata</i>
<i>Sabicea</i> sect. <i>Sessiles</i> ( <i>Sabicea</i> subgen. <i>Eusabicea</i> )	: <i>Sabicea aspera</i> , <i>S. amazonensis</i> , <i>S. brasiliensis</i> , <i>S. burchellii</i> , <i>S. camporum</i> , <i>S. cana</i> , <i>S. cinerea</i> , <i>S. flagenioides</i> , <i>S. guianensis</i> , <i>S. glabrescens</i> , <i>S. glomerata</i> , <i>S. grisea</i> , <i>S. hirsute</i> , <i>S. lindmaniana</i> , <i>S.</i> <i>mollissima</i> , <i>S. pannosa</i> , <i>S. parva</i> , <i>S. velutina</i>
<i>Sabicea</i> sect. <i>Capitatae</i> ( <i>Sabicea</i> subgen. <i>Eusabicea</i> )	: <i>Sabicea mattogrossensis</i> , <i>S. trailii</i> , <i>S. trianae</i>
<i>Sabicea</i> subgen. <i>Stipulariopsis</i>	: <i>Sabicea umbrosa</i> (= <i>Amphidasya umbrosa</i> Standl.)

There has been no disagreement among the Rubiaceae authors in accepting *Sabicea* as a genus, but there are controversies regarding its circumscription. When *Sabicea* was established as a genus of five species from South America and Madagascar, Palisot-

Beauvois (1807) published the African genus *Stipularia* P. Beauv. as a twining plant with 3–5 locular ovaries. Wernham (1914), following Hiern (1877), recognized *Stipularia* as a separate genus on the basis of deeply campanulate involucre. But Hepper (1958), disagreeing with Wernham (1914) and Hiern (1877), introduced the concept that the presence-absence of deeply campanulate involucre is a common character for some *Sabicea* and combined *Stipularia* with *Sabicea*, which was endorsed by Hepper and Keay (1963).

Hallé (1963) viewed *Sabicea* sensu Wernham as overly morphologically heterogeneous but accepted the generic status of *Stipularia*. He argued that a few African *Sabicea* species with non-twining habit, anisophylly, non-fleshy fruits and 2-locular ovaries should be separated out from *Sabicea* and he placed these *Sabicea* in his new genus *Pseudosabicea* N. Hallé. He defined the genus *Sabicea* with usually lianescent, slender and twining habit, large corollas, (4–)5-locular ovaries, fleshy juicy fruits with red carmine pulp, accrescent fleshy axis of ovary, and narrow, thin and sessile placentae.

Hallé (1963) broadly recognized Schumann's (1896) African genus *Ecpoma* K. Schum. containing the bilocular ovaries, though its generic status was rejected by Hepper and Keay (1963). He distinguished this genus with additional characters like shrubby habit, colorless pulp of small fruits, non-acrescent septa, and rounded or twisted to peltate placentae, and transferred five African *Sabicea* species (*S. bicarpellata* K. Schum., *S. cauliflora* Hiern, *S. gigantea* Wernham, *S. gigantostipula* K. Schum. and *S. hierniana* Wernham) to *Ecpoma*.

Hiern (1877) viewed that Hooker (1873)'s genera *Pentaloncha* Hook. f. and *Temnopteryx* Hook. f. might be reducible to the Sri Lankan monotypic genus *Schizostigma* Arn. (Meisner, 1838a, b). But Puff et al. (1998) rejected Hiern's (1877) view and merged *Schizostigma* with *Sabicea*, which is supported by the recent studies (Khan et al., 2007) showing that *Pentaloncha* and *Temnopteryx* belong to subfamily Rubioideae. Though most Rubiaceae systematists including Andersson (1996), Bremer and Thulin (1998), Dessein et al. (2001a, 2001b), and Robbrecht and Manen (2006) seem to accept *Sabicea* sensu Hallé (1963) and recognize *Stipularia*, *Ecpoma*, and *Pseudosabicea* as distinct genera, Khan et al. (2007) argued that *Sabicea*, *Stipularia*, *Ecpoma* and *Pseudosabicea* should be considered as *Sabicea* s.l. to include 170 species, with the corresponding addition of wider morphological variation to the genus description. Khan et al. (2007) also showed that Wernham's (1914) two subgenera (*Sabicea* subgen. *Stipulariopsis* Wernham and *Sabicea* subgen. *Eusabicea*) are unsupported by molecular data.

The conflicts regarding the delimitation of the genus *Sabicea* are ongoing, but there is no controversy among the recent Rubiaceae authors in characterizing Neotropical *Sabicea* (Andersson, 1999; Steyermark, 1974). Wernham (1914) characterized the genus *Sabicea* by its usually shrubby, climbing or prostrate to scrambling habits, isophyllous or anisophyllous leaves, entire to fimbriate or lacinate stipules, axillary inflorescences, (sub-)free bracts, valvate corolla lobes, and (2–)4–5-locular ovaries. In the Neotropics, most *Sabicea* species (47) are described from South America, especially from southeast, central western to

northwest, northern and northeast South America including the Amazonas-Río Negro basin. Only one species, *S. panamensis*, is described from Mesoamerica and two (*S. domingensis* and *S. hirta*) from the Caribbean Islands. The distribution of South American species *S. villosa* in Mesoamerica and Caribbean Islands and the distribution of Mesoamerican species *S. panamensis* in South America are also reported.

Wernham's (1914) work on *Sabicea* is a great contribution to plant systematics. However, his revision was based on a small amount of material and a narrowly typological species concept (Andersson, 1999). Some species described by Wernham (e.g., *Sabicea asperula*, *S. colombiana*, *S. costaricensis*, *S. glomerata*, *S. guianensis*, *S. lindmaniana*, *S. moorei*, *S. pannosa*, *S. paraensis*, and *S. setiloba* etc.) are indistinguishable when they are compared with their close allies. Wernham's treatment, based on typological species concept, is scarred by the avoidance in referring or unawareness in tracing the relationships between the closely allied species. Wernham's key characters such as climbing habit, compactness of inflorescence, pedicel lengths, shape, partitioning and arrangements of bracts, length of corolla tubes, and stipule shapes etc. are either not always invariant or not species specific. Usually it is practically impossible to distinguish a taxon of *Sabicea* in the Neotropics only on the basis of just one such character.

Steyermark (1967, 1974, 1981a), who described 9 new species and 4 new varieties of *Sabicea*, the largest number of new records after Wernham, has not depicted the relationships of his new species (e.g., *Sabicea sastrei*, *S. grandifolia*, and *S. venezuelensis*) and three varieties (varieties of *S. velutina*) with their close allies. Both Wernham and Steyermark were not aware of the important characters like colleter's position in calices and indumentum status inside the stipules, bracts and calyces. Considering the status of existing species circumscriptions of *Sabicea*, Andersson (1999) opined that the genus badly needs a modern revision, because after Wernham, no attempt was undertaken for the revision of Neotropical (as well as Paleotropical) *Sabicea*, though the Rubiaceae of some countries or regions were studied, either in the compilation of floristic works (e.g., Dwyer, 1980; Grisebach, 1864; Macbride, 1936; Standley, 1930, 1931, 1936a; Standley & Williams, 1975; Taylor 2001; Steyermark, 1967, 1972, 1974, 1988; Taylor & Steyermark, 2004; Urban, 1931; Vásquez, 1997) or in checklists or catalogues (Andersson, 1992; Balick et al., 2000; Boggan et al., 1997; Brako & Zarucchi, 1993; Foster, 1958; Molina, 1975; Moraes, 1990; Nelson, 1978).

The use of combination of two or more key characters rather than single characters (used by Wernham for many species) has been stressed by Steyermark (1967, 1974), Andersson (1999), and Taylor (2001, 2002) to key out the species of Neotropical *Sabicea*, presumably because most of the seemingly species-specific characters are overlapping at the extreme limits. The present revision has emphasized this concept in recognizing 37 species out of presently accepted 54 species of Neotropical *Sabicea* and circumscribing 6 new species. The recognition of 5 previously published South American species, known only from their types, is



maintained in this treatment as their key characters are distinct and no specimen close to their types was found.

## DISTRIBUTION

In the Neotropics *Sabicea* is distributed from central Mexico and the Antilles to Bolivia and southern Brazil (Taylor, 2002). This area covers the major parts of Takhtajan (1986)'s central Caribbean (Central America), Guiana Highlands, Amazonean, Brazilian, and Andean floristic regions (Fig. 1: 23-27). In Mesoamerica, *Sabicea* extends from southern Mexico to northeastern Nicaragua, northern Honduras, and Panama; however, it seems to center at the base of Madrean Highlands of Oaxaca to central Gulf-Caribbean slope of Belize and eastern Guatemala (Fig. 1A), Gulf-Caribbean slope of northeastern Nicaragua, Chiriquí-Darién Highlands and Pacific Arid lobe of Costa Rica and Panama (Fig. 1B). In the Caribbean Islands, the distribution of *Sabicea* seems limited to Trinidad, Puerto Rico, central to northeastern Dominican Republic, and Jamaica.

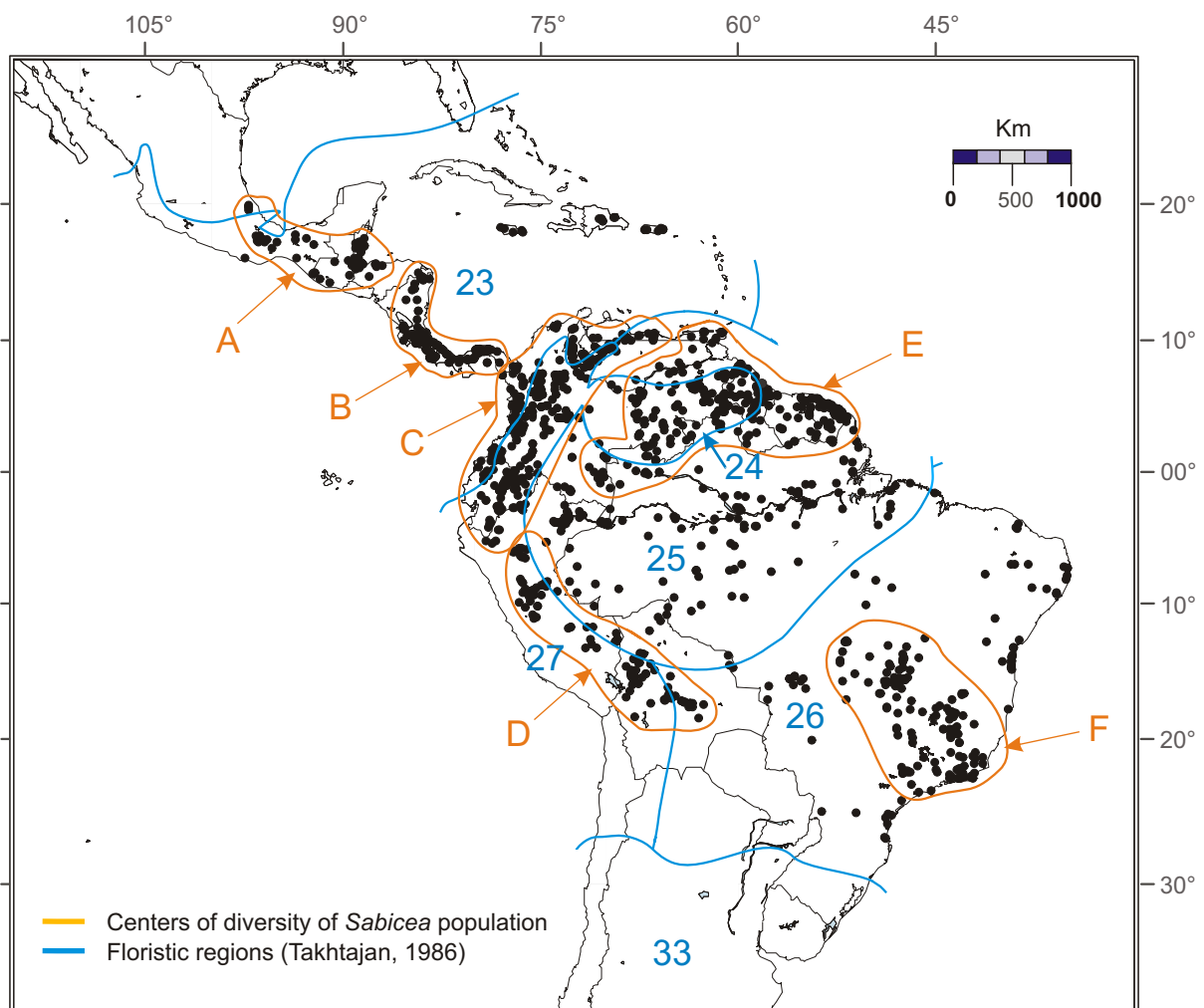


Figure 1. Map of the Neotropics (in part), showing the distribution of *Sabicea* population. 23 = Caribbean (Central America), 24 = Guyana Highlands, 25 = Amazonean, 26 = Brazilian, and 27 = Andean floristic regions of Takhtajan (1986). A = Madrean Highlands and central Gulf-Caribbean Slope; B = Gulf-Caribbean Slope and Pacific Arid Slope; C = Northern Andes; D = Central Andes; E = Amazonia North including Guiana Highlands; F = Central South America to southern Atlantic forest.

In South America, *Sabicea* is widespread in northwestern Colombia, northwestern and central to southern Venezuela, southwestern to northern and eastern Guyana, central and northeastern Suriname, French Guiana, northern, eastern and southern Ecuador, northeastern, central, and southeastern Peru, northwestern to central Bolivia, Amazonas-Río Negro basin, western, and southeastern to eastern Brazil with short and long disjunctions. However, its center of diversity seems to converge to northern Andes (Fig. 1C), northern to northeastern regions of Amazonia North including Guiana Highlands (Fig. 1E), central Andes of Bolivia and Peru (Fig. 1D), central region of Central South America to southern Atlantic forest of Brazil (Fig. 1F), and presumably southern region of Amazonia North to central and southern regions of Amazonia South. The presumably disjunct distribution of *Sabicea* in vast areas of South America (e.g., Amazonas-Río Negro basin) does not indicate that these areas are not rich in *Sabicea*; rather, it might correlate to the collections by different plant collectors. In relation to the distribution of *Sabicea* individuals in the Neotropics, the species richness is different. A total of 37 species are distributed in South America, 5 in Mesoamerica and 4 in the Caribbean Islands (Table. 2). In South America, the highest species richness comprising 17 species occurs in Brazil, followed by Colombia and Venezuela (15 species), Bolivia (12 species), Peru (11 species), Ecuador (7 species), and Guyana, Suriname, and French Guiana (5 species).

In South America, the highest species richness comprising 17 species occur in Brazil (Table 2), followed by Colombia and Venezuela (15 species), Bolivia (12 species), Peru (11 species), Ecuador (7 species), and Guyana, Suriname, and French Guiana (5 species). The highest endemism of *Sabicea* in the Neotropics comprising four species occurs in Brazil (*S. brasiliensis*, *S. burchellii*, *S. trailii*), Bolivia (*S. boliviensis*, *S. cuneata*, *S. erecta*, *S. noellii* sp. nov.) and Venezuela (*S. bariensis*, *S. liesneri*, *S. morillorum*, *S. tillettii*). Three endemic species each are found in Colombia (*S. boyacana* sp. nov., *S. chocoana*, *S. pearcei*, and *S. trianae*), Mexico (*S. chiapensis* sp. nov., *S. liedeeae*, and *S. mexicana*), Peru (*S. klugii* and *S. subinvoluta*) followed by Jamaica and Suriname with one endemic species each. *Sabicea cochabambensis* sp. nov. is found only in Bolivia and Peru, *S. grisea* in Brazil and Paraguay (Wernham, 1914), *S. humilis* in Brazil and Bolivia, *S. novo-granatensis* in Colombia and Venezuela, *S. parva* in Brazil and Venezuela, and *S. velutina* in Venezuela and Roraima (Brazil). *Sabicea cinerea* centered in French Guiana extends to Suriname and Venezuela. *Sabicea mollissima* is found in Suriname, French Guiana and northeastern to central Amazonas and northern Pará of Brazil. Rests of the species are found as widespread in South America (e.g., *Sabicea camporum*, *S. cana*, *S. aspera*), Mesoamerica and South America (e.g., *S. panamensis*) or Mesoamerica, South America and Caribbean Islands (e.g., *S. villosa*).

Table. 2. Species of *Sabicea* recognized here for South America, Mesoamerica and the Caribbean Islands. New species in bold.

	Country	Species	Total
Mesoamerica	Mexico	<b><i>Sabicea chiapensis</i></b> , <b><i>S. liedea</i></b> , <i>S. mexicana</i> , and <i>S. villosa</i>	4
	Guatemala	<i>Sabicea panamensis</i> and <i>S. villosa</i> .	2
	Belize	<i>Sabicea panamensis</i> and <i>S. villosa</i>	2
	Honduras	<i>Sabicea villosa</i>	1
	Nicaragua	<i>Sabicea panamensis</i> and <i>S. villosa</i> .	2
	Costa Rica	<i>Sabicea panamensis</i> and <i>S. villosa</i> .	2
	Panama	<i>Sabicea panamensis</i> and <i>S. villosa</i> .	2
Caribbean Islands	Jamaica	<i>Sabicea hirta</i>	1
	Dominican Republic	<i>Sabicea villosa</i>	1
	Puerto Rico	<i>Sabicea villosa</i>	1
	Trinidad & Tobago	<i>Sabicea aspera</i> , <i>S. oblongifolia</i> , and <i>S. villosa</i> .	3
South America	Colombia	<i>Sabicea amazonensis</i> , <b><i>S. boyacana</i></b> , <i>S. calophylla</i> , <i>S. camporum</i> , <i>S. cana</i> , <i>S. chocoana</i> , <i>S. cuneata</i> var. <i>setiloba</i> , <i>S. mattogrossensis</i> , <i>S. novo-granatensis</i> , <i>S. panamensis</i> , <i>S. pearcei</i> , <i>S. thyrsoiflora</i> , <i>S. trianae</i> , <i>S. velutina</i> , and <i>S. villosa</i> .	15
	Venezuela	<i>Sabicea amazonensis</i> , <i>S. aspera</i> , <i>S. bariensis</i> , <i>S. calophylla</i> , <i>S. camporum</i> , <i>S. cinerea</i> , <i>S. liesneri</i> , <i>S. morillorum</i> , <i>S. novo-granatensis</i> , <i>S. oblongifolia</i> , <i>S. panamensis</i> , <i>S. parva</i> , <i>S. tillettii</i> , <i>S. velutina</i> , and <i>S. villosa</i> .	15
	Guyana	<i>Sabicea aspera</i> , <i>S. oblongifolia</i> , <i>S. parva</i> , <i>S. velutina</i> , and <i>S. villosa</i> .	5
	Suriname	<i>Sabicea cinerea</i> , <i>S. mollissima</i> , <i>S. oblongifolia</i> , <i>S. surinamensis</i> , and <i>S. villosa</i> .	5
	French Guiana	<i>Sabicea aspera</i> , <i>S. cinerea</i> , <i>S. mollissima</i> , <i>S. oblongifolia</i> , and <i>S. villosa</i> .	5
	Ecuador	<i>Sabicea calophylla</i> , <i>S. camporum</i> , <i>S. cana</i> , <i>S. panamensis</i> , <i>S. pyramidalis</i> , <i>S. thyrsoiflora</i> , and <i>S. villosa</i> .	7
	Peru	<i>Sabicea amazonensis</i> , <i>S. boliviensis</i> , <i>S. cana</i> , <i>S. cochabambensis</i> , <i>S. klugii</i> , <i>S. mattogrossensis</i> , <i>S. panamensis</i> , <b><i>S. tayloriae</i></b> , <i>S. subinvoluta</i> , <i>S. umbellata</i> , and <i>S. villosa</i> .	11
	Bolivia	<i>Sabicea boliviensis</i> , <i>S. cana</i> , <b><i>S. cochabambensis</i></b> , <i>S. cuneata</i> , <i>S. erecta</i> , <i>S. humilis</i> , <i>S. mattogrossensis</i> , <b><i>S. noelii</i></b> , <i>S. novo-granatensis</i> , <b><i>S. tayloriae</i></b> , <i>S. umbellata</i> , and <i>S. villosa</i> .	12
	Brazil	<i>Sabicea amazonensis</i> , <i>S. aspera</i> , <i>S. brasiliensis</i> , <i>S. burchellii</i> , <i>S. calophylla</i> , <i>S. cinerea</i> , <i>S. grisea</i> , <i>S. humilis</i> , <i>S. mattogrossensis</i> , <i>S. mollissima</i> , <i>S. oblongifolia</i> , <i>S. panamensis</i> , <i>S. parva</i> , <b><i>S. tayloriae</i></b> , <i>S. traillii</i> , <i>S. velutina</i> , and <i>S. villosa</i> .	17

Most of the Neotropical *Sabicea* (26 species) are found in tropical humid, cloud or rain, primary or secondary, disturbed or virgin, and lowlands or montane forests or forest margins, usually on scrubs or thickets. They are generally found in the grasslands or Savanna (15 species). They are common also besides the roads and highways (13 species), on the banks

of rivers (12 species) and streams (9 species) or in swamps (7 species) on open pastures, scrubs or thickets. Occasionally they grow at the cultivated or abandoned agricultural fields. In the Neotropics, *Sabicea* grows from sea level to high mountains. However, 28 *Sabicea* species are found at 100–1000 m. 8 species of *Sabicea* are recorded from 0–100 m and six species from 1000–3200 m elevation. Only few species that are found at sea level (e.g., *Sabicea aspera*, *S. brasiliensis*, *S. cinerea*, *S. humilis*, *S. panamensis*, *S. velutina*, and *S. villosa*) are also found at higher altitudes. The species which can grow at very high altitudes include *Sabicea aspera*, *S. brasiliensis*, *S. cana*, *S. cochabambensis*, *S. camporum*, *S. cuneata*, *S. hirta*, *S. klugii*, *S. humilis*, *S. liedeeae*, *S. liesneri*, *S. novo-granatensis*, *S. panamensis*, *S. tayloriae*, *S. subinvolucrata*, *S. umbellata*, *S. velutina*, and *S. villosa*.

## MORPHOLOGY

### HABIT

The habit character has been used to distinguish the genera of Sabiceeae and many species of *Sabicea*. Aublet (1775) described *Sabicea* with twining habit. Wernham (1914) mentioned the habit of both African and American *Sabicea* as mostly shrubs and scrambling, unprovided with any climbing device. In the recent studies, Neotropical *Sabicea* have been described as climbing plants with often-subherbaceous stems (Steyermark, 1974), climbing shrubs (Dwyer, 1980), vines, shrubs with clambering branches or erect shrubs (Burger & Taylor, 1993), vines or shrubs with lianescent branches and usually scandent growth habit (Andersson, 1999), and twining (Taylor, 2002). None of these specific characterizations, rather their combination, seems applicable for distinguishing the habit of *Sabicea*. It seems that this genus is usually not restrained to only one habitat. About 25 species of this genus in the Neotropics grow on scrubs or thickets in upland tropical humid forests. The stems and branches of *Sabicea* are usually “scrambling, unprovided with any climbing device”, recognized as the most primitive type of the climbers (Wernham, 1914), that are usually found in forests and along roadsides or riverbanks. Many *Sabicea*, which grow in grasslands, riverbanks, swamps or open forests, are scandent or clambering. Though Hallé (1963) viewed *Sabicea* as non-twining, they are usually twiners (Taylor, 2002) in the Neotropics (e.g., *Sabicea aspera*, *S. cana*, *S. camporum*, *S. calophylla*, *S. cinerea*, *S. choacoana*, *S. liedeeae*, *S. mattogrossensis*, *S. novo-granatensis*, *S. panamensis*, *S. umbellata*, and *S. villosa*). The species with twining habit usually grow in forests, forest edges or remnant patches of forests at or above riverbanks, hillsides or non-flooded lowlands, young secondary vegetation, swamps, roadsides, and savannahs. Sometimes (e.g., *Sabicea amazonensis*, *S. aspera*, *S. boyacana*, *S. calophylla*, *S. humilis*, *S. panamensis*, and *S. villosa*) they are creeping and grow at riversides, roadside to highland forests, open coastal areas, and savannahs. Few

species (e.g., *Sabicea hirta*, *S. amazonensis*, *S. cana*, *S. cinerea*, *S. velutina*, *S. brasiliensis*, *S. panamensis*, *S. parva*, and *S. villosa*) possess trailing habit, though occasionally, and grows at riverbanks, savanna, open uplands, roadsides or in primary forests. Straggling growth habit is rare (e.g., *Sabicea hirta*, *S. velutina*, and *S. villosa*) appeared at riverbanks. Usually *Sabicea brasiliensis* and *S. humilis* (including *S. moorei*, here synonymized with *S. humilis*), and occasionally few other species (e.g., *S. erecta*, *S. panamensis*, and *S. camporum*) growing at hillsides or savannahs possess the erect growth habit. Wernham (1914) recognized these species as the representatives of the erect forms in open situations, the derivative Campos or savannahs. The plants of *Sabicea* are mostly easily visible as "they are usually large plants that cover a lot of area and grow on top of other plants. They apparently are rather seasonal, so in some species at least the stems grow abundantly at some times, like the beginning of the wet season, but then die back" (C. M. Taylor, pers. comm.).

The roots or rootstocks of *Sabicea* are usually woody or they are at least slightly woody at the base. Some species (e.g., *Sabicea aspera*, *S. brasiliensis*, *S. calophylla*, *S. camporum*, *S. humilis*, and *S. subinvolucrata*) possess suffruticose stem. Many species (e.g., *Sabicea aspera*, *S. brasiliensis*, *S. camporum*, *S. humilis*, *S. noelii*, *S. velutina*, and *S. villosa*) appear herbaceous, and may or may not show woody growths. The stems of most of the species do not exceed the length of 10 m, while a few species (e.g., *Sabicea hirta* and *S. setiloba*) can reach up to 15 m. In some species (e.g., *Sabicea aspera*, *S. brasiliensis*, *S. noelii*, *S. parva*, *S. velutina*, and *S. villosa*), stems can be less than 1 m. Most of Neotropical *Sabicea* are richly branched but not self-supporting. Apparently the habit of Neotropical *Sabicea* does not differ from that of African *Sabicea* excluding two trees (e.g., *Sabicea arborea* K. Schum. and *S. gigantea* Wernham; Wernham, 1914). The associated genera of *Sabicea* s.l. (Tribe Sabiceae) are either herbaceous (*Hekistocarpa* Hook. f. and *Virectaria* Bremek.) or shrubby (*Tamridaea* Thulin & B. Bremer).

## INDUMENTUM

Indumentum and trichome types (Hewson, 1988) are the most striking and useful characters in classifying the species of *Sabicea*. The previous authors prove the appreciable value of indumentum in species delimitation within *Sabicea*. Wernham's (1914) first choice of characters for classification of the species was indumentum character. All species of Neotropical *Sabicea* are essentially covered with indumentum, consistent with Wernham (1914). Terminal flowering branchlets, at least apically, upper and lower surface of leaves, outer surface of stipules, petioles, peduncles, pedicels, bracts, and calyces, base of inner surface of stipules, bracts and bracteoles, and inner and outer surface of corolla tubes are always covered with indumentum. Apices or upper part of inner surface of stipules, bracts, bracteoles, and calyx lobes and tubes, pedicels, outer surface of ovary, and basal or lower

part of inner and outer surface of corolla tubes may be glabrous or covered with indumentum. The trichomes on the terminal flowering branchlets, outer surface of stipules, upper and lower surface of leaves, petioles, peduncles, pedicels, and outer surface of bracts, bracteoles, ovary, calyces, corolla tubes, and fruits usually vary within four major groups (Fig. 2), i) long, multicellular, erect to erecto-patent, usually straight to slightly curved or occasionally shallowly flexuous (pilosulous, hirtellous, and villosulous indumenta), ii) long, multicellular, (sub-)appressed, usually straight, occasionally slightly curved or shallowly flexuous (strigulose and sericeous indumenta), iii) short, unicellular to few (usually 3) celled, (sub-)appressed to erecto-patent, straight to flexuous (puberulous and pubescent indumenta), and iv) long, multicellular, (sub-)appressed to patent, curled to tortuous, and usually strongly intertwined (arachnose, floccose, and lanuginose indumenta). Trichomes at the base of inner surface of stipules, bracts, and bracteoles always belong to group-ii (sericeous). Trichomes when present at the upper part of inner surface of stipules, bracts, bracteoles, usually belong to group ii, sometimes iii. Trichomes at orifice and inner surface of corolla tubes are always constricted (Fig. 2R).

Indumentum character of branchlets and its usefulness are hardly known from the previous studies, though sometimes this character is species-specific. In most of Neotropical *Sabicea*, indumentum of branchlets is not confined to only one type (e.g., hirtellous); rather, it is of two to few types (e.g., hirtellous and puberulous or pilosulous, strigulose and arachnoid; Hewson 1988). The trichomes of Neotropical *Sabicea* are 0.05–3 × 0.02–0.1 mm, 2-many celled with usually 0.004–0.01 mm thick wall, whitish to dull brownish-yellow or occasionally rusty brown (e.g., *Sabicea oblongifolia*). In many species, the flowering branchlets are covered with curled to tortuous and intertwined, and additionally, whether barely or plenteously, with either straight and erect trichomes (e.g., *Sabicea amazonensis*, *S. boliviensis*, *S. camporum*, *S. erecta*, *S. liedae*) or straight and appressed trichomes (e.g., *S. bariensis*, *S. boyacana*, *S. calophylla*, and *S. tillettii*) or straight, erect, and appressed trichomes (e.g., *S. cuneata*, *S. klugii*, and *S. subinvolucrata*). In four species (*Sabicea brasiliensis*, *S. cana*, *S. morillorum*, and *S. trianae*), the indumentum of flowering branchlets is comprised of curled to tortuous and intertwined trichomes only. The flowering branchlets of many species are usually devoid of curled, tortuous and intertwined trichomes but they are remarkable for their ambient straight and predominantly erect trichomes (e.g., *Sabicea chocoana*, *S. cochabambensis*, *S. hirta*, *S. humilis*, *S. novo-granatensis*, *S. pearcei*, *S. surinamensis*, and *S. traillii*) or straight and preponderantly appressed trichomes (e.g., *S. aspera*, *S. panamensis*, *S. pyramidalis*, and *S. thyrsiflora*). The indumentum characters of flowering branchlets usually appear as common for two to few species. For example, a pilosulous and isolatedly puberulous indumentum is commonly present in *Sabicea cochabambensis*, *S. pearcei*, *S. surinamensis*, and *S. traillii*, strigulose to hirtellous or pilosulous, and puberulous indumentum in *S. panamensis*, *S. pyramidalis* and *S. thyrsiflora*. The arachnose or lanate to lanuginose indumentum of *Sabicea brasiliensis*, *S. cana*, *S. morillorum*, and *S. trianae* appear synapomorphic for these species.

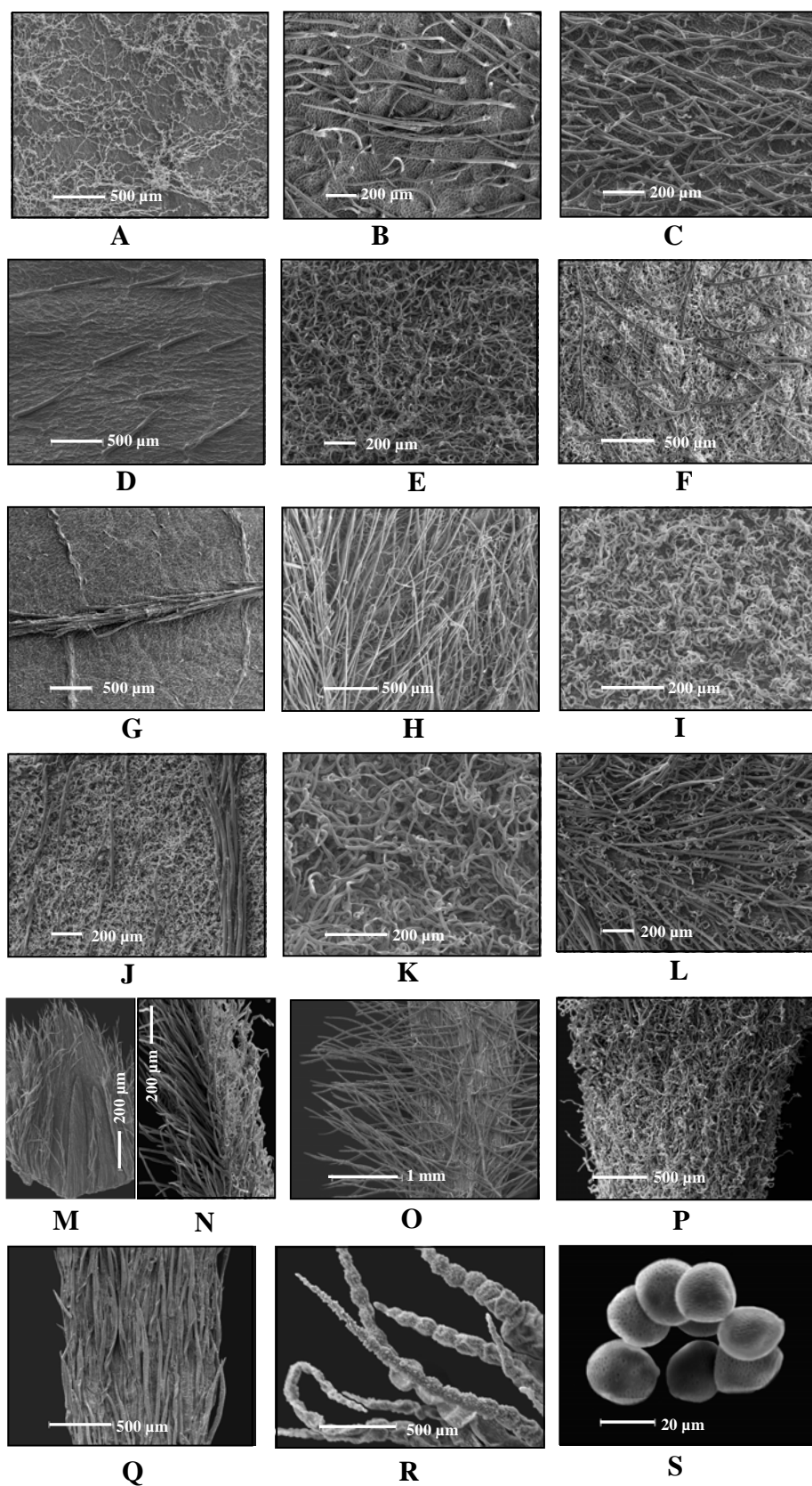


Figure 2. A–S Indumentum types of Neotropical *Sabicea*. —A–E. Upper surface of leaves. —F–K. Lower surface of leaves. —L, Outer surface of stipules. —M. Inner surface of stipules with colleters. —N. Inner and outer surface of calyx lobes. —O–Q. External surface of corolla tubes. —R. Internal trichomes of corolla tubes. —S. Pollens.

There is no previous mention about the variation and usefulness of indumentum characters of stipules, though these have been included in the description of some species by Steyermark (1967) and Andersson (1999). This study depicts that indumentum of stipules, especially of upper inner surface, are sometimes constant and useful for specific delimitation. The base of inner surface of stipules is always densely sericeous (Fig. 11D, 34E). The rest of the surface is glabrous in most of the species, sericeous to strigulose or puberulous (Fig. 5A, 35E) in few species (e.g., *Sabicea amazonensis*, *S. boliviensis*, *S. chocoana*, *S. cuneata*, *S. liesneri*, *S. novo-granatensis*, and *S. oblongifolia*), and sericeous to pilosulous in *S. hirta*. The trichomes of inner surface of stipules are 0.05–3 mm long. Indumentum at inner surface of stipules (excluding the base) may be limited to the apex or upper part only, whether constantly (e.g., *Sabicea cana* and *S. tayloriae*) or inconstantly (e.g., *S. chiapensis*, *S. cinerea*, and *S. klugii*). The outer surface of stipules is usually covered with indumentum all over. In some species (e.g., *Sabicea aspera*, *S. boyacana*, *S. burchellii*, *S. cuneata*, *S. mattogrossensis*, *S. mollissima*, *S. parva*, *S. surinamensis*, and *S. umbellata*), the apex or upper part of outer surface is always glabrous, in few species only occasionally glabrous (e.g., *S. bariensis*, *S. cochabambensis*, *S. hirta*, *S. noelii*, *S. thyrsiflora*, and *S. traillii*). In most of the species, the indumentum of outer surface of stipules is comprised of straight and 0.05–2.3 mm long trichomes that are usually appressed and erect to erecto-patent (e.g., *S. camporum*, *S. chiapensis*, *S. hirta*, *S. liesneri*, *S. mattogrossensis*, *S. novo-granatensis*, *S. panamensis*, *S. pyramidalis*, *S. surinamensis*, *S. thyrsiflora*, *S. traillii*, and *S. villosa*), only appressed (e.g., *S. aspera*, *S. boyacana*, *S. calophylla*, *S. humilis*, *S. noelii*, *S. oblongifolia*, and *S. umbellata*) or only erect to erecto-patent (e.g., *S. amazonensis*, *S. chocoana*, *S. cochabambensis*, *S. erecta*, *S. mexicana*, and *S. pearcei*). In few species (e.g., *Sabicea bariensis*, *S. cuneata*, *S. klugii*, *S. liedea*, *S. mollissima*, *S. morillorum*, and *S. velutina*) indumentum includes straight and appressed to erect and curled to tortuous trichomes (Fig. 2L). In four species (e.g., *Sabicea brasiliensis*, *S. cana*, *S. cinerea*, and *S. tillettii*) the indumentum of outer surface of stipules is composed of curled to tortuous trichomes only.

The indumentum character of leaves was considered by Wernham (1914) as remarkably constant for each species. This study shows that the leaf indumentum is constant for two or more species rather than each species. The indumentum of upper leaf surface is usually solely consisting of one to two types of straight and appressed to erect trichomes (Fig. 2B-D, 5B, 11B, 22B, 32BE). Nevertheless, the indumentum of seven species (e.g., *Sabicea boliviensis*, *S. brasiliensis*, *S. cuneata*, *S. grisea*, *S. klugii*, *S. liedea*, and *S. velutina*) contain curled to tortuous trichomes, whether meagerly or plenteously, in addition to the straight and appressed or erect trichomes (Fig. 2E, 28B). In four species (e.g., *S. cana*, *S. cinerea*, *S. tillettii*, and *S. trianae*) the indumentum of upper leaf surface is exclusively comprised of curled to tortuous trichomes (Fig. 2A, 13B, 21B). In contrast to upper leaf surfaces, the indumentum of lower leaf surfaces of about 24 species is comprised of curled to tortuous trichomes, whether sparsely or densely, loosely or compactly, and usually in addition to



straight and appressed to erect trichomes (Fig. 2F, J, K). In rest of the species, the indumentum of lower leaf surfaces is composed of usually straight and either erect to erecto-patent (e.g., *Sabicea chocoana*, *S. cochabambensis*, *S. hirta*, *S. liesneri*, *S. noelii*, *S. novo-granatensis*, *S. pearcei*, and *S. surinamensis*; Fig. 2H) or (sub-)appressed (e.g., *S. aspera*, *S. bariensis*, *S. mattogrossensis*, *S. mexicana*, *S. panamensis*, *S. pyramidalis*, *S. thyrsoflora*, *S. trailii*, and *S. umbellata*; Fig. 2G) or both erect to erecto-patent and (sub-)appressed trichomes (e.g., *S. parva*, *S. villosa*).

The indumentum of calyces shows a notable range of variation. In few instances indumentum character of calyx is constant for a single or a group of species. Wernham (1914) and Steyermark (1974) emphasized the indumentum character of outer surface of calyces in identifying few species. The variation in indumentum character at inner surface of calyces has not been mentioned previously. The calyces of most of the species of *Sabicea* are isolatedly to densely covered with indumentum inside, whether only apically or almost all over the lobes and tubes. The indumentum is usually composed of shorter trichomes (0.03–1.6 mm) than those of outer surface (0.03–3 mm). In some species (e.g., *Sabicea cana*, *S. chiapensis*, *S. chocoana*, *S. cinerea*, *S. klugii*, *S. noelii*, *S. tayloriae*, *S. tillettii*, and *S. velutina*) merely the apices or upper inner surfaces of lobes are covered with indumentum (Fig. 2N). The indumentum may extend all over the lobes or up to the opening of tubes (e.g., *Sabicea amazonensis*, *S. grisea*, *S. humilis*, *S. liesneri*, and *S. novo-granatensis*; Fig. 5J, 21J) or up to the middle of tubes (e.g., *S. mollissima*, *S. surinamensis*, and *S. trailii*; Fig. 32G, 42I). In *Sabicea boyacana*, the indumentum is limited to the base of tubes. In few species (e.g., *Sabicea brasiliensis*, *S. burchellii*, *S. cuneata*, *S. erecta*, *S. hirta*, *S. morillorum*, and *S. parva*) the inner surface is usually glabrous but sometimes or occasionally the apices are covered with indumentum. The indumentum of inner surface of calyces is usually composed of short, straight and appressed trichomes and additionally merely occasionally of curled trichomes (e.g., *Sabicea brasiliensis*, *S. cinerea*, *S. cana*, and *S. tillettii*). In most of the species, the indumentum of outer surface of calyces is comprised of only straight and appressed or erect trichomes. The indumentum of some species (e.g., *Sabicea bariensis*, *S. boliviensis*, *S. cinerea*, *S. cuneata*, *S. grisea*, *S. klugii*, *S. mollissima*, *S. tillettii*, and *S. velutina*) is consisting of straight and appressed to erect, and curled to tortuous trichomes (Fig. 2N, right side). In *Sabicea brasiliensis*, *S. cana*, *S. morillorum*, *S. tayloriae*, *S. trianae*, the indumentum of outer calyx surface is exclusively comprised of curled to tortuous trichomes.

The type (constricted, ciliate to erect, straight to slightly flexuous) and color (brownish) of trichomes at orifice and inside the tubes of corolla are almost constant for all species (Fig. 2R). The extension of indumentum (1.1–9 mm along the orifice and tube), lengths of trichomes (0.02–0.06 mm), and the number of constrictions (3–36 per trichome) are variable. These variations are mostly convergent and practically almost useless when the tube-length of corolla and the indumentum characters of outer surfaces of corolla tubes are considered. The previous emphasis (e.g., Wernham, 1914) on indumentum characters of corolla tubes

includes the external indumentum. The indumentum of outer surface of corolla tubes is entirely incorporated with straight trichomes in all species except few where the indumentum contains flexuose to tortuous trichomes, with (e.g., *Sabicea cana*, *S. mollissima*, *S. tayloriae*, and *S. velutina*) or without (e.g., *S. brasiliensis*; Fig. 2P) straight trichomes. The erectness of these trichomes is stable for a number of species. For example, in some species (e.g., *Sabicea amazonensis*, *S. aspera*, *S. parva*, *S. cinerea*, *S. grisea*, *S. hirta*, *S. humilis*, *S. novogranatensis*, *S. oblongifolia*, and *S. traillii*), these trichomes are constantly erect to erectopatent (Fig. 2O). In some other species (e.g., *Sabicea bariensis*, *S. calophylla*, *S. camporum*, *S. cuneata*, *S. mexicana*, *S. panamensis*, *S. thyrsoflora*, *S. tillettii*, *S. trianae*, *S. umbellata*, and *S. villosa*), these trichomes are (sub-)appressed (Fig. 2Q) and in few species (e.g., *S. burchellii*, *S. chocoana*, *S. erecta*, *S. liedeeae*, and *S. morillorum*) usually erect and sometimes or occasionally appressed. The ranges of variation in size and number of cells of trichomes of outer surface of corolla tubes fall within  $0.4\text{--}4 \times 0.02\text{--}0.05$  mm and 3–12 respectively. The application of indumentum characters of petioles, peduncles and inflorescence axes, bracts or bracteoles, and of external surface of hypanthium or ovary in taxonomic delimitation is marginally known from the previous studies (Steyermark, 1967, 1974; Wernham, 1914). In this study, a petty variation is found in the indumentum characters of petioles, peduncles and inflorescence axes, styles, and external surface or hypanthium or ovary and fruits in relation to the indumentum of terminal branchlets, stipules or calyces. The indumentum status on styles and external surface ovary and fruits appear to be useful. The style of almost all species is glabrous except in *Sabicea cana*, where it is usually lanuginose to villosulous at least at upper part. In *S. brasiliensis*, the isolatedly distributed trichomes on upper part of styles are found in few specimens only. The free part of filaments is always glabrous. Arachnoid indumentum is absent on the external surfaces of ovary and fruits of most of the species, but present on those of some species (e.g., *Sabicea brasiliensis*, *S. cana*, *S. cinerea*, *S. grisea*, *S. liedeeae*, *S. morillorum*, *S. tayloriae*, *S. subinvoluta*, *S. trianae*, and *S. velutina*), whether isolatedly or densely. The external surfaces of most of the ripened fruits seem glabrescent, even so, the traces of trichome types are usually visible.

Cilia as a source of taxonomically useful characters for the genus were ignored by the previous authors except Steyermark (1967, 1974). The cilia are usually persistent at the margins of stipules, leaves, bracts and calyx lobes of most of the species examined except few exceptions. Sometimes the cilia of stipules (e.g., *Sabicea amazonensis*, *S. aspera*, *S. cana*, *S. camporum*, *S. grisea*, *S. oblongifolia*, *S. panamensis*, and *S. umbellata*), leaves (e.g., *S. cana*, *S. grisea*, and *S. umbellata*), bracts (e.g., *S. amazonensis*, *S. cuneata*, and *S. umbellata*) or calyx lobes (e.g., *S. aspera*, *S. camporum*, *S. panamensis*, *S. umbellata*, and *S. thyrsoflora*) have disappeared due to their deciduousness. However, presence-absence, straightness, and erectness of cilia are constant for a number of species or single species. The stipules, leaves, and bracts of *Sabicea cinerea*, and *S. tillettii* and the calyx lobes of *S. brasiliensis*, *S. calophylla*, and *S. cana* are eciliate. In most of the species, the cilia of stipules,

leaves, bracts, and calyx lobes are usually erecto-patent (Fig. 5D, F, J, 18G, 22G, 35D-H, K). In some species the cilia are (sub-)appressed at stipules, leaves, bracts, and calyx lobes (e.g., *Sabicea bariensis*, *S. burchellii*, *S. panamensis*, and *S. thyrsoiflora*), or to any of these parts (e.g., stipules and leaves of *S. camporum*, *S. mexicana*; calyx lobes of *S. calophylla*, *S. tillettii*, and *S. oblongifolia*). The lengths of cilia at the margins of stipules, leaves, bracts and calyx lobes vary within (0.05–) 0.1–3.5 mm and sometimes the ranges of this variation are found species specific.

The colleters of *Sabicea* are hardly known from previous studies (e.g., Steyermark, 1974), though this structure is commonly present along the adaxial base of stipules, at the margins or adaxial base of bracts and bracteoles, and at the sinus of calyces or inside the calyx tubes of all species examined. The narrowly obconical to cylindrical or subulate shape of colleters is constant for the stipules, bracts and calyces of all investigated species (Fig. 2M, 21D). The size of colleters is almost invariant in relation to the stipules, bracts or calyces of each species, but somewhat variable in respect to the stipules ( $0.3\text{--}1.8 \times 0.05\text{--}0.4$  mm), bracts ( $0.1\text{--}1 \times 0.03\text{--}0.2$  mm) and calyces ( $0.07\text{--}1 \times 0.03\text{--}0.3$  mm). The variation in colleter-number of stipules ([2–]5–28 per stipules) is discrete for a number of species (e.g., colleters 5–7, *Sabicea bariensis*, *S. camporum*, *S. cinerea*, *S. klugii*, *S. morillorum*, *S. oblongifolia*, *S. villosa*; colleters 8–12, *S. cana*, *S. novo-granatensis*, *S. pyramidalis*; colleters 12–18, *S. calophylla*, *S. erecta*, *S. panamensis*, and *S. thyrsoiflora*; colleters 18–24 or 28, *S. hirta* and *S. umbellata*). In most of the species, the presence of 2 colleters at two margins inside the bracts or bracteoles seems constant. In many species, the colleters number vary within 2–30, and this variation is discontinuous in relation to some species (e.g., colleters usually 2–4, *Sabicea cana*, *S. camporum*, *S. cinerea*, *S. chocoana*, and *S. mexicana*; colleters usually 4–7, *S. boyacana* and *S. bariensis*). *Sabicea hirta* is an exception in which 12–30 colleters are present along the base inside of bracts. In calyces, the colleters are usually present in the sinus, where the number varies within 1–4 but in most species within 1–2. Exceptionally, 2–4 colleters are present in each calyx-sinus of *Sabicea hirta*. In few species (e.g., *Sabicea amazonensis*, *S. mollissima*, *S. bariensis*, *S. parva*, and *S. trailii*), colleters occur below (1–6.8 mm) the sinus inside the tubes. All variants of colleters present in *Sabicea* correspond to the standard Rubiaceae colleters (Robbrecht 1988). The colleter characters of *Sabicea* have limited utility in specific or infraspecific delimitation.

No difference between the trichome or cilia characters of African and Neotropical *Sabicea* appears to be notable. The comparison of colleter characters of African and Neotropical *Sabicea* is impossible as the variation in colleter characters of African *Sabicea* is almost unknown. The arachnoid indumentum commonly present in a number of African and Neotropical *Sabicea*, are totally absent in its associated genera. No noticeable difference exists between the straight and flexuous trichomes of *Sabicea* and its associated genera except the completely glabrous upper surface of leaves of *V. angustifolia*, constantly limited number (1–2 per lobe) of trichomes on external surface of calyx lobes of *V. herbacoursi* and

glabrous outside of corolla of *Hekistocarpa*. *Sabicea*, as well as, *Hekistocarpa* and *Tamridaea* can be separated from *Virectaria* by their constricted trichomes at the orifice of corolla in contrast to flat trichomes of *Virectaria*.

## STIPULES

The previous authors have emphasized the characters of stipule in regard to its shape, size, division, and erectness. Palisot-Beauvois (1810) incorporated "large stipule" in recognizing his new genus *Stipularia*. Wernham (1914) stressed large and leafy stipules to key out the subgenus *Stipulariopsis*, as well as, fimbriate or lacinate stipules to identify few African *Sabicea*. Bremekamp (1966) included "simple stipule" in separating *Sabicea* from *Mussaendeae* as the monogeneric tribe Sabiceae. Hallé (1963, 1966) described that stipules are interpetiolar and persistent in all species.

Their persistent, free, ovate to deltate, occasionally widely lanceolate and usually entire stipules appear noticeable. "The stipules are large, and usually pressed against the stem in the bottom part of the stipule and spreading away from the stem in the top part. In the Neotropics, only *Uncaria* Burch. has similar stipules" (C. M. Taylor, pers. comm.). However, the stipule characters are mostly labile in many species of Neotropica *Sabicea*. The variation in size (2–20 × 2–15 mm) of stipules is continuous in respect to a number of species, but seems discrete in some species either in relation to lengths or widths (e.g., 5–10 × 4.5–8 mm, *Sabicea boliviensis*; 10–14 × 4–6 mm, *S. bariensis*; 6–8 × 2.6–3.8 mm; 3.5–4.2 × 2.6 mm, *S. noelii*). The apex of stipules is invariant in a number of species, e.g., subacute to obtuse (e.g., *Sabicea calophylla*, *S. chocoana*, *S. hirta*, *S. morillorum*, *S. parva*, *S. thyrsoiflora*; Fig. 26A, 41D), acute (e.g., *S. burchellii*, *S. erecta*, *S. mexicana*, and *S. noelii*), acuminate (e.g., *S. klugii* and *S. mollissima*), acute to acuminate (e.g., *S. amazonensis*, *S. aspera*, *S. bariensis*, *S. boliviensis*, *S. oblongifolia*, *S. pearcei*, *S. tillettii*, *S. umbellata*, and *S. velutina*; Fig. 5D, 8D, 24D, 44A). The entire and complanate margins of stipules are constant for all species except *Sabicea amazonensis* (Fig. 5D), *Sabicea humilis* and *S. traillii* where sparsely denticulate margins are found. In some plants of *Sabicea panamensis* and *S. mexicana* the margins are slightly wavy but only occasionally. In many species, the uprightness of stipules is inconstant. However, in some species, antrorse and (sub-)appressed stipules (e.g., *Sabicea bariensis*, *S. cana*, *S. cinerea*, *S. grisea*, *S. humilis*, *S. parva*, *S. tayloriae*, and *S. velutina*) and in some others recurved to reflexed stipules (e.g., *S. boliviensis*, *S. brasiliensis*, *S. chocoana*, *S. cochabambensis*, *S. erecta*, *S. mattogrossensis*, *S. novo-granatensis*, *S. thyrsoiflora*, and *S. traillii*) are usually constant. Stipules are constantly undivided except in some species (e.g., *Sabicea amazonensis*, *S. chocoana*, *S. cinerea*, *S. grisea*, *S. humilis*, *S. mattogrossensis*, *S. panamensis*, *S. mollissima*, *S. traillii*, and *S. villosa*) where merely the apex (1–2.7 mm) is occasionally bilobed. The number of main veins (5–24) per stipule seems labile, however, this number is usually limited to (5–)9 in few species (e.g., *Sabicea cinerea*, *S. grisea*, *S. humilis*,

*S. noelii*, and *S. villosa*), 12–14 (e.g., *S. chocoana*, *S. cuneata*, *S. klugii*, and *S. liesneri*), and 14–24 in *S. hirta*. No notable difference between the stipules of Neotropical and African *Sabicea* seems to exist, except their partitioning. Stipules of some Neotropical *Sabicea* are occasionally apically bilobed. Fimbriate or lacinate stipules, commonly present in some African *Sabicea* (e.g., Madagascar *Sabicea*, *S. aurifodinae*, *S. mildbraedii*, *S. dubia*, *S. batesii*, *S. segregata* Hiern, and *S. proselyta*; Wernham, 1914), are totally absent in Neotropical *Sabicea*. The entire stipules of most of *Sabicea* are similar to those of closely allied *Hekistocarpa*, *Tamridaea* and few *Virectaria* (e.g., *V. belingana* and *V. procumbens*). Lacinate or deeply bilobed stipules of some African *Sabicea* are similar to those of few *Virectaria* species (e.g., *V. multiflora* and *V. herbacoursi*).

## LEAVES

The considerable value of leaf-characters in classifying the species of *Sabicea* (Wernham, 1914, Steyermark, 1967, Andersson, 1999) as well as its associated genus *Virectaria* (Dessein et al., 2001b) has been proven previously. The leaves are decussate and petiolate in all species. The shape of leaves varies from narrowly elliptic to widely ovate or lanceolate, even in individual species. However, in many species, the leaves are usually elliptic to oblong and in some species lanceolate or ovate to oblong. Leaf shape is hardly useful in species delimitation. In most of the species, the acute to acuminate leaf apices seem constant. Exceptionally apically usually subacute (e.g., *Sabicea aspera* and *S. humilis*), acute (e.g., *S. burchellii* and *S. morillorum*), acuminate (e.g., *S. pearcei*, *S. tillettii*, and *S. traillii*), and bluntly acuminate (e.g., *S. hirta* and *S. thyrsoiflora*) leaves appeared invariant for the respective species. The application of leaf apex-characters is very limited in the genus. Leaf-base is usually acute to attenuate, and sometimes rounded (e.g., *Sabicea amazonensis*, *S. burchellii*, and *S. klugii*). *Sabicea noelii* appeared as the only species where the leaf-bases are shallowly cordate (Fig. 34A). Thinly papyraceous or membranous leaves are common for the genus except few exceptions (e.g., *Sabicea brasiliensis*, *S. cana*, *S. tayloriae*, and *S. velutina*) where the leaves are thickly papyraceous. The entire and complanate margins seem invariable in all species except *Sabicea calophylla* and *S. panamensis* where margins are occasionally abaxially minutely recurved. The lamina lengths of vary within 0.8–20 cm, but the ranges of variation are mostly overlapping.

In many species lamina lengths usually vary within 2–12 cm, whereas, in two species (e.g., *Sabicea cochabambensis* and *S. umbellata*), these vary within 13–18 cm. Lamina lengths of rest of the species coincide with any of these two ranges. Two ranges of variation in lamina widths (0.5–11 cm) can be recognized for a number of species excluding the too extreme values, 1.2–4 cm (e.g., *Sabicea humilis*, *S. morillorum*, *S. velutina*, and *S. tillettii*) and 4–8.5 cm (e.g., *S. calophylla*, *S. chocoana*, *S. cochabambensis*, *S. subinvolucrata*, and *S. umbellata*).

Costa and secondary veins, which are always protruding at lower leaf-surface, are usually plane and occasionally slightly sunken or prominulous at the upper leaf surface but usually sunken in a few species (e.g., *Sabicea amazonensis*, *S. brasiliensis*, and *S. tillettii*). The ranges of variation in the number of secondary veins per leaf (5–20 pairs) are coinciding in most of the species. Nevertheless, in some species (e.g., *Sabicea amazonensis*, *S. boliviensis*, *S. burchellii*, *S. cana*, *S. cochabambensis*, *S. klugii*, *S. liesneri*, *S. tayloriae*, *S. pearcei*, *S. tillettii*, and *S. umbellata*) the secondary veins are limited to 11–20 pairs, in contrast to 7–11 pairs of few species (e.g., *S. chocoana*, *S. pyramidalis*, *S. trailii*, and *S. trianae*). Tertiary and quaternary veins are usually obscured, plane or indistinct at the upper surface of leaves. At the lower surface of non-arachnoid leaves, tertiary veins are usually distinct or prominulous and occasionally indistinct (e.g., *Sabicea chocoana*), whereas, the quaternary veins are plane, distinct or indistinct. For compactly matted arachnoid leaves, tertiary and quaternary veins are plane to prominulous but usually obscured except in few species (e.g., *Sabicea boliviensis*, *S. brasiliensis*, *S. calophylla*, and *S. cuneata*).

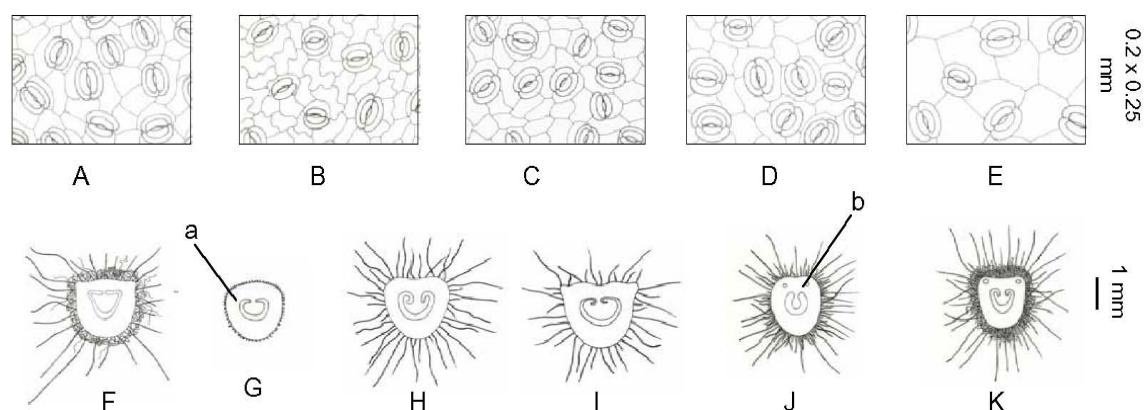


Figure 3. A–E. Epidermal peelings of lower surface of leaves. F–K. Petiole anatomy. —A. *Sabicea cinerea*. —B. *Sabicea liedeeae*. —C. *Sabicea mexicana*. —D. *Sabicea thyrsiflora*. —E. *Sabicea panamensis*. —F. *Sabicea amazonensis*. —F. *Sabicea trailii*. —F. *Sabicea oblongifolia*. —F. *Sabicea mattogrossensis*. —F. *Sabicea burchellii*. —F. *Sabicea novo-granatensis*.

The epidermal cells are usually 4–6 angular (e.g., *Sabicea cinerea*, *S. mexicana*, *S. pyramidalis*, and *S. thyrsiflora*) or wavy (e.g., *S. liedeeae*). The stomata are predominantly paracytic, sometimes hemiparacytic (e.g., *Sabicea mexicana*) or anomocytic (e.g., *S. liedeeae*), and occasionally amphiparacytic (e.g., *S. thyrsiflora*; Fig. 3). The variation ranges of petiole-lengths (0.5–5 cm) are mostly overlapping. In most species, the length of petiole varies within 0.2–1.8 cm, whereas, in two species (e.g., *Sabicea cochabambensis* and *S. umbellata*) it extends from 2 to 5 cm. The diameter of dry petioles is usually 1–2 mm. The medullated arc of the petioles is generally with invaginated ends (Fig. 3H, I, K), one of the common patterns of petiole vasculature described by Radford et al. (1975). In few species a medullated cylinder with straight ends occurs (e.g., *Sabicea amazonensis*, *S. burchellii*, and *S. trailii*; Fig. 3F, G, J). In most of the species, the medullated cylinder is associated with two

distinct and rounded lateral rib traces. These lateral rib traces are absent or indistinct in some species (e.g., *Sabicea aspera*, *S. calophylla*, *S. mattogrossensis*, *S. novo-granatensis*, *S. oblongifolia*, *S. traillii*, and *S. villosa*; Fig. 3F–1). The thickness of the widest part of medullated layer varies from (0.03–) 0.1 to 0.1 mm. In transverse section, the diameter through open ends of medullated ring ranges from 0.2 to 0.8 mm, whereas, the diameter below the open ends ranges from 0.5 to 0.7 mm.

The leaves of the Neotropical *Sabicea* appear to be similar to those of most of the African species. The markedly anisophyllous (e.g., *Sabicea acuminata* Baker, *S. diversifolia* Pers., *S. seua* Wernham, *S. angustifolia* Boivin ex Wernham), and abaxially purple (e.g., *Sabicea capitellata* Benth.), break-read (e.g., *S. carbunica* N. Hallé) or pink (e.g., *S. hierniana* Wernham) colored leaves, present in few African *Sabicea*, are totally absent in Neotropical *Sabicea*, as well as in the associated genera. Apparently the basally oblique (e.g., *Sabicea aurifodinae* (N. Hallé) Razafim., B. Bremer, Liede & Khan, *S. batesii* Wernham, and *S. mildbreadii*) or cordate (e.g., *S. floribunda*, *S. nobilis*, and *S. calycina*) leaves existing in few African species are generally absent in Neotropical *Sabicea*. No Neotropical *Sabicea* has large leaves comparable to the African *S. hierniana* or *S. africana*. On the other hand, the leaves of many *Sabicea* species are rather similar to those of its associated genera, excluding the exceptions just mentioned. However, no *Sabicea* has very narrow and small leaves as those characterizing *V. angustifolia*, and *V. tenella*.

## INFLORESCENCES

The inflorescence characters have been widely used in classifying the species of *Sabicea* and the genera of Sabiceae. Wernham's (1914) evolutionary tree including four sections (Laxae, Sessiles, Capitatae, and Floribundae) of his subgenus *Eusabicea* and designation of many species was based on inflorescence characters. Bremekamp (1934, 1966) added "axillary inflorescence" as one of the distinguishing characters for the tribe Sabiceae.

The inflorescences of *Sabicea* are absolutely axillary, whether one (e.g., *Sabicea amazonensis*, *S. aspera*, *S. camporum*, *S. grisea*, and *S. mollissima*), two (e.g., *S. boliviensis*, *S. calophylla*, *S. cana*, *S. cinerea*, and *S. erecta*) or one and two (e.g., *S. bariensis*, *S. brasiliensis*, *S. chocoana*, *S. mattogrossensis*, and *S. panamensis*) per leaf axis. Modified inflorescences as described in Claßen-Bockhoff (1996) commonly occur in *Sabicea*. The inflorescences are variable from sessile to (sub-)sessile, (sub-)sessile to shortly (3–8 mm long) pedunculate, and always distinctly (1–4.5 cm long) pedunculate. Accordingly, the inflorescence types are comprised of verticillate to glomerulate (e.g., *Sabicea camporum*; Fig. 17A, E), verticillate (e.g., *S. oblongifolia* and *S. villosa*; Fig. 36A, D, 45A, E), capitate (e.g., *S. tayloriae*; Fig. 40A, F), capitate to compact-fasciculate (e.g., *S. burchellii* and *S. noelii*; Fig. 15A, F, Fig. 34A, F), compact-fasciculate (e.g., *S. amazonensis*, *S. brasiliensis*, *S. cana*, *S. cinerea*, *S. grisea*, *S. mollissima*, *S. traillii*, and *S. velutina*; Fig. 5A, E, 32A, D42E), verticillate

to umbellate (e.g., *S. aspera*), umbellate (e.g., *S. hirta*, *S. klugii*, *S. liesneri*, *S. mattogrossensis*, *S. novo-granatensis*, and *S. trianae*; Fig. 26D, 31E, 35F), or paniculate (e.g., *S. cuneata*, *S. panamensis*, *S. pearcei*; Fig. 37E), and laxly paniculate or thyrsoid (e.g., *S. panamensis*, *S. chocoana*, *S. cochabambensis*, *S. pyramidalis*, and *S. thyrsoiflora*; Fig. 22A, 41A). The central inflorescence type in *Sabicea* seems to be the compound panicle (e.g., some *Sabicea panamensis*) or thyrsoid (e.g., *S. thyrsoiflora*, *S. chocoana*, and *S. pyramidalis*), from which the other types appear to be evolved through the reduction of peduncle lengths, lengths and number of inflorescence axes, and pedicel lengths. The range of variation in peduncle length seems convergent or labile for a number of species, which indicate its limitation as a useful character, though, Wernham (1914) widely used peduncle length to key out many species.

Bract characters have been highly emphasized (e.g., Hiern, 1877; Wernham, 1914), or strongly ignored (e.g., Hepper, 1958; Andersson, 1999) in classifying *Sabicea*. The ranges of variation in the characters of bracts, especially their partitioning, are mostly continuous, but sometimes constant. The bracts of Neotropical *Sabicea* are generally undivided and involucre at budding or early flowering stage. Eventually at late flowering stage they are usually completely divided into 2–5 parts and exinvolucre, however, sometimes they remain partially divided or undivided and (sub-)involucre (e.g., *Sabicea amazonensis*, *S. mollissima*, *S. cochabambensis*, *S. hirta*, *S. mattogrossensis*, *S. thyrsoiflora*, *S. traillii*; Fig. 5E, 26D, 32D, 41E, 42F). The ranges of variation in lengths (2.9–18) or diameter (3–22 mm) of (sub-)involucral bracts appear to be stable for few species. In *Sabicea morilloorum*, *S. thyrsoiflora*, and *S. traillii*, the length of bracts usually does not exceed 8 mm, whereas, in *S. amazonensis*, *S. cochabambensis*, *S. mollissima*, and *S. subinvolucrata* it usually ranges from 10 mm to 18 mm. The ranges of variation in involucre diameter in *Sabicea mollissima*, *S. morilloorum*, and *S. thyrsoiflora* seem to remain within 3–8 mm, whereas, usually 11–22 in *S. amazonensis*. The variation in lengths (3.5–30 mm) and widths (1–16 mm) of exinvolucre bracts also appear to be stable for a number of species. Apically usually (sub-)acute to obtuse bract-lobes of few species (e.g., *Sabicea hirta*, *S. mattogrossensis*, *S. morilloorum*, *S. thyrsoiflora*, and *S. traillii*) are easily distinguishable, in contrast to acute to acuminate apices of most of the species. The usually sparsely serrulate to denticulate bract margins of a few species (e.g., *Sabicea cochabambensis*, *S. humilis*, and *S. traillii*) contrast to the constantly entire margins of most species. The bracteoles, located either on pedicels or at the base of hypanthium, are generally exinvolucre and, though variable in size, shape and apex, less striking than bracts.

The range of variation in inflorescence size (1–8 × 0.7–7.5 cm, excluding peduncles) of this genus is notable. Steyermark (1974) mentioned the variation in inflorescence size for few species. The size of the (sub-)sessile inflorescences in some species (e.g., *Sabicea brachycalyx*, *S. brasiliensis*, *S. cana*, *S. camporum*, *S. oblongifolia*, and *S. villosa*) varies within the range of 1–2 × 0.7–2.5 cm, and in few species (e.g., *S. cinerea*, *S. grisea*, *S. traillii*,



and *S. velutina*) within 2–3 × 1–4 cm. In *Sabicea cochabambensis*, *S. pyramidalis*, *S. thyrsoiflora*, and *S. panamensis*, the size of laxly paniculate or thyrsoid inflorescences ranges within 3–7.5 × 2–8 cm (excluding peduncles). The inflorescence sizes of other species overlap with any of these ranges. The range of variation in inflorescence size is high and continuous in few species (e.g., *Sabicea novo-granatensi* and *S. panamensis*); however, the inflorescences of some species (e.g., *Sabicea oblongifolia* and *S. villosa*) show little and more or less constant ranges of variation. The length of primary axis (0.1–6.5 cm) shows a considerable range of variation, extending up to 0.8 cm in the compact to moderately lax inflorescences and up to 6.5 cm in the lax inflorescences. There are 2–6(–8) lateral axes of 1–6 mm length. The number and lengths of main axes (in umbellate inflorescences) vary within 3–5 and 1–6 mm respectively. The variation in flower number (1–88) per inflorescence in this genus, just mentioned before for few species (Steyermark, 1974; Andersson, 1999), is remarkable. In many species, the flower numbers per inflorescence vary within 3–12, whereas, in many other species within 12–64.

Wernham (1914) was the first who mentioned that the plants he considered ancestral to the genus, i.e. his section *Primosabicea*, comprise species with lax inflorescences and prevails simultaneously in Africa and America, a hypothesis which is unsupported by the results of Khan et al.'s (2007) molecular study. This molecular study showed that species bearing both congested (e.g., *Sabicea fulva* Wernham, *S. nobilis* Good) and lax inflorescences (e.g., *S. venosa* Benth. and *S. segregata*) have radiated from a group of African *Sabicea* with congested inflorescences (e.g., *S. batesii* Wernham, *S. becquetii* (N. Hallé) Razafim., B. Bremer, Liede & Khan, *S. mildbraedii* Wernham). Wernham (1914) plotted all Neotropical *Sabicea* in three sections *Laxae*, *Capitatae*, and *Sessiles* of his evolutionary tree constructed mainly according to inflorescence types. The placements of *Sabicea asperula*, *S. colombiana*, *S. costaricensis*, *S. panamensis*, and *S. paraensis*, in his section *Laxae* are not supported by this study.

Variation in inflorescence characters and other parts of these presumed species is continuous, also including *Sabicea reflexa*. Of the species of section *Laxae*, Dwyer (1980) merged *Sabicea costaricensis* with *S. panamensis*, and later, Andersson (1999), following Dwyer, synonymized *S. colombiana*, *S. costaricensis*, *S. mexicana*, *S. paraensis*, and *S. reflexa* under *S. panamensis*. The present study comes to the same conclusion; only *Sabicea mexicana* should be maintained as a separate species due to its antrorse to sprteading and long calyx lobes. The position of *Sabicea humilis* and *S. moorei* (here synonymized with *S. humilis*) is not also supported because their inflorescences are transitional between *Capitatae* and *Sessiles*. The positioning of *Sabicea mattogrossensis*, *S. trianae*, and *S. traillii* together and with mostly African *Capitatae* (Wernham, 1914) is inconsistent with this study. The inflorescences of these species are not truly capitate, rather, compactly to moderately lax-umbellate (e.g., *Sabicea mattogrossensis* and *S. trianae*) compactly lax-umbellate (e.g., *S. trianae*), and capitate to compact-fasciculate (e.g., *S. traillii*). Their calyx lobes are also very

different. *Sabicea mattogrossensis* and *S. trianae* should be placed in section *Laxae*, and *S. traillii* in sect. *Sessiles*. The position of *Sabicea burchellii* in section *Sessiles* is contrasting to its capitate to compactly fasciculate inflorescences. There is no Neotropical species of *Sabicea* with a constantly capitate inflorescence. The only Neotropical species with usually capitate inflorescence is *Sabicea tayloriae* with a peduncle length varying from 1 to 15 mm. *Sabicea cana* with usually compactly sessile inflorescences rarely has also capitate inflorescences with 2–18 mm long peduncles. The capitate to compact-fasciculate inflorescences occur in the new species *Sabicea noelii*. The inflorescences of *Sabicea mexicana* and of some *S. panamensis* specimens are not always lax. Also, variation in inflorescence size seems considerable in Neotropical *Sabicea* (e.g., *Sabicea novogranatensis* and *S. panamensis*). Therefore, Wernham's (1914) inflorescence based classification for and explanation of the affinities within *Sabicea*, including the Neotropical species, are widely unsupported, which coincides with the results of the molecular study by Khan et al. (2007).

The inflorescence characters of African and Neotropical species of *Sabicea* appear similar with some exceptions. For example, capitate inflorescences are frequent in African *Sabicea*, but rare in Neotropical *Sabicea*. Single-flowered inflorescences (e.g., *Sabicea cordata*, *S. liberica*, and *S. solitaria*), long peduncles (e.g., *S. bigerrica* and *S. calycina*), large (e.g., *S. dewevrei* and *S. najatrix*) and deeply campanulate (e.g., *S. africana*, *S. elliptica*, *S. gabonica*, and *S. urceolata*) bracts exist in a few African *Sabicea* but are generally absent in Neotropical *Sabicea*. Claßen-Bockhoff (1996) reported the occurrence of extra-floral semaphylls in few African *Sabicea* (*Sabicea africana*, *S. floribunda*, *S. gigantistipulata*, and *S. segregata*) that are absent in Neotropical *Sabicea*. Only one exceptional single-flowered inflorescence was found in the South American *Sabicea mollissima*, all other inflorescences examined had 3–5 flowers. The inflorescences of the only one Asian species *Sabicea ceylanica* are also solitary. The difference between the inflorescences of *Sabicea* and its associated genera is clear-cut. The inflorescence of *Hekistocarpa* is an axillary, but scorpioid cyme, which seems totally absent in *Sabicea*. The inflorescences of both *Tamridaea* and *Virectaria* are terminal. The elongated-monochasial branches existing at late flowering or fruiting stage, in few species of *Virectaria* (e.g., *Virectaria belingana*, *V. herbacoursi*, *V. major*, and *V. multiflora*) are also absent in *Sabicea*.

## FLOWERS

The flowers of *Sabicea* are actinomorphic, hermaphrodite, and homostylous or heterostylous. They are usually pentamerous, but occasionally with variable number in any of the floral parts. Their aestivation is generally valvate and ample floral disc is undivided. Most of the species are known to produce flowers throughout the year. The floral parts that have proven to be of considerable importance in classifying *Sabicea* include the lengths of

pedicels, calyx tubes and lobes, corolla tubes, stigmatic lobes, and locules of ovaries. Many Neotropical *Sabicea* species seem to contain usually pedicellate flowers, some others (16 species) sessile to subsessile flowers, and five species sessile flowers (e.g., *Sabicea brasiliensis*, *S. parva*, and *S. oblongifolia*). The ranges of variation in pedicel lengths (0.5–15 mm) are mostly coinciding and distinct only in a few species (e.g., 1–3 mm long, *Sabicea aspera*, *S. boliviensis*, *S. burchellii*, *S. humilis*, and *S. klugii*; pedicels 3–10 mm long, *S. chocoana*, *S. hirta*, *S. novo-granatensis*, *S. pyramidalis*, and *S. thyrsiflora*).

The calyces of Neotropical *Sabicea* are usually green and campanulate calyx (34 species). An infundibuliform calyx is constant for only four species (e.g., *Sabicea amazonensis*, *S. mollissima*, *S. surinamensis*, and *S. traillii*; Fig. 5H, J, 32E, G, 42E, G, I), while the rest of the species (e.g., *S. bariensis*, *S. cinerea*, *S. grisea*, *S. parva*, and *S. tillettii*) show campanulate to shortly infundibuliform calices. The lengths and diameters of campanulate calyx tubes of most the species vary within 0.3–3 mm and 0.8–3.5 mm respectively, whereas, in the infundibuliform calyces within 3–11 mm and 2–6.5 mm respectively. Though the calyces of Neotropical *Sabicea* are commonly united, however, the campanulate calyces of some species appear to be almost free (e.g., *Sabicea burchellii*, *S. cochabambensis*, *S. cuneata*, *S. erecta*, *S. humilis*, *S. klugii*, *S. liedeeae*, *S. liesneri*, *S. morillorum*, *S. pearcei*, *S. pyramidalis*, and *S. thyrsiflora*) due to their mostly indistinct (0.3–1.2) mm tubes. The number of lobes per calyx shows a considerable range of variation (3–10). In many species, the number of five lobes per calyx is constant, other species possess 4–6 lobes. Only *Sabicea mattogrossensis* shows a decreased lobe number of three, while it is increased up to 7–10 in a few species (e.g., *S. camporum*, *S. cinerea*, *S. humilis*, *S. mollissima*, and *S. villosa*). The variations in lengths (0.2–15 mm) and widths (0.1–7 mm) of calyx lobes in *Sabicea* are proved as noteworthy, though sometimes labile. The calyx lobes of few species (e.g., *Sabicea brasiliensis*, *S. calophylla*, *S. chocoana*, and *S. morillorum*) usually do not exceed the length of 2.5 mm. In few species (e.g., *Sabicea cuneata*, *S. klugii*, *S. liesneri*, *S. thyrsiflora*, *S. velutina*, and *S. villosa*) the calyx lobes are 2.5 or 3 mm to 6 mm long, in *S. liedeeae*, *S. mattogrossensis*, *S. mexicana*, *S. trianae*, 6–10 mm and in *S. chiapensis*, 10–15 mm.

The variations in lengths of calyx lobes of other species usually coincide with any of these ranges. In 27 species, the calyx lobes usually do not exceed the width of 2 mm, though in few species (e.g., *Sabicea amazonensis*, *S. hirta*, *S. mattogrossensis*, and *S. traillii*) they extend from 2 mm to 4–7 mm. Markedly unequal calyx lobes exist in few species (e.g., *Sabicea bariensis*, *S. burchellii*, *S. cana*, *S. humilis*, *S. liesneri*, *S. mattogrossensis*, and *S. tayloriae*). The shape of calyx lobes varies even within a species. However, sometimes they appear to be constant. Ample elliptic or obovate to lingulate calyx lobes exist in some species (e.g., *Sabicea hirta*, *S. mattogrossensis*, *S. novo-granatensis*, *S. trianae*, and *S. thyrsiflora*; Fig. 26A, G, 31E, HJ), widely lanceolate to triangular or ovate calyx lobes in some other species (e.g., *S. amazonensis*, *S. bariensis*, *S. parva*, *S. surinamensis*, and *S. traillii*; Fig. 5J, H, 8E, J), and lanceolate to linear calyx lobes in a third group of species (e.g., *S. chiapensis*, *S.*

*cochabambensis*, *S. cuneata*, *S. klugii*, *S. oblongifolia*, *S. pearcei*, *S. tillettii*, and *S. velutina*; Fig. 18E, D, G, 22G, H, 29E, F, H). The erectness of calyx lobes shows a considerable range of variation. Calyx lobes are usually antrorse (e.g., *Sabicea amazonensis*, *S. burchellii*, *S. brasiliensis*, *S. cinerea*, *S. grisea*, *S. novo-granatensis*, and *S. thyrsiflora*; Fig. FJ, H, 13E, I, 21H, J, 25D, E, G), antrorse to spreaded (e.g., *S. bariensis*, *S. chiapensis*, *S. cochabambensis*, *S. liedae*, *S. mattogrossensis*, *S. mollissima*, *S. noelii*, and *S. tayloriae*), spreaded to slightly reflexed (e.g., *S. morillorum*, and *S. erecta*, Fig. 33F, H, 24F, H), recurved to reflexed, occasionally antrorse (e.g., *S. aspera*, *S. chocoana*, *S. panamensis*, *S. pyramidalis*, and *S. villosa*; Fig. 37E, G, I). In most plants of the genus, the calyx lobes are apically acute and/or acuminate, sometimes they are (sub-)acute (e.g., *Sabicea cinerea* and *S. tayloriae*; Fig. 21H, J) or obtuse to rounded (e.g., *S. mattogrossensis*, *S. thyrsiflora*, *S. hirta*, and *S. morillorum*; Fig. 31E, H, J, 33F, H). The margins of calyx lobes are usually entire, but entire to serrulate in *Sabicea erecta*, *S. pearcei*, *S. cochabambensis*, *S. subinvoluta*, entire to irregularly slightly wavy in *S. amazonensis* and *S. mexicana*, and sparsely denticulate in *S. humilis*, *S. klugii*, *S. surinamensis*, *S. humilis*, *S. moore*, and *S. traillii*. The number of veins in calyx lobes varies from 1–7 per lobe, though 3–5 in most of the plants. Rarely their number is increased up to 6 (e.g., *Sabicea mattogrossensis*) or 7 (e.g., *S. hirta*).

The range of variation in corollas is less extensive than in calyces (Wernham, 1914). Essentially the indumentum, and the lengths of corolla tubes and lobes appear to be stable. A narrow variation exists in tube diameter, lobe width, and corolla color. Corolla tube lengths, varying from 2.7 mm up to 25 mm in the genus, remain within 7–12 mm in most species, within 3–6.5 mm in some others, but within 12–25 mm only in four species (*Sabicea amazonensis*, *S. cinerea*, *S. grisea*, and *S. surinamensis*). Tube lengths under these ranges of variation appear to be species-specific for some species. In 30 species, corolla tube diameters vary between 1 and 2 mm (at widest part) and merely in few species between 2–12 mm (e.g., *Sabicea amazonensis*, *S. cuneata*, *S. hirta*, *S. mattogrossensis*, and *S. thyrsiflora*). Corolla lobe lengths seem to be constantly homomorphic, ranging from 1.5 to 2.5 mm in 9 species, and 2.5 to 7 mm in 17 species. In few species (e.g., *Sabicea panamensis*, *S. pearcei*, *S. thyrsiflora*, and *S. tillettii*), the lobe lengths do not exceed 1.5 mm. These ranges of corolla lobe lengths are overlapping in other species. The ranges of variation in corolla lobe widths seem to be stable for some species. In 35 species, the width of corolla lobes generally vary between 0.8 to 2 mm, and exceptionally between 2 to 2.5 mm in *Sabicea amazonensis*. The lobe-widths in other species are overlapping with these ranges. The corolla lobes are usually ovate (length-width ratio <2) in most of the species and widely lanceolate to narrowly ovate (length-width ratio >2) in some species (e.g., *Sabicea amazonensis*, *S. bariensis*, *S. calophylla*, *S. cinerea*, *S. cuneata*, *S. erecta*, *S. humilis*, *S. liedae*, *S. mattogrossensis*, and *S. surinamensis*). The corollas of Neotropical *Sabicea* are commonly whitish. Yellow corollas are known merely from *Sabicea aspera* and pale or dull rose corolla lobes are known from *S. velutina*.

The number of stamens is commonly 5 per flower in all examined species excluding few exceptions. Sometimes in *Sabicea brasiliensis*, *S. tayloriae*, and *S. villosa* or rarely in *S. aspera* and *S. novo-granatensis*, the stamen-number is decreased to 4 per flower. In *Sabicea villosa*, up to 10 stamens per flower are found, but rarely. In all species examined the anthers are generally included in the corolla tubes (Fig. 15J, 23G, 31I, 37H), yet in few species (e.g., *Sabicea amazonensis*, *S. aspera*, *S. oblongifolia*, and *S. traillii*; Fig. 5I, 36G, 42H) they are apically slightly exerted from the corolla tubes. Stamens generally are attached to corolla tube at its upper part. Insertion points of stamens in corolla tubes (at 1.8–20 mm from the base of tubes) show a considerable range of variation. In some species, the stamens are inserted at 2–5 mm from the base of tubes. The filaments of stamens are inserted at 2–5 mm from the base of tubes in 16 species, and at 6–11 mm in 17 species. They are also inserted at 12–16 mm (e.g., *Sabicea cinerea*, *S. grisea*, and *S. traillii*) and 16–21 mm (e.g., *S. amazonensis* and *S. surinamensis*) from the base of tubes. In each flower, the anthers are always homomorphic and undivided or merely basally divided. The variation in anther's lengths (0.8–4 mm) in different species is notable. In about 30 of the species, anther-lengths appear to range from 1.1 to 2 mm, in some species from 2 to 2.7 mm, and in two species (e.g., *Sabicea amazonensis* and *S. cinerea*) from 3 to 4 mm. The free part of filaments is glabrous and shorter and slender (0.07–1 × 0.06–0.2 mm) than anthers.

The flowers of Neotropical *Sabicea* appear to be generally homostylous, sometimes heterostylous (e.g., *Sabicea cochabambensis*, *S. calophylla*, *S. novo-granatensis*, *S. oblongifolia*, and *S. panamensis*). Andersson (1999) and Teixeira & Machado (2004) reported the heterostyly in *Sabicea panamensis* and *S. cinerea* respectively. A considerable range of variation exists in the lengths of style, number and lengths of stigmas, and locule number per ovary. The number of stigmas per flower and the diameter of style and stigmas are barely variable. The ranges of variation in style-lengths (1–20 mm) appear to be mostly species-specific. However, in 26 species, the style-length generally ranges from 3 to 10 mm. In some species it remains usually limited to 1.5–3 mm (e.g., *Sabicea erecta*, *S. klugii*, *S. liesneri*, and *S. subinvoluta*), in contrast to 11–20 mm in *S. cinerea* and *S. grisea* or 19–20 mm in *S. amazonensis*. The number of stigmas per flower is generally 5 in about 34 of the species, and 4–5 in few species (e.g., *Sabicea brasiliensis*, *S. calophylla*, *S. noelii*, *S. novo-granatensis*, and *S. tayloriae*). Stigma number per flower rarely increases up to 6 (e.g., *Sabicea aspera* and *S. mollissima*) or 10 (e.g., *Sabicea villosa*). The stigmas are usually homomorphic for a number of species. They are filiform to narrowly oblong in many species, oblanceolate in some species (e.g., *Sabicea brachycalyx*, *S. burchellii*, *S. cana*, *S. klugii*, *S. hirta*, *S. mattogrossensis*, *S. mollissima*, and *S. tayloriae*), and filiform or oblong to oblanceolate in some other species (e.g., *S. boliviensis*, *S. brasiliensis*, *S. humilis*, *S. morillorum*, *S. novo-granatensis*, *S. parva*, *S. thyrsoflora*, *S. umbellata*, and *S. velutina*). The stigmas are apically generally obtuse in almost all species and additionally (sub-)acute (e.g., *Sabicea noelii*, *S. trianae*, and *S. velutina*) or gently truncate (e.g., *S. brasiliensis* and *S. calophylla*). The

variation in stigma lengths (0.7–5 mm) is not as extensive as in style lengths. Stigma length ranges from 1.1 to 2.5 mm or 2 to 3.5 mm in many species. The two extreme ranges are 0.7–0.9 (e.g., *Sabicea erecta* and *S. liesneri*) and 4–5 mm (e.g., *S. amazonensis*). The ovary is commonly ellipsoidal to turbinate. Its length and diameter generally vary between 1 and 2 mm in 34 of the species, and 2 to 3.5 mm in few species (e.g., *Sabicea bariensis*, *S. cinerea*, *S. grisea*, and *S. novo-granatensis*).

The taxonomic utility of locule number is controversial. Wernham (1914) mentioned that the ovary of *Sabicea* is usually 4–5-locular and that in most of the species of subgen. "*Stipulariopsis*" and two or three species of subgenus "*Eusabicea*" is bilocular. Wernham (1914) did not emphasize on locule-number as a character in classifying *Sabicea* except for *S. arborea*. Hallé (1963) was the first who stressed the locule number in classifying *Sabicea* s.l. Hallé (1963) restricted *Sabicea* to species with 4–5-locular ovary, and recognized *Ecpoma* and *Pseudosabicea* for species with 2-locular ovary. Hallé's (1963) circumscription was contested by Steyermark (1974) who reported that locule number (3–5, rarely 2 per ovary) is variable in Neotropical *Sabicea*, and following Wernham, he did not give emphasis on locule number in classifying the genus. Finally, the recognition of genera within *Sabicea* alliance has been rejected by Khan et al. (2007). However, most Rubiaceae authors (e.g., Andersson, 1999, Dessein et al., 2001a; Robbrecht & Manen, 2006) maintained Hallé's concept emphasizing locule-number in delimitation of *Sabicea* from its associated genera. In contrast, Khan et al. (2007) showed that the delimitation of *Sabicea* associated genera based on the characters including locule number is not supported. In Neotropical *Sabicea*, the locule number appears to be constantly five (Fig. 5M, 27J) in about 27 species. In contrast, its number seems to be labile in some species. It ranges from 4 to 5 in some species (e.g., *Sabicea aspera*, *S. calophylla*, *S. humilis*, *S. noelii*, *S. oblongifolia*, *S. parva*, *S. tayloriae*, and *S. velutina*), 5 to 6 in few species (e.g., *S. cana*, *S. mollissima*, *S. pyramidalis*, and *S. villosa*), 3 to 5 in *S. brasiliensis*, and 4 to 6 in *S. cinerea*. In 30 species, the ovaries of are uneven to shallowly 5-lobed at outside and in the rest of the species they are plane or uneven. Locule length (0.5–2.5 mm) and diameter (0.2–1.5 mm) are not strikingly variable. Locule length is limited to 0.8–1.5 mm in 30 species, and 1.5–2 mm in few species (e.g., *Sabicea cana*, *S. hirta*, *S. mexicana*, *S. mollissima*, and *S. novo-granatensis*). Locule diameter is variable between 0.4 and 0.8 mm in 35 species.

Pollen morphology, pollination and floral visitors for the Neotropical *Sabicea* are little known. Dessein et al. (2001a) mentioned that pollen grains of *Sabicea* (Fig. 2S) are 3–4-colporate to 3–4(–5)-porate. In *Sabicea* pollens appear to be released as monads. Teixeira et al. (2004) reported that in *Sabicea cinerea* anthesis begins at about 5.00 a.m. and nectar production (24% sugar concentration; 8 µl per day) continues until 4.00 p.m. Two species of hummingbird (*Phaethornis ruber* and *Amazilia* sp.), several species of Apidae, Anthophoridae and Halictidae bees, HesperIIDae and Nymphalidae butterflies and Syrphidae flies are reported as visitors of *Sabicea cinerea* flowers and *Phaethornis ruber* as the main

pollinator (Teixeira & Machado, 2004). Butterflies also are reported as the visitors of *Sabicea*, especially *S. villosa* (Keber, 1997). Ramírez et al. (2002) listed 30 species of Neotropical euglossine bees *Eufriesea*, *Euglossa*, *Eulaema*, and *Exaerete*, (Hymenoptera: Apidae), thought to be important long distance pollinators of several plant families, that visited *Sabicea* plants (e.g., *Sabicea* spp., *S. aspera*, *S. brasiliensis*, *S. velutina*, and *S. villosa*), mostly for nectar and nesting materials.

The floral characters of African and Neotropical *Sabicea* appear to be almost similar excluding few exceptions. For example, the long and narrowly linear calyx lobes (e.g., *Sabicea pilosa*, and *S. xanthotricha*), longer corolla lobes (e.g., *S. hierniana*, *S. pilosa*, *S. speciosa*, and *S. speciosissima*), externally glabrous corolla tubes (e.g., *S. calycina*, *S. geantha*), two and laterally dilated stigmas (e.g., *S. aurifodinae*, *S. floribunda*, *S. marojejyensis*, *S. nobilis*, and *S. proselyta*), and bilocular ovaries (e.g., *S. floribunda*, *S. hierniana*, *S. nobilis*, *S. segregata*, *S. mildbraedii* Wernham, *S. marojejyensis* S. G. Razafimandimbison & J. S. Miller, *S. nobilis* Good, *S. proselyta* (N. Hallé) Razafim., B. Bremer, Liede & Khan) exist in few African *Sabicea*, but are totally absent in Neotropical *Sabicea*. Floral characters of *Sabicea* differ with those of its related genera in some extents. Heterostyly is present in *Tamridaea* (Bremer & Thulin, 1998), but absent in *Hekistocarpa* and *Virectaria* (Dessein et al., 2001a). Slightly obcordate and apically truncate, emarginate or mucronate corolla lobes occur in *Tamridaea*, reduplicate-valvate aestivation in *Hekistocarpa* and *Tamridaea*, truncated (no distinct lobe) stigmas in *Virectaria*, usually completely exerted anthers and upper part of filaments and style in *Virectaria*, and divided floral discs in three species (e.g., *V. herbacoursi*, *V. multiflora*, and *V. tenella*) of *Virectaria* while all these characters are totally absent in *Sabicea*.

## FRUITS AND SEEDS

Fruit characters are presumably never emphasized in classifying the species of *Sabicea*, but in recognizing its generic status in the tribe Sabiceae (Wernham, 1914; Hallé, 1963, 1966; Bremekamp, 1966; Andersson, 1996; Bremer and Thulin, 1998; Dessein et al., 2001a). Wernham (1914) noted that the fruits of *Sabicea* differ from those of *Stipularia* by their smaller size and rounded shape. Hallé (1963) separated out few species of *Sabicea* containing scanty fleshy fruits with colorless pulp, non-fleshy center and oblong, peltate and fleshy placenta as his new genus *Pseudosabicea*, though, afterwards, he (Hallé, 1966) keyed out *Pseudosabicea* from *Sabicea* only by its 2-locular ovary and non-fleshy fruits. Neither the circumscription of *Stipularia* by Wernham (1914) nor the split of *Sabicea* by Hallé (1963, 1966), based on the characters including those of the fruits, was supported by the recent molecular study (Khan et al., 2007). The fruit characters- indehiscence, fleshiness, rounded external surface, and several to numerous seeds per locule appear to be constant for the genus *Sabicea*, whereas, only the indumentum (already noted under the text on indumentum)

and presumably the shape (Hallé, 1963) appears to be stable for some species. The fruits of Neotropical *Sabicea* are indehiscent berries, generally moderately fleshy with juicy pulp, non-fleshy or fleshy center and oblong, peltate and thin or thick placenta. They are subglobose, usually rounded, and rarely shallowly 5-lobed at outside and 4–6-locular with several to numerous seeds in each locule. The colour of fruits generally varies from pale to dark red or crimson (e.g., *Sabicea aspera*, *S. bariensis*, *S. brasiliensis*, *S. cinerea*, and *S. panamensis*), pinkish (e.g., *S. brasiliensis*, *S. cinerea*, *S. oblongifolia*, and *S. villosa*), purplish (e.g., *S. aspera*, *S. brasiliensis*, *S. cana*, *S. chocoana*, *S. tayloriae*, *S. pyramidalis*, and *S. velutina*), violet (e.g., *S. cana*, *S. oblongifolia*, and *S. velutina*), and maroon (e.g., *S. villosa*). The ripened fruits show a considerable range of variation in size (5–18 × 5–18 mm). In most species, fruit-length or diameter ranges between 5 and 12 mm, and in few species it extends up to 15 (e.g., *Sabicea cinerea*, *S. grisea*, and *S. villosa*) or 18 mm (e.g., *Sabicea brasiliensis*).

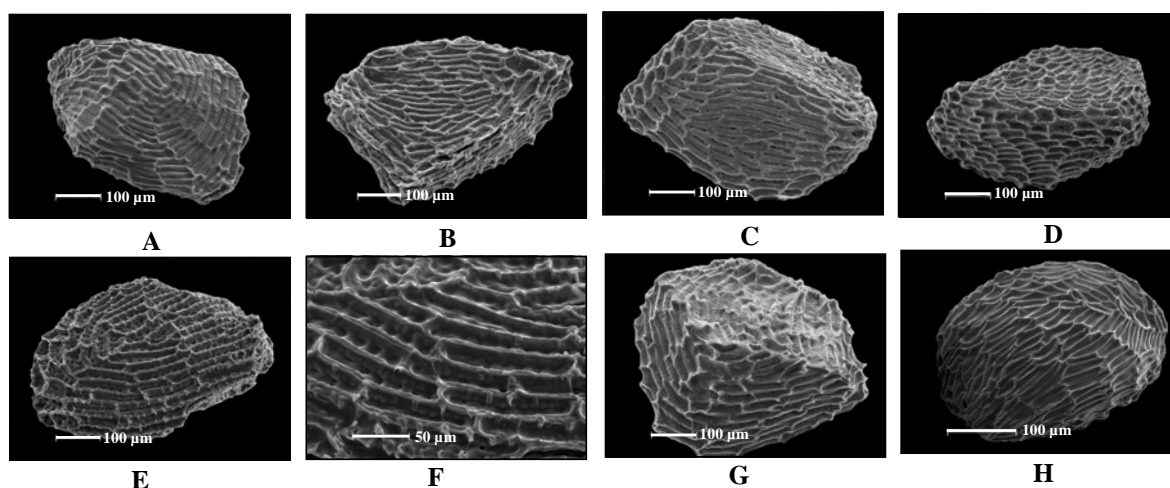


Figure 4. A–E. Elongated exotesta cells of Neotropical *Sabicea* seeds showing verrucate thickenings on radial wall with few large perforations (—F). —A. *Sabicea*. —B. *Sabicea*. —C. *Sabicea*. —D. *Sabicea*. —E. *Sabicea panamensis*. —F. *Sabicea amazonensis*. —F. *Sabicea traillii*. —F. *Sabicea oblongifolia*. —F. *Sabicea mattogrossensis*. —F. *Sabicea burchellii*. —F. *Sabicea novo-granatensis*.

The utility of seed characters is proven in tribal and generic classification of *Sabicea* and its associated genera. Bremekamp (1934, 1966) added “the very narrow testa cells” for recognizing his monogeneric tribe Sabiceae. Andersson (1996) distinguished the seeds of Sabiceae s.l. as irregularly angular to subglobose. Bremer and Thulin (1998) stressed on seed characters in recognizing their new genus *Tamridaea*. Dessein et al. (2001a) listed seed characters of *Sabicea* s.l. and its associated genera (e.g., *Hekistocarpa*, *Tamridaea*, and *Virectaria*), as valuable. The seeds of *Sabicea* are variously angular, usually irregularly or unevenly trigonal to tetragonal or flattened subglobose. Their exotesta cells are narrow and elongated (Fig. 4A–H), with few to many rounded or to suborbicular pits, and verrucose thickenings on radial wall (Fig. 4E, F). The ranges of variation in size of seeds (0.3–1 × 0.2–



0.8) seem very narrow and unstable for most of the species. A brownish orange color of seeds is constant for all species. Seed dispersal mechanism of *Sabicea* is very barely known. Solórzano et al. (2002) mentioned that the diaspore type of *Sabicea villosa* is sarcochores (fruits with soft and fleshy outer layers or seeds with arils) and dispersal syndrome is zoochory.

The fruits of Neotropical *Sabicea* are similar to those of African *Sabicea*, except few 2-locular and turbinate fruits (e.g., *Sabicea mildbraedii* and *S. nobilis*; Hallé, 1963, 1966) or 2–3-locular fruits (e.g., *S. angustifolia* and *S. marojejensis*, Razafimandimbison and Miller 1999). The seeds of African *Sabicea* are not known, except from Hallé (1966) and Dessein et al. (2001a). African and Neotropical *Sabicea* are similar in shape and size of seeds and type of exotesta cells including perforations on inner tangential wall. The seeds of *Sabicea* show marginal differences to those of *Hekistocarpa*, and perhaps very minor difference to *Virectaria*, and are identical with those of *Tamriddaea* (see Dessein et al., 2001a, b).

Karyology of *Sabicea* has not been investigated in this study. Kiehn (1995), based on the investigation in eight species of *Sabicea*, reported the basic chromosome numbers 9 and 11, and a ploidy level of 4x.

## MATERIALS AND METHODS

This revision is based on the study of herbarium specimens from B, BM, BR, BRLU, F, G, HUH, L, MO, M, NY, P, S, U, UPS, US, VEN, W, WAG, and WIS. All descriptions were originally generated from DELTA (Dallwitz et al., 1999). The length of stem was included when its measurements were available on the label information. The internodes, stipules, leaves, inflorescences, peduncles, bracts, pedicels, fruits, and seeds were measured in the dried specimens. The floral parts, when available, were measured in wet condition using boiled water. The flowers of few species, known only from the type specimen/s, were measured directly in the dried specimens, and sometimes in wet condition if these or their parts were available in the specimen folder. The trichomes, cilia and colleters were preferably measured in wet condition. The distribution maps are based on the longitude-latitude values either available on the specimen labels or estimated from the locality descriptions of the labels and Microsoft Encarta World Atlas 2001, and Global Gazetteer Version 2.1. All maps are originally created at the OMC input form using the decimal co-ordinates ([www.aquarius.geomar.de/www.aquarius.ifm-geomar.de](http://www.aquarius.geomar.de/www.aquarius.ifm-geomar.de)) and edited in CorelDRAW12. All illustrations are based on the observation of type specimen/s or non-type specimens mostly matching with the type/s. The line drawings of petiole anatomy and leaf epidermis, trichomes, floral parts, and seeds are done through using the camera lucida. In the illustration indicating the morphological features, mostly a tiny part of branchlets was preferred over relatively longer branchlets with many leaves or larger size of inflorescences and floral parts were prioritized over their natural size for showing the possible closer surface view with

indumentum, the most important source of characters for classifying the genus. Trichomes and seed morphology are studied through compound light microscope and SEM (Philips XL-30). The terminology for indumentum used in this study follows mostly Hewson (1988).

The key to all species is mostly based on the characters of indumentum, calyx lobes, and inflorescences and scantily on floral parts. Based on the availability of the specimens, the cited vouchers showing morphological variation are chosen for indicating the general distribution within the departments or states, as well as, within the country. Appendix I includes the list of all collections studied with their identification.

## TAXONOMY

**Sabicea** AUBL. Hist. Pl. Guiane, 1: 192. t, 75. Jun.-Dec. 1775. TYPE: *S. cinerea* Aubl.

*Cephaëlis* O. Swartz, Prodr. 3, 45 ('*Cephaelis*'). 20 Jun-29 Jul 1788 (*nom. cons.*).

TYPE: *C. muscosa* (N. J. Jacquin) O. Swartz (*Morinda muscosa* N. J. Jacquin) (*typ. cons.*).

*Paiva* Vellozo, Fl. Flum., 104. 7, Sep-28 Nov 1829 ('1825'). TYPE: *P. verticillata* Vellozo.

*Stipularia* P. Beauv., in Fl. Oware 2: 26 (1807). TYPE: *Stipularia africana* P. Beauv. (G!).

*Ecpoma* K. Schum. syn. nov., in Bot. Jahrb. 23: 430 (1896). TYPE: *Ecpoma apocynaceum* K. Schum. (K, photo!).

*Pseudosabicea* N. Hallé syn. nov., in Adansonia III (1963). TYPE: *Pseudosabicea nobilis* (R. Good) N. Hallé (P, photo!, K, photo!).

*Schizostigma* Arn. -- in Ann. Nat. Hist. iii. 20 (1839). TYPE: *Schizostigma hirsutum* Arn. (not designated).

Plants usually vines or lianas, sometimes suffruticose to (sub-)shrubs with pendent or spreading branches, occasionally herbs; stems 0.3–15 m, soft to woody, usually branched, erect to twining, scandent, sprawling or straggling. Terminal flowering branchlets 0.3–1.1 m, bark green to rusty brown, isolatedly to densely pilosulous to hirtellous, strigulose, puberulous or pubescent and/or arachnose to lanuginose, eventually glabrate, internodes 0.8–38 cm long. **Stipules of flowering branchlets** persistent, 2–20 × 2–15 mm, usually ovate to widely deltate, membranous to thickly papyraceous, narrowly lingulate or oblong to lanceolate or triangular, sometimes cordate or suborbicular, rarely elliptic, appressed and antrorse to reflexed or apically slightly curved, usually not lobed, apically sometimes bilobed, usually acuminate to (sub-)acute, sometimes obtuse to rounded, basally usually obtuse, sometimes truncate, occasionally cordate; marginally usually entire and complanate, occasionally widely denticulate to wavy or uneven, adaxially densely sericeous at the base, glabrous or isolatedly to sparsely puberulous to strigulose at upper or lower part or all over, abaxially isolatedly to densely strigulose or puberulous to pubescence, pilosulous or villosulous or arachnose to lanuginose at lower part to almost all over, (5–)9–18(–24)-veined; veins parallelodromous,

eventually reticulate, usually plain adaxially, slightly raised abaxially, colleters (2–)5–24(–28) along the adaxial base,  $0.3\text{--}1.8 \times 0.05\text{--}0.4$  mm, subulate to obconical or cylindrical to flattened, apically acute to obtuse. **Leaf blades of flowering branchlets** narrowly elliptic to obovate or oblong, ovate to lanceolate, occasionally oblanceolate, rarely (sub-)orbicular to obcordate, (0.7–)2–18(–20)  $\times$  (0.5–)1.5–11 cm, apically usually acute to acuminate, sometimes mucronate or obtuse, rarely shallowly obcordate, basally attenuate or cuneate to rounded, rarely oblique or (sub-)cordate, membranous to thickly papyraceous, margins usually entire and complanate, occasionally shallowly wavy or slightly curved to reflexed towards the abaxial surface, eciliate to ciliolate, adaxially usually light to dark green, isolatedly to densely hirtellous to pilosulous or villosulous or strigulose or puberulous to pubescence, occasionally floccose or discontinuously arachnose at lamina and secondary veins, usually densely so at costa, abaxially light green, isolatedly to densely pilosulous to villosulous or strigulose or arachnose to lanuginose, sometimes puberulous to pubescent at lamina, usually densely so at the secondary veins or costa; secondary veins (5–)8–16(–20) pairs, obscured to plain or slightly sunken adaxially and protruding abaxially, tertiary and quaternary veins usually obscured, rarely distinct adaxially, obscured to slightly prominulous abaxially; petioles (0.5–)2–40(–50)  $\times$  (0.8–)1–2 mm, indumentum same to those of branchlets or leaf costa. **Inflorescences** axillary, one to two per node, (1–)3–76(–88)-flowered, compact-verticillate or fascicled to glomerulate, capitate to umbellate or lax paniculate to thyrsoid cymes, sessile to pedunculate, (1–)1.5–8  $\times$  (0.7–)1.5–8 cm excluding peduncles; primary axis, when present, 1–50(–65) mm long; peduncles when present  $0.6\text{--}6.5 \times 0.5\text{--}0.3$  cm, indumentum including the orientation and straightness of trichomes nearly same to those of terminal flowering branchlets; bracts usually (sub-)involucrate or campanulate at budding, usually exinvolucrate and incompletely isolated into 2–5 parts or (sub-)involucrate, sometimes campanulate at flowering, usually thinly papyraceous; involucre (5–)8–25  $\times$  (4–)6–22 mm, 3–5-lobed, isolated parts 3–30  $\times$  3–16 mm, 0–6-lobed, lobes  $0.5\text{--}16(–27) \times 0.2\text{--}8(–12.5)$  mm, ovate to deltate or widely lanceolate to triangular or lingulate, occasionally elliptic or suborbicular, apically acute or acuminate to obtuse, margins entire or uneven to widely denticulate or serrulate, campanulate to slightly undulate or wavy, eciliate to ciliolate, involucre (3–)5–18(–24)-ribbed, usually parallelodromous at the base, eventually reticulate towards the apex, adaxially plain, abaxially plain to slightly prominulous, bracteoles 0–2 per flower or per pedicel or per inflorescence branch, exinvolucrate,  $0.5\text{--}12 \times 0.1\text{--}10$  mm, ovate to lanceolate, linear to lingulate, deltate to triangular, elliptic to oblanceolate or cymbiform, apically acute to acuminate or obtuse, usually not lobed, occasionally with 1–2 lateral lobes, margins entire to shallowly denticulate or serrulate, eciliate or ciliolate, (0–)1–9-ribbed, colleters usually present in bracts and bracteoles, 1–3 at each margin of adaxial base, occasionally along the adaxial base, rarely up to 30 along the adaxial base,  $(0.1\text{--})0.2\text{--}1 \times (0.03\text{--})0.1\text{--}0.2$  mm, obconical to cylindrical or subulate. **Flowers** homostylous, sometimes heterostylous, sessile

to pedicellate; pedicels, when present, (0.5–)1–15 × (0.3–)0.5–1.5 mm long, indumentum, including orientation and straightness of trichomes, almost as on terminal flowering branchlets; **calyx** campanulate to infundibuliform, usually green, (3–)4–5(–8)-lobed, tubes (0.2–)0.6–9(–11) × (0.6–)1.5–5(–6.5) mm, lobes (0.2–)1–11(–15) × (0.1–)0.5–4(–7) mm, antrorse to reflexed, usually lanceolate, elliptic to obovate, and linear to lingulate, sometimes ovate or triangular, occasionally deltate, rarely suborbicular, apically acute to acuminate or obtuse, basally truncate to (sub-)acute, margins entire to sparsely denticulate or serrulate or irregularly crenulate, cilia (0.05–)1.2–2(–3) mm long, appressed to erecto-patent, straight to flexuous, occasionally curled or tortuous, adaxially glabrous or the upper part of tubes and lobes or only the apex of lobes isolatedly to sparsely puberulous to strigulose or sericeous, abaxially usually isolatedly to densely pilosulous or hirtellous to strigulose or sericeous, sometimes puberulous to pubescent or arachnose to lanuginose, occasionally glabrescent, tubes 9–15-ribbed at the base, 15–21 in upper part, lobes (1–)3–5(–7)-ribbed, ribs usually distinct or occasionally obscured, parallelodromous, eventually occasionally interconnected, colleters usually 1–2(–4) in each sinus or 1–6.8 mm below each sinus inside the tube, (0.07–)0.4–1 × (0.03–)0.05–0.3 mm, subulate to obconical or cylindrical, apically acute to obtuse; **corolla** usually white to creamy, occasionally pink to purple, salverform or hypocrateriform, tubes (2.7–)3–22(–25) × (0.8–)1–3(–3.5) mm, lobes ovate to lanceolate or lingulate to elliptic, (0.8–)1.5–6(–7) × (0.6–)1–2.5(–3) mm, usually antrorse to spreaded, sometimes slightly recurved to reflexed, apically (sub-)acute, sometimes obtuse, basally truncate to obtuse, margins entire and complanate, sometimes slightly recurved, adaxially lobes usually papillate, densely moniliform at the orifice, gradually sparsely to isolatedly up to the upper lower part of the tubes, abaxially usually pilosulous to villosulous or hirtellous or sericeous to strigulose, occasionally arachnose to lanuginose or pubescent excluding the glabrous base or lower part (1–11 mm) of tubes; stamens ([4–]5[–10]) per flower, included in corolla tubes with or without protruding apices of anthers beyond the tube, attached to the corolla tubes at (1.8–)2–16(–20) mm from the base, anthers dorsifixed at the middle, usually oblong, creamy or whitish to grayish or dull-yellowish, rarely dull-brownish, (0.8–)1.5–3.5(–4) × 0.2–0.6 mm, apically (sub-)acute to obtuse, basally usually bifurcated with obtuse ends, occasionally with short tapering tails, each bifurcated part 0.2–1.2 × 0.06–0.3 mm, free part of filament 0.07–1 × 0.06–0.2; style (1.5–)2–16(–20) × 0.07–0.4 mm long, included in corolla tube, whitish to yellowish, filiform, stigmatic lobes 4–5(–10), (0.8–)1.1–4(–5) × 0.2–0.4 mm, narrowly oblanceolate or elliptic to filiform or oblong, occasionally narrowly lanceolate, apically obtuse to (sub-)acute, completely included in or apically exerted from corolla tubes; ovaries ellipsoid to subglobose, (1–)1.5–2.1(–3) × (0.8–)1.2–2.5 mm, abaxially evenly or unevenly rounded to shallowly 4–5-lobed, usually densely, occasionally isolatedly hirtellous to pilosulous or strigulose to pubescence, sometimes arachnose to lanuginose, 4–5(–7)-locular, each locule 0.5–1.5(–2.5) × 0.2–0.1(–1.5) mm, stalk of placenta 0.1–0.4 × 0.02–0.2 mm, wall of ovary incl. hypanthium

0.04–0.9 mm thick, partition walls of locules 0.02–0.2 mm. Fruits indehiscent berries, ellipsoid to turbinate or subglobose, not ripened fruits 3–6 × 3–6 mm, ripened fruits 5–18 × 5–18 mm, red to red-purple or dull-rose to dark violet, black or maroon, usually rounded, occasionally shallowly 4–5-lobed, usually covered with indumentum similar to those of hypanthia but less densely, sometimes glabrescent; seeds variously angular, 0.3–1 × 0.2–0.8 mm, brownish orange, exotesta cells narrow and elongated, with few to many rounded pits, radial wall with verrucose thickenings.

*Schwenkfelda* Schreb., (Gen. Pl 1:123, 1789) was described based on *Sabicea* Aubl. On the other hand, both of *Schwenkfeldia* Wild. (Sp. Pl, 4 [Post reichardianum Quinta]: 982, 1797) and *Schwenkfelda* Sw. (Fl. Ind. Occid. 1: 448-452, 1797) were described based on *Schwenkfelda* Schreb., due to which these names are considered as the illegitimate names. Aublet (1775) described the genus *Sabicea* with two species (*Sabicea aspera* and *S. cinerea*) without designating any type. Swartz (1797) cited “Mufeo Banks, in fepibus Cayennae, Guianae, Aublet von Rohr.” as only one specimen with *Schwenkfelda cinerea* (Aubl.) Sw., which is an illegitimate name, although correlated to *Sabicea cinerea* Aubl. In North American Flora, *Sabicea cinerea* Aubl. is designated as the lectotype for the genus (by P. C. Standley, N. Amer. Fl. 32: 148. 10 May 1921; Index nominum genericorum).

The genus *Sabicea* of the Neotropics predominantly comprises vines, lianas or shrubs with lianescent branches, occasionally erect herbs to suffruticose or (sub-)shrubs. They can also be recognized by the combination of their usually opposite decussate, petiolate, entire, narrowly ovate to elliptic leaves, axillary, verticillate to laxly paniculate or thyrsoid inflorescences subtended by exinvolucrate to involucrate bracts, valvate aestivation, shortly campanulate to infundibuliform calyx with usually 4–5 lobes, hypocrateriform, usually white to occasionally pink or purple corollas with short or long tubes, (sub-)globose- to ellipsoid- ovary with usually 4–5 locules, ripened fruits usually red-purple or dull-rose to dark violet ripened fruits with numerous and variously angular seeds. Their terminal flowering branchlets, stipules, leaves and almost all parts of inflorescences are covered with appressed to erect and straight to tortuous trichomes and the margins of their stipules, leaves, bracts, and calyces are usually ciliate. They have few to many, subulate or bluntly obconical colleters along the adaxial base of stipules, usually 2–6 at the margins of adaxial base or occasionally few or many along the adaxial base of bracts, and 1–2 in or below each sinus of calyx.

Neotropical *Sabicea* was often confused with *Amphidasya* Standl. until its separation from *Sabicea* by Standley (1936a). The Neotropical *Sabicea* are readily distinguishable from *Amphidasya* by their usually entire, only occasionally apically bilobed stipules, axillary inflorescences, and its entire, smooth or eciliate corolla lobes (in contrast to deeply lacinate to fimbriate, pseudoaxillary or lateral inflorescences, multicellular, tuberculate to filamentous appendaged margins of *Amphidasya*; Steyermark, 1972, Taylor & Clark, 2001).

KEY TO THE NEOTROPICAL SPECIES OF *SABICEA*

- 1a. Curled to tortuous trichomes entirely absent at the upper surface of leaves, or rarely isolatedly present at the costa (e.g., *Sabicea boliviensis*, *S. cuneata*, *S. grisea*)
- 2a. Calyces campanulate, calyx tubes generally 0.3–3 mm long, with L/D 0.2–1; colleters located in sinus or at inner tube surface near the sinus, not associated with trichomes; inflorescences thyrsoïd, paniculate, umbellate, capitate, fascicled, verticillate or glomerulate
- 3a. Inflorescences thyrsoïd to paniculate; if umbellate, then curled to tortuous trichomes present or calyx lobes lanceolate to narrowly lingulate, recurved to reflexed and the abaxial trichomes of corolla appressed; flowers always pedicellate
- 4a. Curled to tortuous trichomes absent or isolatedly to sparsely and partially present, straight trichomes always present over the whole lower surface of leaves
- 5a. Curled to tortuous trichomes absent; inflorescences lax, calyx lobes antrorse, elliptic to widely lingulate or inflorescences lax to moderately lax, calyx lobes recurved to reflexed, rarely antrorse; calyx lobes if antrorse then < 4 mm long
- 6a. Trichomes appressed at lower leaf surface and outer surface of inflorescences including hypanthia
- 7a. Inflorescences elongated- and lax-thyrsoïd; bracts subinvolucrate; calyx lobes elliptic to lingulate, antrorse; bracts and calyx lobes apically subacute to obtuse  
 .....**37. *S. thyrsoïflora***
- 7b. Inflorescences lax-thyrsoïd to compact-paniculate, rarely umbellate; bracts usually exinvolucrate; calyx lobes lanceolate to linear or ovate to triangular, usually recurved to reflexed; bracts and calyx lobes apically acute to acuminate
- 8a. Lateral branches usually > 6 mm long and not more than 7-flowered; inflorescences never compact-paniculate or umbellate; corolla tubes 4.5–5 mm long  
 .....**33. *S. pyramidalis***
- 8b. Lateral branches usually < 6 mm long and always more than 7-flowered or not more than 7-flowered but inflorescences compact-paniculate or rarely umbellate

- 9a. Inflorescences compact-paniculate to elongated-thyrsoid; calyx lobes lanceolate to lingulate, ovate to triangular, straightened, recurved to reflexed, sometimes antrorse; corolla tubes usually 7–14 mm long.....**30. *S. panamensis***
- 9b. Inflorescences compact-paniculate; calyx lobes narrowly lanceolate to linear, shallowly bent and divaricately spreading; corolla tubes usually 5–6.5 mm long.....**41. *S. umbellata***
- 6b. Trichomes erecto-patent at lower leaf surface and outer surface of inflorescences, appressed or erecto-patent at hypanthia
- 10a. Trichomes generally uniform; stipules apically obtuse to rounded; stipules, bracts and calyces adaxially apically covered with trichomes; calyx lobes elliptic to lingulate or narrowly ovate, reflexed; abaxial trichomes of corolla [0.07–]0.2–0.8 mm long  
.....**12. *S. chocoana***
- 10b. Trichomes generally of several kinds; stipules apically acute to acuminate; stipules, bracts and calyces adaxially apically glabrous; calyx lobes lanceolate to lingulate or linear, antrorse to spreading; abaxial trichomes of corolla 0.9–2.5 mm long
- 11a. Petioles 2–4 cm long, lamina 13–17.5 × [2–]5–9 cm; peduncles 1.2–4.5 cm long, excluding peduncle 3–6 × 2–6 cm with 0.5–3.5 cm long primary axis; calyx lobes lanceolate to lingulate  
.....**14. *S. cochabambensis***
- 11b. Petioles 0.4–0.7 cm long, lamina 7–12 × 2.5–4.3 cm; peduncles 0.4–0.7 cm long, excluding peduncle 2–2.5 × 2 cm, with 0.2–0.4 cm long primary axis; calyx lobes narrowly lanceolate to linear.....**32. *S. pearcei***
- 5b. Curled to tortuous trichomes absent or present at lower leaf surface; inflorescences moderately lax, calyx lobes divaricately spreading, triangular to ovate or inflorescences compact, calyx lobes antrorse; calyx lobes if antrorse then ≥ 6 mm long
- 12a. Inflorescences moderately lax- to compact-paniculate or verticillate; calyx tubes 2–3 mm long, lobes [0.7–]1.5–6

- mm long, triangular or ovate to widely lanceolate, colleters located inside the tubes below the sinus
- 13a. Inflorescences moderately lax- to compact-paniculate; calyx lobes usually divaricately spreading; abaxial trichomes of corolla tubes appressed.....**3. *S. bariensis***
- 13b. Inflorescences verticillate; calyx lobes antrorse to gently reflexed, not divaricately spreading; abaxial trichomes of corolla tubes erecto-patent.....**31. *S. parva***
- 12b. Inflorescences compact-paniculate to umbellate; calyx tubes 0.6–1.7 mm long, lobes  $\geq 6$  mm long, widely linear to narrowly lanceolate or lingulate to elliptic, colleters located in the sinus
- 14a. Straight trichomes of lower leaf and outer corolla tube surface erecto-patent; calyx lobes 8–15 mm long, adaxially isolatedly to sparsely covered with straight trichomes.....**11. *S. chiapensis***
- 14b. Straight trichomes of lower leaf and outer corolla tube surface appressed; calyx lobes 6–7.7 mm long, glabrous inside.....**24. *S. mexicana***
- 4b. Curled to tortuous trichomes continuously and usually densely present over the whole lower surface of leaves, straight trichomes usually distinct on the costa and secondary veins, distinct or indistinct in between
- 15a. Curled to tortuous trichomes of lower lamina surface moderately dense and diffused; straight trichomes erecto-patent; inflorescences thyrsoid with compact lateral axes or compact-paniculate to umbellate; corolla tubes 3–4.8 mm long
- 16a. Stipules 7–10  $\times$  6–11 mm; inflorescences cylindrical to pyramidal-thyrsoid; bracts usually subinvolucrate with 3.5–16 mm long lobes; > 4.5 mm long calyx lobes present.....**34. *S. subinvolucrata***
- 16b. Stipules 5–8  $\times$  4–6 mm; inflorescences umbellate; bracts exinvolucrate with 2–3.5 mm long lobes; > 4.5 mm long calyx lobes absent.....**16. *S. erecta***
- 15b. Curled and tortuous trichomes of lower lamina surface dense and matted; straight trichomes appressed or erecto-patent; inflorescences moderately lax- to compact-paniculate or umbellate; corolla tubes 6–11.7 mm long



- 17a. Adaxially the upper part of stipules and bracts covered with trichomes; bracts apically acute to acuminate; calyx lobes narrowly linear to lanceolate, apically acute to acuminate
- 18a. Straight trichomes appressed at upper surface and secondary veins of lower surface of leaves, and outer corolla tube surface; calyx lobes adaxially apically glabrate; inflorescences moderately lax-paniculate.....**15. *S. cuneata***
- 18b. Straight trichomes erecto-patent at upper surface and the secondary veins of lower surface of leaves and outer corolla tube surface; calyx lobes adaxially apically covered with trichomes; inflorescences compact-umbellate.....**4. *S. boliviensis***
- 17b. Adaxially stipules glabrous, bracts glabrous or covered with trichomes on the upper part; bracts apically acute to obtuse; calyx lobes narrowly lingulate or elliptic to rounded, apically obtuse to rounded or (sub-)acute
- 19a. Inflorescences moderately lax- to compact-paniculate; calyx lobes usually < 2.5 mm long with L/W 1–2 and apically obtuse to rounded; curled or tortuous trichomes present at peduncles, abaxial surface of bracts, and pedicels
- 20a. Trichomes exclusively curled to tortuous at abaxial surface of stipules, bracts, hypanthia and calyces; petioles 5–10 mm long; calyx lobes ciliolate.....**26. *S. morillorum***
- 20b. Trichomes straight, with or without associated curled trichomes at abaxial surface of stipules, bracts, hypanthium and calyces; petioles 13–36 mm long; calyx lobes eciliate.....**8. *S. calophylla***
- 19b. Inflorescences compact-paniculate to umbellate; calyx lobes usually >2.5 mm long with L/W 2–3 and apically (sub-)acute; curled or tortuous trichomes absent or present at peduncles, outer surface of bracts and pedicels
- 21a. Calyx lobes widely linear to elliptic, shallowly bent, usually 6–9 mm long, adaxially

- glabrous; curled or tortuous trichomes present at peduncles, out side of bracts, and pedicels.....**21. *S. liedea***
- 21b. Calyx lobes lingulate to ovate, straightened, usually 2.5–6 mm long, tubes adaxially with trichomes at the base or glabrescent; curled or tortuous trichome absent at peduncles, outside of bracts, and pedicels.....**5. *S. boyacana***
- 3b. Inflorescences umbellate, capitate, fascicled, verticillate or glomerulate; rarely compact-paniculate when the abaxial trichomes of corolla erecto-patent; flowers pedicellate or sessile
- 22a. Inflorescences moderately lax- to compact-umbellate, curled to tortuous trichomes absent, calyx lobes usually elliptic to lingulate, antrorse to moderately spreading
- 23a. Inflorescences variously branched; trichomes erecto-patent at lower leaf surface, and outer surface of inflorescences excluding hypanthia; calyx lobes larger than 2.5–5.5 × 0.5–1.8 mm absent, markedly unequal; abaxial trichomes of corolla < 0.6 mm long.....**22. *S. liesneri***
- 23b. Inflorescences unbranched; trichomes appressed or erecto-patent at lower leaf surface, and outer surface of inflorescences excluding hypanthia; calyx lobes larger than 2.5–5.5 × 0.5–1.8 mm present, usually equal; abaxial trichomes of corolla > 0.6 mm long
- 24a. Trichomes appressed at lower leaf surface, and outer surface of inflorescences including hypanthia; peduncles, pedicels and hypanthia eventually glabrate; stipules, bracts and calyces adaxially glabrous excluding the base.....**23. *S. mattogrossensis***
- 24b. Trichomes erecto-patent at lower leaf surface, and outer surface of inflorescences excluding hypanthia; peduncles, pedicels and hypanthia constantly covered with trichomes; stipules, bracts and calyces adaxially apically covered with trichomes or glabrous
- 25a. Stipules not wider than long, basally obtuse, adaxially trichomes present at the apex; bracts exinvolucrate with 1–3 colleters at the margins of adaxial base; calyx lobes apically acute to acuminate, 1–2 colleters in each sinus

- .....**28. *S. novo-granatensis***
- 25b. Stipules wider than long, basally obtuse to gently cordate, adaxially glabrous at the upper part; bracts (sub-)involucrate, adaxially with numerous colleters along the base; calyx lobes apically obtuse to rounded, 2–4 colleters in each sinus
- .....**18. *S. hirta***
- 22b. Inflorescences compact-umbellate, capitate, fascicled, verticillate or glomerulate, rarely compact-paniculate; curled to tortuous trichomes absent or present; calyx lobes usually lanceolate to triangular or linear to narrowly elliptic to lingulate, antrorse to reflexed
- 26a. Curled to tortuous trichomes absent or indistinct
- 27a. Calyx lobes widely lanceolate to narrowly elliptic or lingulate, antrorse to spreading, usually 5–11 mm long, bracts and calyx lobes adaxially apically covered with trichomes; inflorescences capitate to compact-fasciculate
- 28a. Stipules [3–]10–14 × [3–]7–11 mm, trichomes not uniform, 0.8–1.3 mm long trichomes commonly present on upper leaf surface; calyx tubes 0.2–1.2 mm long, corolla tubes 6–11.5 mm long, external trichomes usually 0.7–1.1 mm long, appressed.....**7. *S. burchellii***
- 28b. Stipules 3.5–4.2 × 2.6 mm, trichomes uniform, 0.8–1.3 mm long trichomes absent from upper leaf surfaces; calyx tubes 1.5–1.8 mm long, corolla tubes 12–13 mm long, abaxial trichomes usually 1.2–1.5 mm long and erect.....**27. *S. noelii***
- 27b. Calyx lobes narrowly lanceolate, usually reflexed and < 5 mm long; bracts and calyx lobes adaxially glabrous; inflorescences non-capitate or loosely fasciculate
- 29a. Corolla tubes 8–12 mm long, abaxial trichomes erecto-patent; inflorescences loose-fasciculate to verticillate, umbellate, rarely compact-paniculate
- .....**2. *S. aspera***
- 29b. Corolla tubes 3.5–5[–7] mm long, abaxial

trichomes appressed; inflorescences verticillate

.....**43. *S. villosa***

26b. Curled to tortuous trichomes manifestly present and distinct at least all over the lower leaf surfaces

30a. Inflorescences capitate to fasciculate; curled to tortuous trichomes absent or present at outer surface of stipules, bracts and calyces; calyx lobes antrorse to spreading

31a. Petioles < 5 mm long; lower leaf surface densely covered with long and straight trichomes and isolatedly to sparsely with curled to tortuous trichomes; calyx lobes marginally denticulate, narrowly elliptic to lingulate or lanceolate

.....**19. *S. humilis***

31b. Petioles usually > 5 mm long; lower leaf surface densely and compactly covered with curled to tortuous trichomes only or in addition isolatedly to sparsely with short straight trichomes; calyx lobes marginally entire, linear to deltate

32a. Inflorescences usually capitate; calyx lobes triangular to ovate or lingulate to deltate, usually one lobe per calyx is smaller; corolla tubes 3.5–6.2 mm, lobes 1.8–2.5 mm long, abaxial trichomes curled to tortuous and straight.....**40. *S. tayloriae***

32b. Inflorescences compact-fasciculate; calyx lobes linear to narrowly lingulate, elliptic, lanceolate to triangular, almost equal; corolla tubes  $\geq 8$  or 9 mm long, lobes  $\geq 2.5$  mm long, trichomes straight or straight to curled and tortuous

33a. Upper leaf surfaces non-velvety, straight trichomes present at lower leaf surfaces; calyx lobes usually linear or narrowly lingulate to elliptic or lanceolate, apically (sub-)acute to obtuse; abaxial trichomes of corolla erecto-patent.....**17. *S. grisea***

33b. Upper leaf surfaces moderately

- velvety, straight trichomes absent at lower leaf surfaces; calyx lobes narrowly lanceolate to triangular, apically acute to acuminate; abaxial trichomes of corolla appressed, flexuous to curled.....**42. *S. velutina***
- 30b. Inflorescences verticillate or verticillate to glomerulate; curled to tortuous trichomes absent at outer surface of stipules, bracts and calyces; calyx lobes antrorse to spreading or reflexed
- 34a. Abaxial indumentum of corolla erecto-patent; corolla tubes 8–12[–16] mm long; calyx lobes narrowly triangular to lanceolate; stipules apically acute to acuminate; rusty brown to maroon indumentum present, indumentum of lower leaf surface.....**29. *S. oblongifolia***
- 34b. Abaxial indumentum of corolla appressed; corolla tubes 3–6[–7] mm long; calyx lobes lanceolate to lingulate; stipules apically (sub-)acute to obtuse; rusty brown to maroon indumentum absent, indumentum of lower leaf surfaces matted.....**9. *S. camporum***
- 2b. Calyces infundibuliform, calyx tubes generally 3–11 mm long, with L/D1.5–2.2; colleters located near the middle of inner tube surface below the sinus, associated with trichomes; inflorescences fascicled to capitate (*S. traillii*) or only fascicled
- 35a. Curled and tortuous trichomes absent; indumentum of lower surface of leaves, flowering branchlets and outer surface of bracts and calyces composed of straight trichomes
- 36a. Leaf blades shorter than 3 mm present; trichomes appressed at lower leaf surfaces, mostly 0.7–1.5 mm long; corolla tubes usually 9–14 mm long.....**39. *S. traillii***
- 36b. Leaf blades shorter than 3 mm absent; trichomes erecto-patent at lower leaf surfaces, usually 1.6–2.5 mm long; corolla tubes 17–22 mm long.....**35. *S. surinamensis***
- 35b. Curled and tortuous trichomes densely present at the lower leaf surfaces, at the flowering branchlets, and outer surface of bracts and calyces in association with straight trichomes
- 37a. Trichomes of upper leaf surfaces 1.2–3 mm long; inflorescences

- generally 2.5–3.5 mm long; curled to tortuous trichomes absent at outer stipule surface; indumentum of upper adaxial calyx surfaces non-shaggy; corolla tubes 14–22[–25] mm long  
 .....1. *S. amazonensis*
- 37b. Trichomes of upper leaf surfaces 0.1–1.5 mm long; inflorescences generally 1.5–2.3 mm long; curled to tortuous trichomes present at outer stipule surface; indumentum of upper adaxial calyx surface shaggy; corolla tubes 7–14[–15] mm long  
 .....25. *S. mollissima*
- 1b. Curled to tortuous trichomes present at entire upper surface of leaves, sparsely to densely on lamina and always densely at the costa
- 38a. Inflorescences umbellate; straight trichomes manifestly present at lower leaf surface; calyx lobes lanceolate or elliptic to lingulate; when calyx lobes lingulate then flowers shortly pedicillate and corolla tubes < 9 mm long
- 39a. Trichomes of upper leaf surface both curled to tortuous and straight; calyx lobes lanceolate, [1.5–]2.5–5 × 0.4–1.2 mm, marginally denticulate, corolla tubes 4–5 mm and lobes 1.8–2.1 mm long, abaxial trichomes erecto-patent.....20. *S. klugii*
- 39b. Trichomes of upper leaf surface exclusively curled to tortuous; calyx lobes elliptic to lingulate, 5.9–9.4 × 1.8–2.9 mm, marginally entire, corolla tubes 8–8.6 mm and lobes 2.9–3.1 mm long, abaxial trichomes appressed  
 .....40. *S. trianae*
- 38b. Inflorescences compact-fasciculate, rarely capitate (*S. cana*); straight trichomes usually absent from lower leaf surface; calyx lobes triangular or ovate to lingulate or deltate to ovate or lingulate; when calyx lobes lingulate then flowers sessile or corolla tubes ≥ 9 mm long
- 40a. Plants erect herbs; trichomes of upper leaf surfaces curled to tortuous and straight to flexuous; petioles < 8 mm long; curled to tortuous trichomes present at outer corolla surface.....6. *S. brasiliensis*
- 40b. Plants vines or lianas; trichomes of upper leaf surfaces exclusively curled to tortuous, rarely isolatedly associated with straight trichomes (*S. cinerea*); petioles < 8 mm long only when curled to tortuous trichomes absent at outer corolla surface

- 41a. Calyx lobes usually 1.1–3 mm long, triangular to ovate or shortly lingulate; corolla tubes 3.4–5.5[–6.5] mm, abaxial trichomes curled and tortuous; upper part of style and stigmas covered with straight to curled trichomes.....**10. *S. cana***
- 41b. Calyx lobes usually > 3 mm long, widely linear, narrowly elliptic or lanceolate; corolla tubes > 6.5 mm long, abaxial trichomes straight; upper part of style and stigmas glabrous
- 42a. Calyx lobes oblong to lanceolate or narrowly elliptic, apically (sub-)acute to obtuse, corolla lobes > 3 mm long, abaxial trichomes erecto-patent.....**13. *S. cinerea***
- 42b. Calyx lobes narrowly lanceolate, apically acuminate, corolla lobes < 3 mm long, abaxial trichomes (sub-)appressed...**38. *S. tillettii***

**1. *Sabicea amazonensis*** Wernham, Monogr. *Sabicea* 47, t 5, f. 3, 4. 1914. TYPE. Brasil. Amazonas: Rio Negro, *E. Ule* 5117 (lectotype, designated here, G!; duplicate, K, B, not seen, L!, photo NY!), no date. Figure 5A–0.

Spreading or climbing woody shrubs or vines; terminal flowering branchlets sparsely pilosulous to hirsutulous, sparsely to densely arachnose, trichomes 1.5–2 mm long. *Stipules* (6–)8–12(–15) × (5–)8–12(–14) mm, antrorse to recurved or reflexed, ovate to widely ovate or deltate, rarely bifid, apically usually (sub-)acute to acuminate, ciliate with 1.7–2.3 mm long cilia, adaxially glabrous excluding the basal part, abaxially densely villosulous to pilosulous almost all over, trichomes (0.2–)1.4–2.3 mm long, 9–12(–14)-veined, colleters 3–9, 0.5–1.5 mm long. *Leaf blades* elliptic to widely lanceolate or oblong, (2–)5.4–10(–13.5) × (1.5–)2.2–5(–7.5) cm, apically usually acute to acuminate, occasionally mucronate, membranous or papyraceous, cilia 0.6–2.2 mm long; adaxially sparsely to densely pilosulous or villosulous, costa additionally sparsely puberulous, trichomes (1.2–)1.8–3 mm long; abaxially densely pilosulous to villosulous, and arachnose or lanate to lanuginose, trichomes 1.5–2.5 mm long, secondary veins 11–15 pairs, obscured to plain or slightly sunken adaxially and protruding abaxially, tertiary veins usually obscured, occasionally distinct abaxially; *petioles* 5–12(–18) mm long, densely pilosulous to hirtellous, and arachnose, trichomes 1.8–2.3 mm long. *Inflorescences* one per node, 3–5(–6)-flowered, compact-fascicled, (2–)2.5–3.5 × 1–2(–3) cm; *peduncles* 0(–1.5) mm long; *bracts* (sub-)involucrate or campanulate, 10–18 × (8–)11–22 mm,

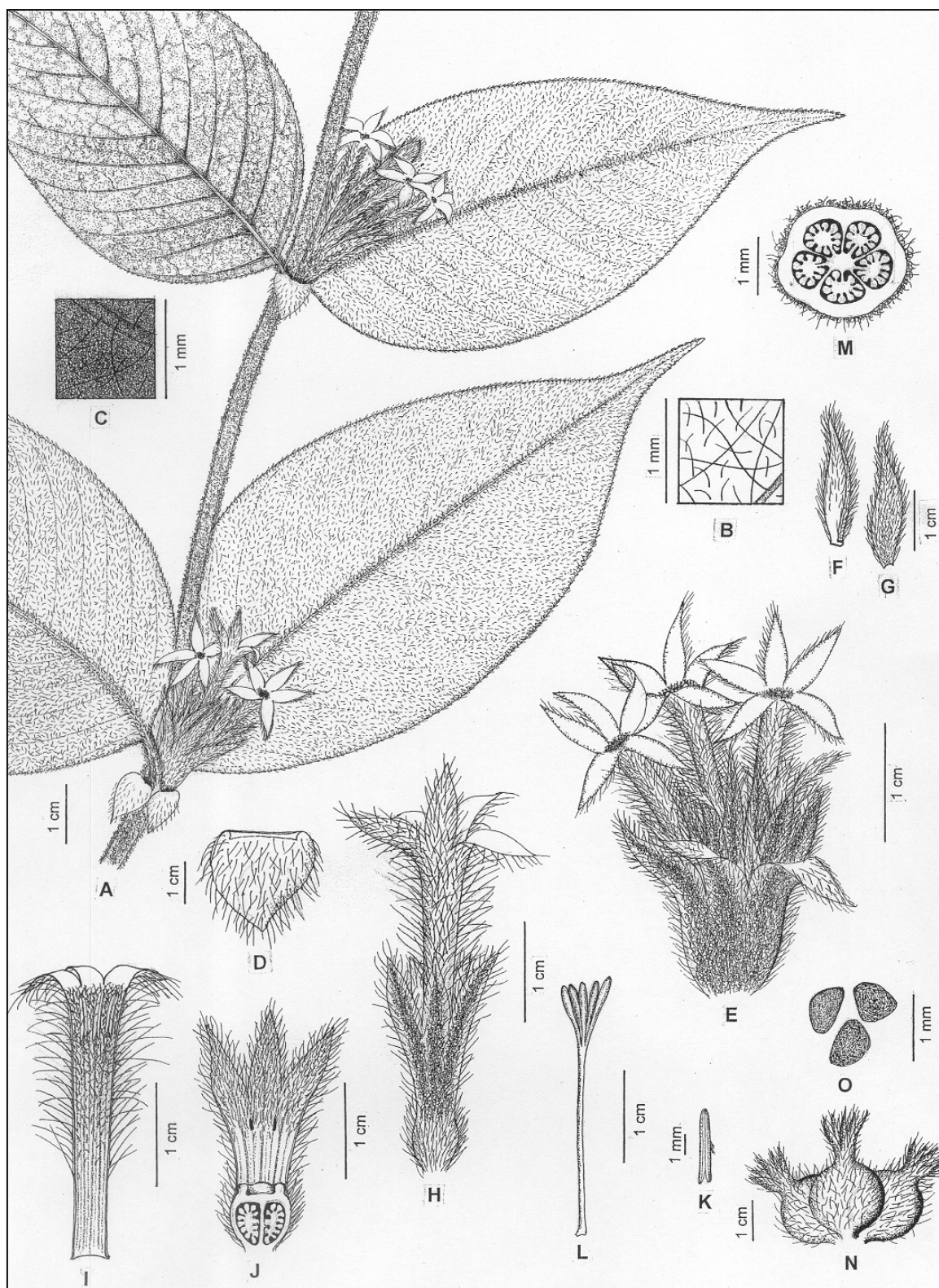


Figure 5. A–N. *Sabicea amazonensis*. —A. Part of flowering branchlet. —B. Indumentum of upper surface of leaf. —C. Indumentum of lower surface of leaf. —D. Outer surface view of stipule. —E. Inflorescence. —F. Internal surface view of bracteole. —G. External surface view of bracteole. —H. Flower. —I. Internal surface of corolla. —J. Longitudinal section of calyx and ovary. —K. Style and stigmata. —L. Anther. —M. Transversal section of ovary. N. Fruits.



3–5-lobed, lobes 1–8 × 1–6 mm, ovate to widely ovate, apically acute or acuminate, margins entire or uneven to slightly undulate or denticulate and ciliate to ciliate with 0.3–2 mm long cilia, adaxially the apices or upper parts sparsely strigulose to pilosulous, abaxially usually densely pilosulous to hirtellous almost all over, the middle and upper part sparsely to densely arachnose, 15–18-ribbed, bracteoles 5–10 × 1–2.5 mm, narrowly ovate to lanceolate, apically acute or acuminate. *Flowers* (sub-)sessile; *pedicels* 0–0.5 mm long; *calyx* elongated-infundibuliform, 5-lobed, tubes (4–)5–11 × 3–5 mm, lobes (2–)4–9(–11) × 2–2.5(–4) mm, antrorse, lanceolate to triangular, apically acute to acuminate, margins entire to irregularly slightly wavy and ciliate with (0.3–)1.2–2 mm long cilia, adaxially at least upper part sparsely to densely strigulose, lower part glabrous, abaxially densely to sparsely pilosulous to hirtellous or strigulose, sparsely to densely arachnose at usually at the middle, trichomes 1.5–2.5(–3) mm long, tubes 12–14-ribbed, ribs obscured or distinct adaxially, distinct or plain abaxially, colleters 5, (2.1–)2.6–5.9 mm below the sinus, (0.1–)0.4–0.6 mm long; *corolla* salverform or hypocrateriform, tubes 14–22(–25) × 2–2.5 mm, lobes (3–)4–5 × (1–)2–2.5 mm, widely lanceolate to narrowly ovate, apically acute, adaxially the indumentum of orifice extends up to 7–9 mm of tubes, abaxially pilosulous to hirsutulous and glabrous up to 5–11 mm of the lower part, trichomes (0.3–)1–3.6 mm long; *stamens* 5 per flower, attached to corolla tube at (16–)18–20 mm from the base, anthers 3–4 × 0.4–0.5 mm; *styles* 19–20 mm long, stigmatic lobes 4–5 × 0.2–0.4 mm; *ovaries* 1.8–2.5 × 1.8–2.5 mm, abaxially shallowly 5-lobed or uneven, 5-locular, each locule 0.9–2 × 0.4–1.5 mm. *Fruits* red to pink, 8–11 × 7–10 mm when mature, abaxially isolatedly to sparsely pilosulous to hirsutulous, and arachnose; *seeds* 0.5–0.8 × 0.5–0.8 mm.

*Phenology, distribution and habitat.* Collected in flower and fruit in December or January to October. *Sabicea amazonensis* is widespread in the areas along the upper Amazon River and its tributaries, mostly belonging to the Amazonas State of Brazil, Amazon and Vaupes Departments of Colombia and Amazonas State of Venezuela. This species is reported mostly from forest or open areas besides the rivers and roads, occasionally from cultivated areas. It has been found in clay to sandy soil; 20–250 m (Fig. 6).

*Discussion.* *Sabicea amazonensis* is characterized by the combination of its subinvolucrate fascicled inflorescences, arachnose flowering branchlets, non-arachnose stipules, adaxially pilosulous to villosulous and abaxially densely arachnoid indumenta of leaf blades, elongated-infundibuliform calyces, long (usually 4–9 mm) and lanceolate to triangular calyx lobes, long (14–22[–25] mm) corolla tubes, erecto-patent cilia and external trichomes of bracts and calyces, erecto-patent external trichomes of corolla tubes, non-shaggy indumentum of upper adaxial surface of calyces, and colleters located near the middle or basal part inside the calyx tubes below the sinus (Fig. 5A–H, J). In the original description of

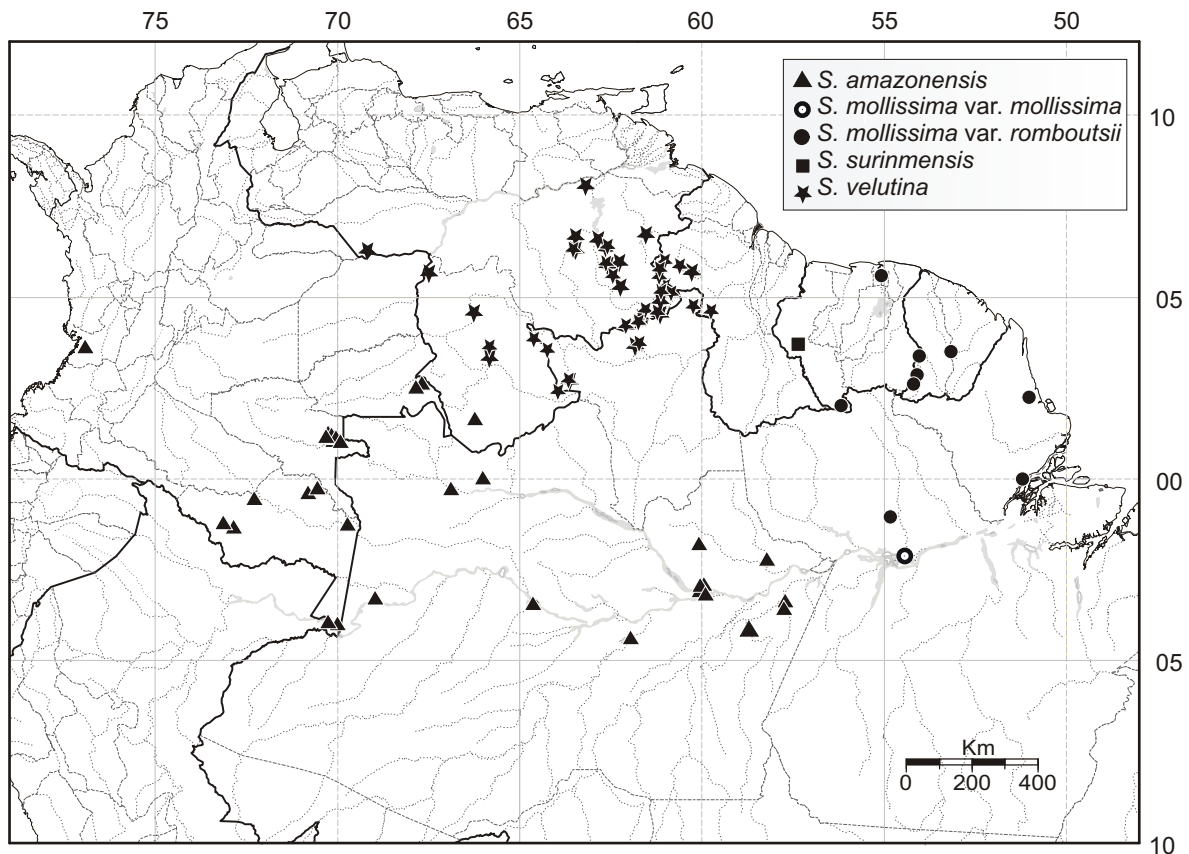


Figure 6. Map of the central and northern South America (in part), showing the distribution of the *Sabicea amazonensis*, *S. mollissima*, *S. surinamensis*, and *S. velutina*.

*Sabicea amazonensis*, Wernham (1914) mentioned that this species is distinct from its allies in habit, compact subinvolucrate inflorescences, and large, far exerted corolla. *Sabicea mollissima*, most closely allied to *S. amazonensis*, has the same habit and inflorescences but less exerted corolla. *Sabicea amazonensis* differs from *S. mollissima* by its longer corolla (14-22[-25] mm in contrast to (7-10[-14] mm) and accordingly longer inflorescences (usually 2.5-3.5 cm contrast to 1.5-2.3 cm), pilosulous to villosulous adaxial leaf blades, abaxially non-arachnose stipules and non-arachnose or glabrous areas near the margins of bracts and calyces, and non-shaggy indumentum at upper adaxial surface of calyces which usually doesn't cover the colleters (Fig. J). *Sabicea amazonensis* can be easily set apart from its closely related *S. cinerea* by its adaxially pilosulous to villosulous leaf blades, infundibuliform calyces with longer ([4-]5-11 mm in contrast to 1.2-3[-4] mm) calyx tubes that are adaxially covered with indumentum, abaxially pilosulous to hirtellous calyx lpbes, and location of colleters near the middle or basal part inside the calyx tubes. *Sabicea amazonensis* seems close also to *S. grisea* from which it differs by its pilosulous to villosulous indumentum of adaxial leaf blades comprised of apparently longer trichomes ([1.2-]1.8-3 mm in contrast to 0.1-1.1 mm), widely lanceolate calyx lobes, longer ([4-]5-11 mm in contrast to 1-3 mm) calyx tubes adaxially covered with indumentum and collator's location inside the calyx tube, much below the sinus.

Among Neotropical *Sabicea*, only *Sabicea amazonensis*, *S. mollissima*, *S. surinamensis* and *S. traillii* have elongated-infundibuliform calyx tubes. Yet, *Sabicea amazonensis* can easily be distinguished from *S. surinamensis* and *S. traillii* by their arachnose indumentum on branchlets, lower leaf surfaces, and on the abaxial side of bracts and calyces. *Schultes & Cabrera 12594* (F, US) and *Hill 13010* (NY) have exceptionally short (2–5 mm long) calyx lobes and tubes (4–5 mm long) but their other characters support their inclusion in *Sabicea amazonensis*.

Wernham (1914) has not designated a holotype but cited six syntypes: *Koch 92* (K, B, G, not seen, F [type fragments!]; Manaus, Río Negro, Dec 1900, *Gwynne-Vaughan 25* (K, B, G, not seen), *Traill 389* (K, B, G, not seen); *Poeppig 2514* (K, B, not seen, G!, F!, photo MO!). *Spruce s.n.* (syntype, K, B, G, not seen). *Ule 5117* has been selected as lectotype because it is in a well-preserved condition with several leaves, and inflorescences including flowers.

*Selected specimens examined.* BRASIL. Amazonas: E bank of Rio Abacaxis, Francisco Ceará, *Hill 13010* (NY); Manaus, Antiga do Passarinho, *Chagas 4484* (F, U), Cachoeirinha, P.J.M. & *Maas 216* (F, U, WIS), Forquilha, *Rodrigues & Chagas 2.020* (US), Manaus-Bilhares Chapada, *Rodrigues 762* (F, U), Manaus and Vicinity, Cachoeira baixa Taruma, Beside Igarape Taruma, *Forero et al. 4634* (F, M, NY, S, U), Manaus-Caracará road, Km 16–20 of BR-174, 1 km N of junction with Manaus-Itacoatiara road, *Todzia et al. 2201* (MO, NY), along Manaus-Caracará road, 2 km north of the junction in road to Tacoatiara, *Croat 62224* (MO), near the Eduardo Gomes International Airport, *Tsugaru et al. B-577* (MO, NY), Manaus-Itacoatiara, Reserva Florestal Ducke, Km 26, *Assunção 106* (MO, NY), *Costa & Nascimento 136* (NY), *Costa et al. 207* (NY); Yucabí, on the Rio Negro, *Tate 18* (F, NY); São Pauls de Olivença, *Ducke 34991* (F); Missao Religiosa de Paricachoera, Alto Rio Negro, *Baksta s.n.* (US); Rio Xie, proximo a cochoeira de Cumati, afluyente do Rio Negro, *Silva et al. 1390* (US); Maués, across from Guaraná factory, *Campbell et al. P22037* (MO, NY, S, U); Atalaia do Norte, Rio Javari, Pau Mari c, 0,5 hrs above Atalaia, *Andersson et al. 2147* (MO, NY, S); Km 26, Lateral Oeste-Igarapé do Acará, Campina, *Sothers & Silva 840* (MO). **Roraima:** Cachoeira Caranguejo, Rio Cauabury, *Holt & Blake 427* (BM, F, NY). COLOMBIA. **Amazonas:** Río Popeyacá (tributary of Apaporis between Río Piraparaná and Raudal Yayacopi), near mouth, *Schultes & Cabrera 15586* (F, US, NY); Río Miritiparana, *Schultes & Cabrera 16442* (HUH, US); Corregimiento de Araracuara, Río Caquetá, *Galvis 1101* (MO); Leticia, Km 04 of the trail to Calderón from Km 21 on the Via Tarapacá, *Andersson et al. 2177* (NY, S), Corregimiento de Tarapacá, Parque Nacional Natural Amacayacu, Cabaña Pamaté, alrededores de la Cabaña, *Rudas et al. 2800* (MO); Río Igaraparana (affl. Río Putumayo), La Chirrerá, Territoire des indiens WITOTO Jitomagaró, 17 km en aval de La Chorrera, Jofoi 6, *Gasche & Desplats 1148* (G); La Pedrera, ca. 2 km en el camino entre La Pedrera y Tarapaca, *Galeano et al. 2036* (NY). **Vaupés:** Mitú and vicinity, Río Vaupés, Río Kubujei, *Schultes et al. 24289* (HUH, MO), *Schultes et al. 26066* (HUH, NY, U), ca. 2 km along dirt

road SE of Mitú, *Croat 56821* (MO), Bajo Vaupes, Terra de Urania, *Gutierrez & Schultes 979* (HUH), bosque orilla Vaupes, *Arbelaez & Cuatrecasas 6788* (F); Camino desde Mitú hacia el cerro urania, borde del camino, *Cortés 1594* (NY); Río Piraparana (Tributary of Río Apaporis), Cano Teemeena, *Schultes & Cabrera 17268* (F, HUH, US); Río Apaporis, entre el Río Pacoa y el Río Kananari, *Schultes & Cabrera 12594* (F, US). PERU. **Loreto:** Florida, Río Putumayo, at mouth of Río Zubineta, *Klug 2085* (BM, F, HUH, US, NY, S). VENEZUELA. **Amazonas:** Bosque a lo largo del río Yatua al pie del Cerro Araucaua, *Styermark & Bunting 102512* (F, US); Río Guainia, Maroa, *Williams 14363* (F); Guinia, along road from Maroa to Yabita, vicinity of old trail to Pimichin, *Acevedo-Rodriguez et al. 10370* (MO, US).

**2. *Sabicea aspera*** Aubl. Hist. Pl. Guiane 1: 194, t. 76. 1775. TYPE: French Guiana. Ad ripam fluvii Sinémari, *J. B. C. F. Aublet s.n.* (lectotype, designated by Steyermark [1967], BM!, photo NY!). *Schwenkfelda aspera* Wild. Spec. pl. i. 982. 1797. TYPE: Based on *Sabicea aspera* Aubl.

Ascending, twining to scrambling herb, shrubs to suffruticose vines or lianas, stems 0.6–5 m long; *terminal flowering branchlets* densely strigulose to pubescent, rarely isolatedly arachnose, trichomes 0.2–1.2(–1.5) mm long. *Stipules* lanceolate to narrowly lingulate or ovate to deltate, antrorse to reflexed, 5–8(–10) × 2.4–11 mm, apically (sub-)acute to acuminate, membranous, ciliolate with 0.2–0.9 mm long cilia, adaxially glabrous excluding the basal part, abaxially sparsely to densely strigulose to puberulous at the base or lower part, sparsely towards the upper part, eventually glabrous, trichomes (0.2–)0.6–1.5(–1.8) mm long, 5–9(–12)-veined, veins plain both adaxially and abaxially, colleters 5–9, (0.6–)0.9–1.3 mm long. *Leaf blades* usually narrowly elliptic to oblong or lanceolate, sometimes widely elliptic to oblong, (1.5–)5–16.5 × (0.8–)2–6(–8) cm, apically usually (sub-)acute, occasionally obtuse, membranous or papyraceous, cilia 0.5–1.5 mm long; adaxially lamina isolatedly to sparsely strigulose to hirtellous, costa and secondary veins densely strigulose and sparsely puberulous, trichomes 0.07–0.7(–1.1) mm, lamina abaxially isolatedly to sparsely strigulose to pubescent, occasionally isolatedly arachnose, costa and secondary veins densely strigulose and puberulous to sericeous, trichomes 0.07–1.3 mm long, secondary veins 8–12 pairs, plain adaxially and protruding abaxially, tertiary veins prominulous abaxially; *petioles* (3–)5–15(–25) × 0.8–1.5 mm, densely puberulous to hirtellous or pubescent, rarely isolatedly arachnose, trichomes 0.07–1.3 mm long. *Inflorescences* one per node, 4–12(–32)-flowered, loosely fascicled or verticillate to compact-umbellet or occasionally moderately lax-paniculate, (1–)1.5–3.5 × (1–)1.5–3.5 cm; *peduncles* 0–5 mm long, primary axis or main inflorescence branches 0(–6) mm long, main lateral axes 0(–4) mm long; *bracts* exinvolucrate, membranous, incompletely isolated into 2–3 parts, isolated parts (1.8–)2.5–4.5(–9.5) × (0.9–)1.2–5.5 mm, 0–6-lobed, lobes 0.3–4.8 × 0.5–2.8 mm, narrowly triangular to widely

lanceolate, apically acute to acuminate, ciliolate with 0.1–0.3 mm long cilia, adaxially glabrous excluding the basal part, abaxially sparsely to densely strigulose at lower part, isolatedly to sparsely at upper part, bracteoles 2–3.5 mm long, colleters 2, 0.1–0.2 mm long. *Flowers* sessile or pedicellate, *pedicels* 0–3(–8) mm long; *calyx* campanulate, 4–5(–6)-lobed, tubes (0.8–)1–1.8(–2.2) × (1–)1.5–2.2 mm, lobes 0.3–5(–6) × 0.3–0.9 mm, usually reflexed, occasionally antrorse, usually narrowly lanceolate, occasionally linear or narrowly lingulate or triangular, apically acute to acuminate, ciliolate with 0.1–0.6(–1) mm long cilia, adaxially glabrous, abaxially sparsely to densely strigulose, trichomes 0.1–0.7 mm long, colleters 1(–4) in each sinus, 0.2–0.3 mm long; *corolla* yellow or white, salverform, tubes (6.5–)8–12 × (1–)1.5–2.7 mm, lobes 2–3.6 × 1–1.8 mm, ovate, antrorse, apically (sub-)acute to obtuse, adaxially the indumentum of orifice extends up to (3–)5.5–7.8 mm inside the tubes, trichomes 0.2–0.5 mm long, abaxially densely pilosulous at tubes, pilosulous to serious at lobes, trichomes (0.9–)1.2–2(–2.4) mm long; *stamens* 5(–6) per flower, attached to corolla tube at 6–11 mm from the base, anthers (1.5–)2–2.7 × 0.4–0.6 mm apically; *style* (4.4–)5.2–7.5 mm long, stigmatic lobes 4–5(–6), (1.5–)2.8–3.6 × 0.2–0.3 mm; *ovaries* 1.3–2 × 1.2–2(–2.5) mm, abaxially uneven, 4–5-locular, each locule 0.9–1.1 × 0.3–0.8 mm. *Fruits* dark burgundy, dull crimson to blackish purple or red to violet, 6–10 × 6–10 mm when mature, abaxially sparsely strigulose; *seeds* 0.5–0.9 × 0.4–0.6 mm.

*Phenology, distribution and habitat.* Flowering throughout the year. Fruiting January to March and June to December. *Sabicea aspera* var. *aspera* is widely distributed in the Guiana Shield region excluding Venezuela. Its distribution extends up to the southern region of Amazonas and southeast to southwestern regions of Pará State of Brazil. *Sabicea aspera* var. *glabrescens* is widespread in the Guiana Shield region, southern Amazonas, southwestern Rondônia, southeast region of Pará and northern region of Maranhão of Brazil, and in Trinidad and Tobago. *Sabicea aspera* is collected from forests, swamps, scrub thickets and roadside areas, and from plain land to Rocky Mountains. It is found in clayish to sandy or rocky soil; 0–1060 m (Fig. 7).

*Discussion.* Steyermark (1967) mentioned the type protologue “Ad ripam fluvii Sinémari, French Guiana”, which does not include any specimen, but correspond to the collection *Aublet. s.n.* (BM).

*Sabicea aspera* is characterized by its erect to erecto-patent trichomes on abaxial surface of corolla tubes, appressed and short trichomes on branchlets, abaxial surface of stipules, leaves, and calyx lobes, and exinvolucrate, usually few-flowered compact inflorescences. Wernham (1914) noted that the shape of stipules of *Sabicea aspera* is quite unusual for the genus. But similar stipules are present in *Sabicea bariensis*, *S. boliviensis*, and *S. brasiliensis* and few others as well. *Sabicea glabrescens* and *S. trinitensis* do not differ from each other in

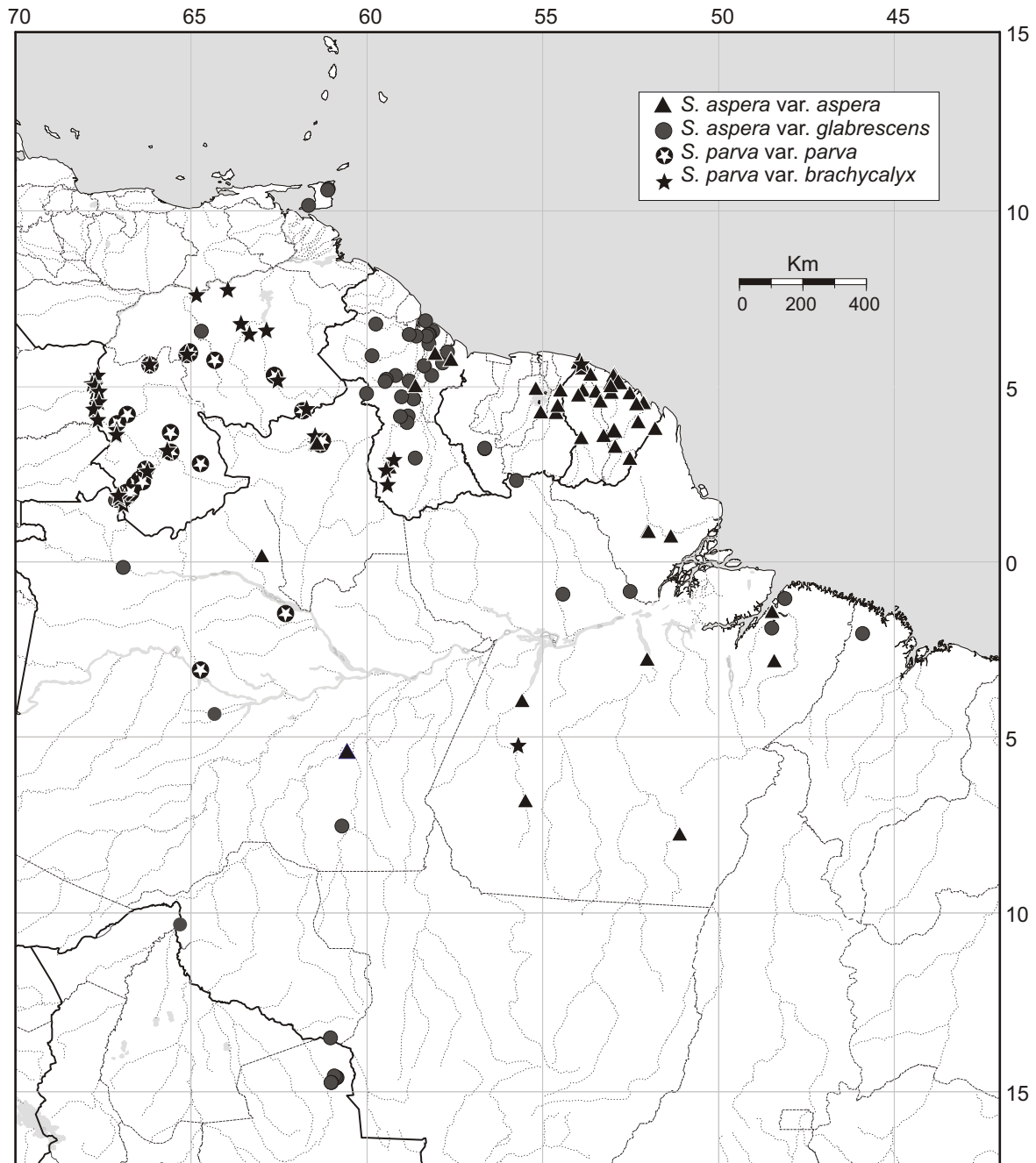


Figure 7. Map of the Guiana Highland and Amazon Basin including northeast Bolivia, and western and central Brazil (in part), showing the distribution of *Sabicea aspera* and *S. parva*.

any notable character and on the other hand, they do not differ from *S. aspera* in any character except stipule shape. The narrow difference of *Sabicea glabrescens* and *S. trinitensis* with *S. aspera* doesn't support these as a distinct species, rather seems to permit their infraspecific delimitation under *S. aspera*. Therefore, we transfer *Sabicea glabrescens* and *S. trinitensis* under *S. aspera* as a variety instead of recognizing them as a separate species. Wernham (1914) recognized *Sabicea aspera* var. *latifolia*, which does not differ from *S. glabrescens*. It has been included here with *Sabicea aspera* var. *glabrescens*. Schumann's (1889) *Sabicea aspera* var. *scandens* do not differ

from *S. villosa* in any noticeable character due to which we synonymized it under *S. villosa*.

Close to *Sabicea aspera* is *S. noelii*, from which it is distinct by its glabrous upper inner surface of bracts and calyx lobes, appressed trichomes, colleter's location at sinus, and manifestly shorter calyx lobes (see *S. Sabicea noelii*). *Sabicea aspera* with short peduncles and pedicels is confusable with some *S. panamensis* bearing few-flowered compact-paniculate inflorescences from which it can only be distinguished by its erecto-patent trichomes at outside of corolla tubes. *Sabicea aspera* var. *glabrescens* is somewhat similar to *S. parva*, from which it differs by its narrowly lanceolate to lingulate or linear and usually reflexed calyx lobes, short (usually < 2 mm in contrast to 2–3[–3.5] mm) calyx tubes and colleters location in sinus. *Sabicea aspera* appears very close to *S. villosa* var. *adpressa*, from which it differs by its longer (usually 8–12 mm, in contrast to usually 3.5–5 mm) corolla tubes and erecto-patent trichomes at outside the corolla tubes.

The collections *Ek et al. 1031* (MO, U), *Taylor 12059* (MO, U, US), *Holt & Blake 584* (F, US, NY), *Dahlgren & Sella 780* (F, HUH, US), *Rosa & Vilar* (NY), and *Knab-Vispo & Rodriguez 462* (MO, WIS) seem intermediate between *Sabicea aspera* var. *glabrescens* and *S. parva*. The collections *Maguire et al. 22957* (F, HUH, NY, US, U), *Cruz 2638* (F, HUH, NY), *Clarke et al. 10918* (MO) and *Pipoly et al. 11704* (NY) are found to share the distinguishing characters of *Sabicea aspera* var. *glabrescens* and *S. villosa* var. *adpressa*.

#### Key to the varieties:

- 1a. Stipules usually widely lanceolate to lingulate.....2a. *S. aspera* var. *aspera*  
 1b. Stipules usually ovate to deltate.....2b. *S. aspera* var. *glabrescens*

#### 2a. *Sabicea aspera* Aubl. var. *aspera*

*Sabicea aspera* var. *genuina* Schumann Fl. Bras. 6(6): 307. 1889.

*Selected specimens examined.* BRASIL. **Amapá:** Serra do Navio, Rio Amapari, Fritz Akerman Ore Body, *Cowan & Maguire 38092* (HUH, NY, U), Rio Amapari, at beginning of Terezinha-Reservatorio Trail, *Cowan 38316* (NY, U); In forest behind Oyapock Airfield, *Cowan 38686* (NY, U); Rio Araguari, 20 minutes downriver from Porto Platon, 0°44'N, 51°22'W, *Pires et al. 51003* (NY); Area do Gaúcho, ca. 5 km, mais Oeste na estrada Perimetral, *Austin et al. 7157* (HUH, US, NY). **Amazonas:** Rio Vista, Rio Branco, *Lehman 3398* (U); Rio Oiapoque, ilha perto da cachoeira do Carratá, *Frôes 25761* (U); São Luiz, along Rio Negro between Manaus and São Gabriel, 63°00'N, 00°10'W, *Pode 1705* (NY); Maranhão, Região Gurupi, *Frôes 34515* (U). **Pará:** Belém, *Huber 644* (G); Northeast woods of the I, A, N, Belém, *Blake 7772* (F, NY), *Archer 7772* (F, NY), Pedreiras, *Costa 170* (F), South woods, I,A,N, *Archer 8056* (F, NY), South woods Agronomico do Norte, at lands of Instiuto Agronomico do Norte, *Silva 165* (NY, US); *Schubert 2246* (US); Santo Antonio,

Embrapa, 2°50'S, 48°25'W, *Rosa 1761* (NY), Maguary E,F,B, Capoeira, *Sneathlage 107* (F, HUH); vicinity of Pará, *Baker 73* (BM, F, G[-3], M, S, U), near Pará, *Killip & Smith 30364* (F, NY, US); Reserva Florestal De Gorotire, surroundings of Gorotire village at Rio Fresco, 7°47'S, 51°7'W, W, *Gottsberger & Posey 25-18183* (US); Itaituba, Santarém-Cuiabá, BR 163, Km 1115, 6°50'S, 55°30'W, *Amaral et al. 778* (NY). FRENCH GUIANA. **Cayenne:** Rivière Comté, sur la crique Bagot a environ 14 km de son confluent, *Oldeman B-2036* (U); Ilets de Saut Émerillon, sur le Grand Inini, *Granville C102* (U); Rives gauche du Yaroupi, 4 km en amont de son embouchure, *Oldman 3122* (US); Sur la Riviera Sinnamary, Environ 5km avant d'arrives à la station hydrologique de la Crique Grégoire, *Granville B5111* (US); Sommet sud du ic Natecho, 30 km NE de Saül, *Granville 3344* (U); Sinnamary, piste de Ste Elie, Km 2 coupe forestière, 5°22'N, 52°57'W, *Billiet & Jadin 1119* (BM, BR, NY, U, US), Saut Kawène, Crique Kourcibo-Bassin du Sinnamary, 4°53'N, 53°30'W, *Hoff et al. 6518* (NY), Camp Eugène-Bassin du Sinnamary, 4°51'N, 53°4'W, *Granville & Cremers, 12837* (MO, U); Cacao, piste de Coralie, *Billiet & Jadin 1520* (BR); Montagne de Kaw, Route de Kaw, P, K, 47, 4°33'N, 52°9'W, *Granville 9145* (NY, US); Piste de Saint-Elie, pk 25, 5°9'N, 53°3'W, *Hoff 6885* (MO); Saut Kawène, Crique Kourcibo-Bassin du; Pic Coudreau. Monts Bakra, Région des Émerillons, 03°18'N, 52°57'W, *Granville & Cremers 11795* (NY, U); Montagne de Kaw, E end ca. 10 km from end of road, 4°32'N, 52°07'W, *Andersson et al. 1941* (MO, NY, S, U); Roche Touatou, bassin de L'Oyapock, 2°57'N, 52°32'W, *Granville & Cremers 12980* (MO); Kaw Mts, Trésor, Favard Creek, 4°36'N, 52°18'W, *Jansen-Jacobs 5327* (U); Piste se Saint-Elie-Interfluve Sinnamary-Counamama, Piste du PK 22, debut de piste, 5°20'N, 53°00'W, *Prévost, 3402* (G, MO, U, NY). **Saint-Laurent-Du-Maroni:** Saut Sabbat, Halle, 522 (U), Petit Laussant sur sable blanco, *Granville B5324* (U), Piste de Saint-Laurent vers Paul Isnard, km 30, *Billiet & Jadin 1717* (BR), PK 70 environ, Piste Sosacaba, *Granville 5348* (BR), environ du PK Km 25, *Cremers 8183* (BR); Monts de l'Observatoire, sommet EST, a 2 km de Ouanary environ, *Granville 6739* (BR, U); Montagne de la Trinité, sommet NE top of Table Mountain, *Granville et al. 6476* (BR, G, US, NY, U); Montagnes de la Trinité, Inselberg Nord Ouest, Pied d'une falaise granitique à la base de la paroi sud, *Granville et al. 6152* (BR, NY, WIS, US, U), Inselberg an NW du Massif, Forêt à la base oe L' Inselberg, 04°36'N, 53°22'W, *Granville et al. 6077* (U), Futur nouvelle RN 1, a 3 km vers l'est a partir du pk 16 de la route de'acces vers Petit Saut, *Billiet & Jadin 4371* (BR), Inini, Mont Atachi Bacca-Région de l'Inini, Sud du plateau sommital, 12 km SE de Gobaya Soula, 3°33'N, 53°55'W, *Granville et al. 10787* (G, NY, US, U), Route de l'Acarouany-Bassin de la Mana, Piste forestière vers Les Roches, 5°34'N, 53°51'W, *Cremers & Hoff 11349* (NY, US, U); Route de Paul Isnard, Km 40, *Andersson et al. 2003* (NY, S). SURINAME. In montibus, qui dicuntur Nassau, In forest, Km 3.8, *Lanjouw & Lindeman 2349* (NY, U); Brokopondo, Natuurpark Brownsberg, *Verden 13697* (U); Lely Mts., along forest road, northward from airstrip, *Lindeman et al. 389* (NY, U), along airstrip, *Lindeman et al. 20* (U), SW plateaus covered by ferrobaxite, *Lindeman et al. 807* (U), SW plateaus covered by ferrobaxite, along forest road, northward from airstrip, *Lindeman*



*et al.* 694 (U).

**2b. *Sabicea aspera* Aubl. var. *glabrescens* (Benth.) Schumann, Fl. Bras. 6(6): 307. 1889.**

*Sabicea glabrescens* Benth., J. Bot. (Hooker), 3: 219. 1841. TYPE: Guyana: Río Quitaro, 1838 (fl), *R. Schomburgk* 538 (holotype, G[2]! ; isotypes, NY!, US!, WI!, photo HUH!, NY!).

*Sabicea aspera* var. *latifolia* Wernham, Monogr. *Sabicea* 57. 1914. TYPE: French Guiana, Cayenne, no date (fl), *Martin* 63 (holotype, BM!, photo NY!).

*Sabicea trinitensis* Standl. Bull. Torrey Bot. Club, 48(12): 339. 1921 [1922]. TYPE: Trinidad: O'Meara Savanna, 22 Mar. 1921, *N. L. Britton & E. G. Britton* 2489 (holotype, US!; isotype, NY!).

*Selected specimens examined.* BRASIL. **Maranhão:** Turiacu, Km 6 da BR 106 Maracaçumé-Sta, Helena, fazenda Maracaçumé Agro Industrial Grupo, *Rosa & Vilar* 2798 (NY). **Pará:** Rio Maicuru, between Lageira and Macau airstrip, 0°55'S, 54°26'W, *Strudwick et al.*, 3625 (NY); Parque Ineigena do Tumucumaque, Rio Paru de Oeste, Missao Tiriyo, 2°20'N, 55°45'W, *Cavalcante* 2443 (NY-2). **Rondônia:** Km 282 Madeira-Mamoré railroad, 12 km north of Riberão, basin of Rio Madeira, *Prance et al.* 6714 (F, NY[2] U, S). GUYANA. **Cuyuni-Mazaruni** (Region): Along the upper Mazaruni River, *Leng* 199 (NY); Cuyuni River, Crab Fall, *Tutin* 16a (BM, NY, U, US); Aurora, along track ca. 0,5 km S of camp, 6°47'30"N, 59°44'30"W, *Gillespie & Tiwari* 2172 (MO, NY, U). **Demerara-Mahaica:** East Coast Water Conservancy, southeast of Georgetown, canal southeast of Lamaha Stop-off, *Hitchcock* 16999 (HUH, US, NY, S); Demerara, Haiama, West Bank Demerara, *Davis* 62 (NY), Demerara River, *Jenman* 4711 (NY); near Timehri airport, 6°30'N, 58°15'W, *Gillespie & Tiwari* 825 (MO, NY, U), south of Timehri, *Maas & Westra* 3593 (F, MO, NY, U, S); West Damerara, Cieba Biological Centre Just west of Soesdyck-Linden Highway, about 7,6 km S of Timehri Airport turnoff, 06°29'55"N, 58°13'09"W, *Taylor et al.* 12105 (MO, US), south of Dora, at the Loo River, 06°14'03"N, 58°14'41"W, *Taylor* 12059 (MO, U, US), Waraputa logging consession, 5°11'N, 51°48'W, *Raes et al.* 26 (MO, NY). **Mahaica-Berbice:** Margins of Berbice River, S of New Dageraad, 6°0'N, 57°43'W, *Maas et al.* 5471 (F, NY, S). **Potaro-Siparuni:** Indian clearing, Kangaruma, *Gleason* 193 (HUH, NY), Tumatumari, *Gleason* 158 (HUH, NY); Potaro River, mining camp (dredge), 6 km below Kaieteur Falls, 5°13'N, 59°27'W, *Kvist et al.* 168 (U, US); Kaieteur Falls National Park, 5°10'N, 59°29'W, *Hahn et al.* 4764 (MO); Essequibo River at Karupukari crossing, 4°40'N, 58°41'W, *Hoffman et al.* 1336 (MO, NY, U, US); Pakaraima Mts., upper Ireng R, 0.5 km E of Cipo settlement and adjacents savanna ridges, 4°49'N, 60°01'W, *Henkel et al.* 1847 (MO); Iwokrama Rainforest Reserve, 1 km N of Surama, 4°10'N, 59°03'W, *Ehringhaus* 106 (MO, NY, U); Iwokrama Rain Forest Reserve, Karupukari, 4°25'N, 58°50'W, *Mori et al.* 24480 (MO). **Upper Takutu-Upper Essequibo:** Rewa River, Summit of unnamed peak, 5.6 km W of camp, 02°58'N, 58°38'W,

*Clarke* 3713 (US); Makarapan MT., at base of Southern side, 0–1 km of camp, 3°56.59'N, 058°52.03'W, *Clarke et al.* 6931 (MO, US). **Upper Demerara-Berbice:** In and about the village, Rockstone, *Gleason* 496 (HUH, NY, US); Malali, Demerara River, *Cruz* 2638 (F, HUH, MO, NY); Labbakabra Ck, Tiger Ck, Essequibo River, *Sandwith* 1175 (S); east bank of Essequibo River near end of Mabura Road, 4°40'N, 58°40'W, *McDowell* 3254 (MO, US); west Pibiri Compartment, Pibiri main road, 5°20'N, 58°10'W, *Ek et al.* 1031 (MO, U); Zion, Dubulary Ranch, 05°41'N, 57°51'W, *Mutchnick* 1376 (MO). FRENCH GUIANA. **Saint-Laurent-Du-Maroni.** Sopaie, *Hallé* 766 (NY). SURINAME. **Sipaliwini** (District): 45 km above confluence with Lucie Rivier, *Irwin et al.* 57508 (F-2); Kayser Airstrip, 25 km above confluence of Lucie Rivier, 3°10–20'N, 56°39'W, *Irwin et al.* 57640 (NY, US); Zuid Rivier, Kayser Airstrip, 45l m above confluence of Lucie Rivier, 3°15'N, 56°39'W, *Irwin et al.* 57640 (NY). TRINIDAD AND TOBAGO. Auora forest via Saugos Graude, *Broadway* 5382 (BM, F). **Saint George:** Arcadia Estate, Caura Valley, *Britton & Hazen* 1195 (HUH, NY, US). **Saint Andrew:** Melajo forest reserve, c. 1.5 km., North of Orupuche Village, 0°37'N, 61°6'W, *Barnard et al.* 561 (MO). VENEZUELA. **Bolívar:** Reserva Forestal Imataca, selva pluvial Río Cuyuní, Puesto (GN) Akarabisí, hasta la Quebrada de Akarabisí, *Stergios et al.* 3326 (MO); Salto Para, Río Caura, stretching from sandy beach to top of Salto Para, 6°03'N, 65°04'W, *Horner et al.* 333 (MO); Cedeño, Río Caura, Boca del Río Nichare, 6°37'N, 64°45'W, *Knab-Vispo et al.* 462 (MO, WIS [2]).

- 3. *Sabicea bariensis*** Steyerl. Ann. Missouri Bot. Gard. 75(1): 350. 1988. TYPE: Venezuela: Territorio Federal Amazonas: upper Río Baria, mostly non-inundated area along riverside, 00°55'N, 66°16'W, 140 m, 09 May 1984 (fl), *A. Gentry & B. Stein* 47314 (holotype, MO!; isotypes, NY!, VEN, not seen). Figure 8A–K.

Lianas or vines, branches pendent, terminal flowering branchlets densely strigulose, and sparsely to densely lanuginose, strigulose trichomes, 0.5–1.1(–1.2) mm long. *Stipules* narrowly ovate to widely lanceolate, antrorse, 10–14 × 4–6 mm, ciliolate with 0.1–0.7(–1.1) mm long cilia, adaxially glabrous excluding the basal part, abaxially densely strigulose, occasionally isolatedly lanuginose at the lower part, trichomes 0.1–0.8 mm long, colleters 5–7, 0.8–1.4 mm long. *Leaf blades* elliptic to oblong, 4.8–14.5 × 1.8–6.5 cm, apically acute to acuminate, cilia 0.4–1.2(–1.3) mm long; lamina and secondary veins isolatedly to sparsely and costa sparsely to densely strigulose to puberulous, trichomes 0.1–1.3 mm long; abaxially lamina isolatedly to sparsely, costa and secondary veins densely sericeous to strigulose or pubescent, or in addition isolatedly to densely lanuginose or arachnose, trichomes 0.2–1.1(–1.4) mm long, secondary veins 10–12 pairs, plain adaxially or protruding abaxially, tertiary veins prominulous and quaternary veins sometimes distinct abaxially; *petioles* 1.5–4 mm long, densely strigulose. *Inflorescences* one to two per node, (12–)28–36(–64)-flowered, moderately lax- to compact-paniculate, 2–4.8 × 3.5–4 cm excluding 3–7 mm long peduncles,

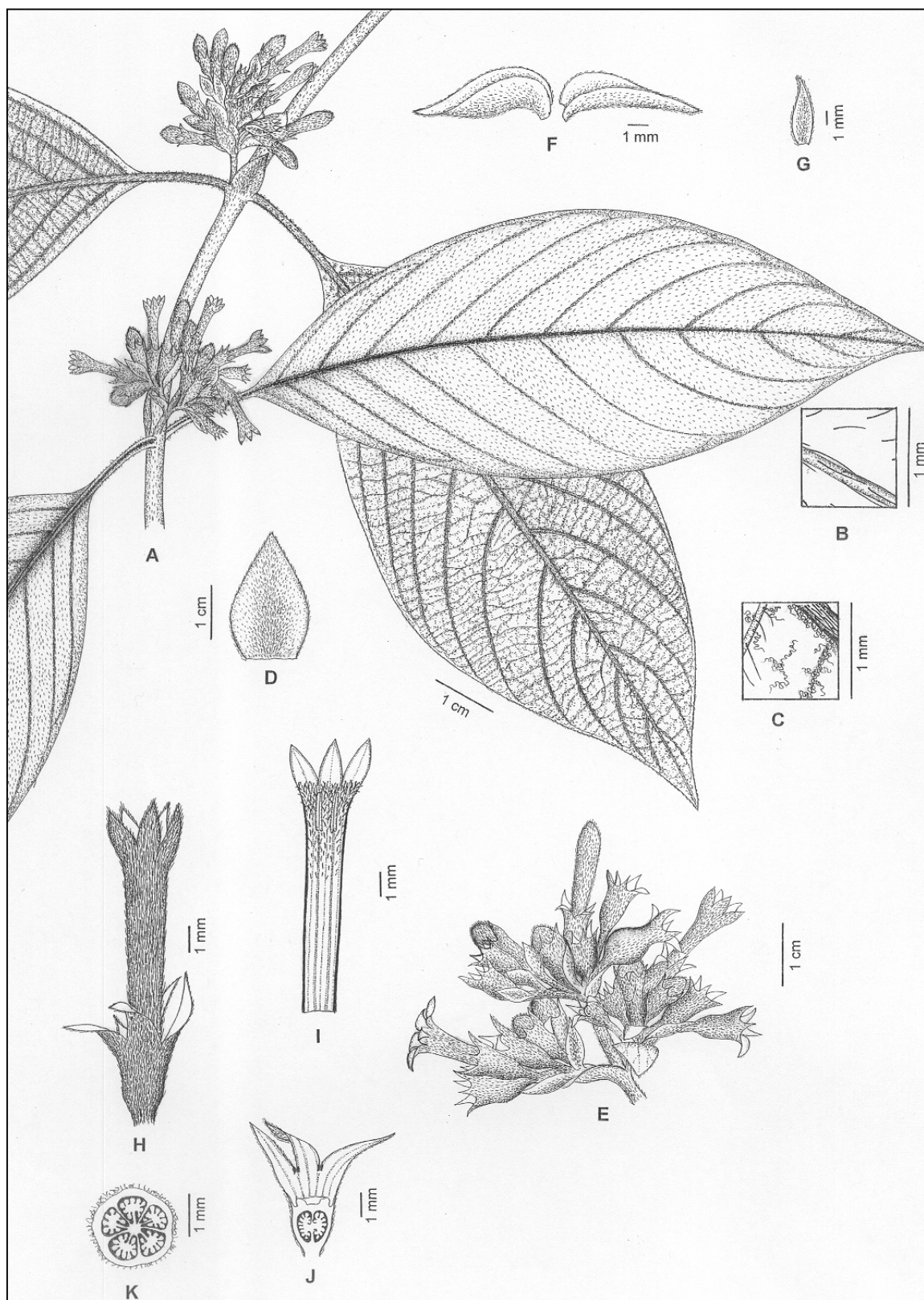


Figure 8. A–K. *Sabicea bariensis*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Outer stipule surface. —E. Inflorescence. —F. Side view of bract. —G. Outer bracteole surface. —H. Flower. —I. Inner corolla surface showing anther's position. —J. Longitudinal section through calyx and ovary. —K. Transversal section through ovary.

trichomes 0.4–1.1 mm long, primary axis 1.5–2 mm long, main lateral axes 4, 1.8–2.8 mm long; *bracts* (sub-)exnvolucrate, membranous, incompletely isolated into 2–3 parts, isolated parts 4–7 × 3–4 mm, ovate, apically acute to acuminate, ciliolate with 0.1–0.6 mm long cilia, adaxially glabrous excluding the basal part, trichomes (1.4–)1.8–2.1 mm long, abaxially densely strigulose at the lower and middle part, isolatedly to sparsely lanuginose at the base, trichomes abaxially 0.1–0.9 mm long, 5–7-ribbed, bracteoles 2–8.5 mm long, 1–3 mm, lingulate to ovate or triangular, apically acute, colleters 4–6, 0.4–0.6 mm long. *Flowers* pedicellate, pedicels 2–7 mm long; *calyx* campanulate, 5-lobed, tubes 2–3 × 2–3 mm, lobes (0.7–)1.5–6 × (0.6–)1–2.5 mm, antrorse to divaricately spreaded, triangular or ovate to widely lanceolate, apically acute, ciliolate with 0.1–0.4 mm long cilia, adaxially glabrous, abaxially densely pubescent to strigulose, isolatedly to sparsely lanuginose at tubes and lower and middle part of lobes, trichomes 0.4–1.1 mm long, plain both abaxially and adaxially, colleters 1–2, slightly (0.2–0.6 mm) below the sinus, 0.2–0.4 mm long; *corolla* white, salverform, tubes 10–10.5 × 0.8–1.5(–1.8) mm, lobes (1.8–)2–3 × (0.7–)1.2 mm, widely lanceolate to narrowly ovate, antrorse to spreaded, apically (sub-)acute, indumentum of orifice extends up to 3.5–4.4 mm inside the tubes, abaxially densely sericeous, trichomes (0.2–)0.6–2.2 mm long, (sub-)appressed to clinate; *stamens* 5 per flower, attached to corolla tube at 7.1–9.5 mm from the base, anthers 2.2–2.5 × 0.3–0.4 μm; *style* 5.3–7.6 mm, stigmatic lobes 2.5–3.5 × 0.1–1.8 mm; *ovaries* (1.8–)2–2.5(–3) × (1.8–)2–2.5 mm, abaxially 5-lobed or uneven, densely strigulose and isolatedly to sparsely lanuginose, trichomes 0.2–1.1(–1.2) mm long, 5-locular, each locule 0.6–0.8 × 0.6–0.7 mm. *Fruits* red, 3–4 mm when immature, abaxially isolatedly to sparsely strigulose and lanuginose; *seeds* 1.2–1.5 × 0.7–1.2 mm.

*Phenology, distribution and habitat.* Flowering in March–May and December. *Sabicea bariensis* is reported from the southern Amazonas state of Venezuela. It is collected from non-inundated or swampy areas along riversides (Fig. 9).

*Discussion.* Steyermark (1988) described *Sabicea bariensis* as non-arachnoid species, though the lamina and hypanthia of holotype and the hypanthia of paratype (e.g., *Liesner 16967*) are abaxially isolatedly to sparsely lanuginose to arachnoid (Fig. 8C). In this treatment, *Sabicea bariensis* has been defined on the basis of the combination of its unequal and widely lanceolate to triangular or ovate calyx lobes (Fig. 8H, J) and arachnoid indumentum at the adaxial surface of leaves and/or on hypanthium. *Sabicea bariensis* differs from *S. panamensis* by its isolated to sparse, lanuginose to arachnoid indumentum at least outside the hypanthia, larger (2–4 × 2–3 cm in contrast to 0.8–2.1 × 1.4–2 cm) calyx tubes, and usually widely lanceolate to triangular and divaricately spread calyx lobes. *Sabicea bariensis* seems close to *S. calophylla* with larger calyx lobes and non-arachnose to sparsely arachnose indumentum. It is distinct from *Sabicea calophylla* by its unequal calyx lobes,

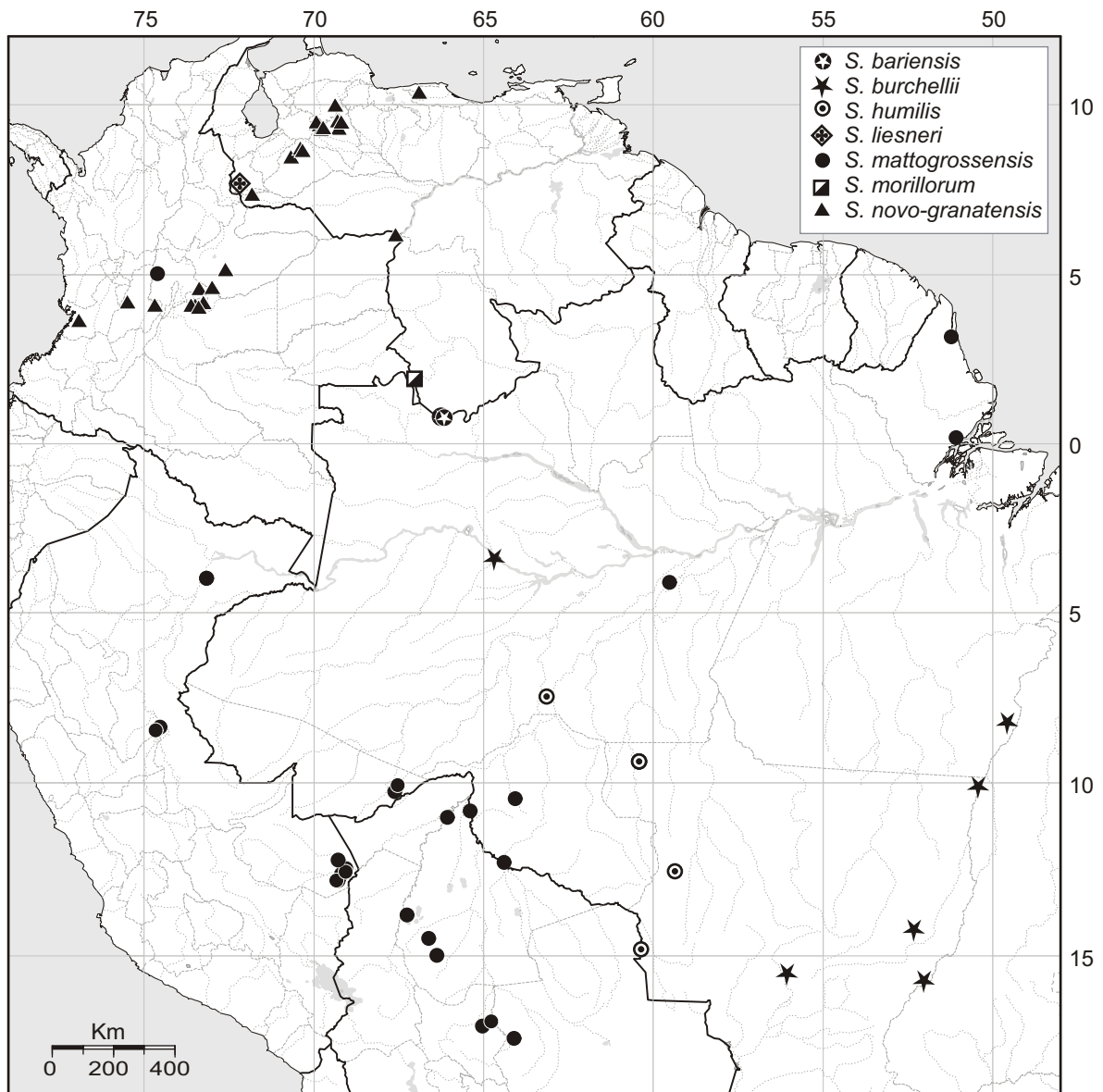


Figure 9. Map of South America (in part), showing the distribution of *Sabicea bariensis*, *S. burchellii*, *S. humilis*, *S. liesneri*, *S. mattogrossensis*, *S. morillorum*, and *S. novo-granatensis*.

longer (2-4 mm in contrast to 0.8-1.5 mm) calyx tubes and larger (2-4.8 x 3.5-4 cm in contrast to usually 2-3 x 2-3 cm) inflorescences of irregular shapes. Steyermark (1988) mentioned that *Sabicea bariensis* mainly differs from *S. morillorum* by its non-arachnoid pubescent. We disagree, because Steyermark's (1988) *Sabicea bariensis* is not really a non-arachnoid species. Yet, it is very distinct from *Sabicea morillorum* by its apically acute to acuminate and abaxially non-arachnoid or isolatedly to sparsely lanuginose at tubes and lower and middle part of lobes, occasionally only basally isolatedly to sparsely lanuginose stipules and bracts, widely lanceolate to triangular, apically acute and abaxially non-arachnoid calyx lobes, and larger (2-4 x 2-3 mm in contrast to 0.5-1 x 1.5-2.1 mm) calyx tubes. The collection *Gentry & Stein 47313* with adaxially densely arachnoid leaves, close to *Sabicea calophylla*, is included in *S. bariensis*, because such specimens in *S. calophylla* would make *S. Bariensis* indefinable.

*Additional specimens examined.* VENEZUELA. **Amazonas:** Río Negro, Gravel banks of main channel of Río Mawarinuma, 3–4 kms upstream from Neblina Base Camp, *Kral 71981* (MO), upper Caño Baria, swampy area between Río Mawarinuma and head waters of Río Baria, *Liesner 16967* (U).

**4. *Sabicea boliviensis*** Wernham, Monogr. *Sabicea* 37. 1914. TYPE: Bolivia: Yungas, 1890, *M. Bang 384* (holotype, BM!, isotypes FI!, GI!, HUH!, KI!, MI!, NY!, US!, W!).

Scandent; terminal flowering branchlets densely pilosulous, to pubescent and arachnose to lanuginose, trichomes, (0.1–)0.4–1.1(–1.3) mm long. *Stipules* ovate to widely lanceolate, reflexed, (5–)7–10 × 4.5–8 mm, apically acute to acuminate, ciliolate with 0.1–0.5(–0.9) mm long cilia, adaxially sparsely to densely sericeous to strigulose, abaxially densely to sparsely pubescent almost all over, trichomes 0.1–0.8 mm long, 12-veined. *Leaf blades* usually lanceolate, sometimes narrowly elliptic, (3.5–)6.5–15.2 × (1.5–)3.5–4.7 cm, apically acute to acuminate, cilia 0.2–0.7(–0.8) mm long; adaxially lamina pilosulous to puberulous, costa densely pilosulous or pubescent to puberulous, rarely lanuginose, trichomes 0.1–1.4 mm long; abaxially albescent to ochroleucous, at lamina sparsely to densely pilosulous to pubescent, densely lanuginose, costa and lateral veins densely pilosulous to pubescent and lanuginose, trichomes (0.2–)0.7–1.2(–1.5) mm long, secondary veins 11–12 pairs, costa and secondary veins plain adaxially and protruding abaxially, tertiary veins distinct or prominulous and quaternary veins usually distinct abaxially; *petioles* (5–)8–15 mm long, densely puberulous or pubescent, and arachnose. *Inflorescences* two per node, 9–18-flowered, compact-umbellate, (1.5–)2–2.4 × (1.5–)2–2.4 cm; *peduncles* (5–)6–15 mm long; *bracts* exinvolucrate, papyraceous, isolated into 2–3 parts, isolated parts 5–8.3 × 2–3(–4.1) mm, 1–2(–3)-lobed, lobes 0.8–5 × 0.3–2.6 mm, ovate to lanceolate, apically acute to acuminate, ciliolate with 0.1–0.6 mm long cilia, adaxially pubescent to sericeous, trichomes 0.1–0.8 mm long, abaxially sparsely to densely pubescent, bracteoles (1.5–)4–5(–6.5) × (0.3–)1–1.5 mm, narrowly lanceolate or linear, apically acute to acuminate. *Flowers* (sub-)sessile, pedicels 1–3(–6) mm long; *calyx* campanulate, 5-lobed, tubes 0.6–1.2 × 1.4–2.1 mm, lobes (1.2–)2.5–3.5(–6) × 0.2–0.8(–1.1) mm, antrorse to spreaded, occasionally slightly reflexed, narrowly lingulate to lanceolate, apically acute to acuminate, ciliolate with 0.2–0.6(–1.1) mm long cilia, adaxially usually isolatedly-sparsely pubescent to sericeous or glabrescent, trichomes 0.1–0.6 mm long, abaxially densely pubescent, occasionally isolatedly arachnose to lanuginose, trichomes (0.2–)0.6– (1.1) mm long, colleters 1 in each sinus, 0.2–0.3 mm long; *corolla* salverform, tubes 7–8.5 × 1.5–1.7 mm, lobes 1.8–2.1 × 1.2–1.7 mm, ovate, antrorse, apically acute, abaxially densely pilosulous, trichomes (0.2–)0.8–1.4(–1.6) mm long; *stamens* 5 per flower, attached to corolla tube at 6.8–7 mm from the base, anthers 1.5–1.7 × 0.2 mm; *style* 5.2–5.6 mm long, stigmatic lobes 2.6–3.5 × 0.2–0.3 mm; *ovaries* 1.5–1.8 × 1.5–1.8 mm,

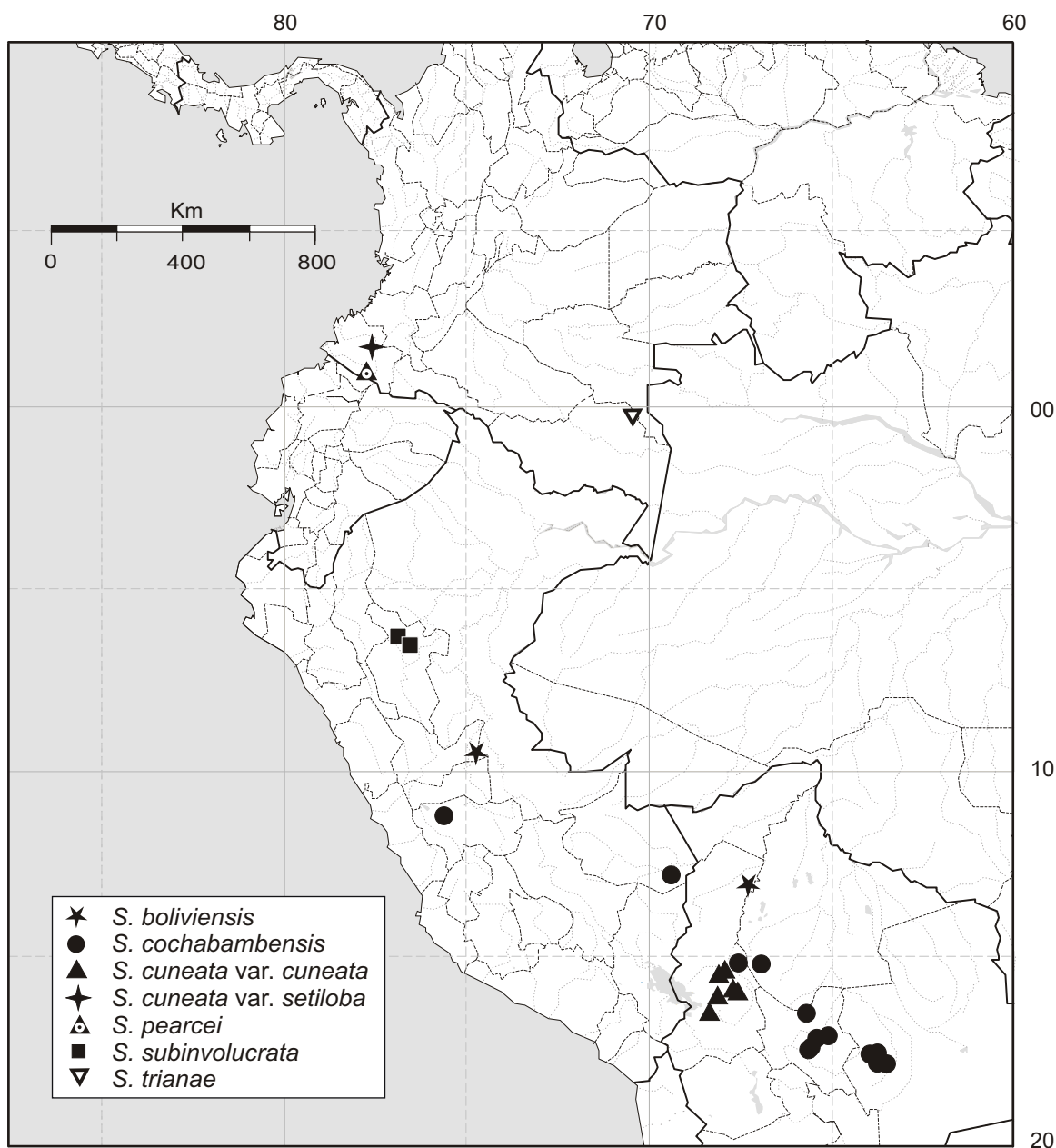


Figure 10. Map of western South America (in part), showing the distribution of *Sabicea boliviensis*, *S. cochabambensis*, *S. cuneata*, *S. pearcei*, *S. subinvoluta*, and *S. trianae*.

Abaxially uneven to slightly 5-lobed, pilosulous, or pubescent and arachnose to lanuginose.

*Phenology, distribution and habitat.* The phenology, distribution and habitat of *Sabicea boliviensis* are not well-known. Flowering in April, known from one specimen. Though Wernham (1914) reported *Sabicea boliviensis* from Bolivia, the collection *Wallnöfer 1528488* (W) indicates the distribution of this species also in Huánuco, Peru. Information on habitat and flowering time in respect to the type specimen is unknown. *Wallnöfer 1528488* was collected from red latosols with thick humus layer in the mountain rain and primary cloud forests; 1700 m (Fig. 10).



*Discussion.* *Sabicea boliviensis* is confusable with *Sabicea cuneata*. Wernham (1914) keyed out this species against *Sabicea cuneata* and *S. setiloba* by “peduncles 2–3 times as long as the inflorescences (2 cm or more)” in contrast to “peduncles barely as long as the inflorescences”. We measured the peduncles of *Sabicea boliviensis* as (5–)6–15 mm long and those of *S. cuneata* as (1–)2–7(–9) mm long which indicate that the distinction of these species based on peduncle lengths is not clear-cut. However, we maintain *S. boliviensis* and *S. cuneata* as separate species because too few specimens of these two species were available for study. Moreover, the type specimen of *Sabicea boliviensis* differs from that of *S. cuneata* by its erecto-patent trichomes at abaxial surface of corolla tubes, and adaxial surface and abaxial secondary veins of leaves, marginally ciliolate, and mostly lanceolate leaves, compact-umbellate inflorescences, and calyx lobes adaxially apically covered with trichomes.

*Additional specimen examined.* PERU. **Huánuco:** Pachitea, region of Pucallpa, western part of the “Sira Mountains” and adjacent low land; c. 24 km SE to c. 26 km ESE of Puerto Inca, from the beginning of the mountain rain forests next to ‘Campamento Pato Rojo [9°27′S, 74°46′W]’, *Wallnöfer 15–28488* (W).

**5. *Sabicea boyacana*** Liede, Meve & Khan, sp. nov. TYPE: Colombia. Boyacá. Region of Mt. Chapon, extreme western part, 100 miles NW of Bogotá, in high forest, 1005.84 m, 02 Jul. 1932 (fl), A. E. Lawrance 282 (holotype, S!; isotypes, BM!, F!, G!, HUH!, MO!, NY!). Figure 11A–I.

*Ad S. camporum, S. trianae, et S. burchellii similis, sed differt in tubis calycum abaxialibus basaliter sericeis et tubis corollarum crassis.*

Creeping vines, 6.1 m long; terminal flowering branchlets densely strigulose, and isolatedly to sparsely puberulous to lanuginose, trichomes (0.07–)0.1–1.3(–1.7) mm long, *Stipules* widely ovate, antrorse or with reflexed apices, (3.5–)6–8 × (3–)4–7 mm, apically (sub-)acute, basally obtuse, papyraceous, ciliolate with 0.1–0.2 mm long cilia, adaxially glabrous excluding the sericeous base, abaxially densely strigulose, at the lower part, eventually glabrescent at the apices and near the margins, trichomes (0.07–)0.1–0.7 mm long, (5–)9–11-veined, veins plain adaxially, slightly raised abaxially, colleters 9–12, 0.5–0.9 mm long. *Leaf blades* narrowly elliptic to lanceolate, 3.2–4(–9.5) × (1–)1.5–4.2 cm, apically acute to acuminate, basally obtuse to acute, papyraceous, ciliolate with 0.2–0.9(–1.1) mm long cilia, adaxially isolatedly to sparsely strigulose at secondary veins and lamina, densely strigulose and puberulous at costa, trichomes 0.1–0.8(–1.1) mm long, straight; abaxially isolatedly strigulose, to puberulous, sparsely to densely lanate to lanuginose at lamina, and sparsely to densely strigulose to sericeous, isolatedly to sparsely lanuginose, at costa and secondary veins, trichomes (0.1–)0.7–1.5(–1.7) mm long, secondary veins 11–12 pairs, obscured or plain



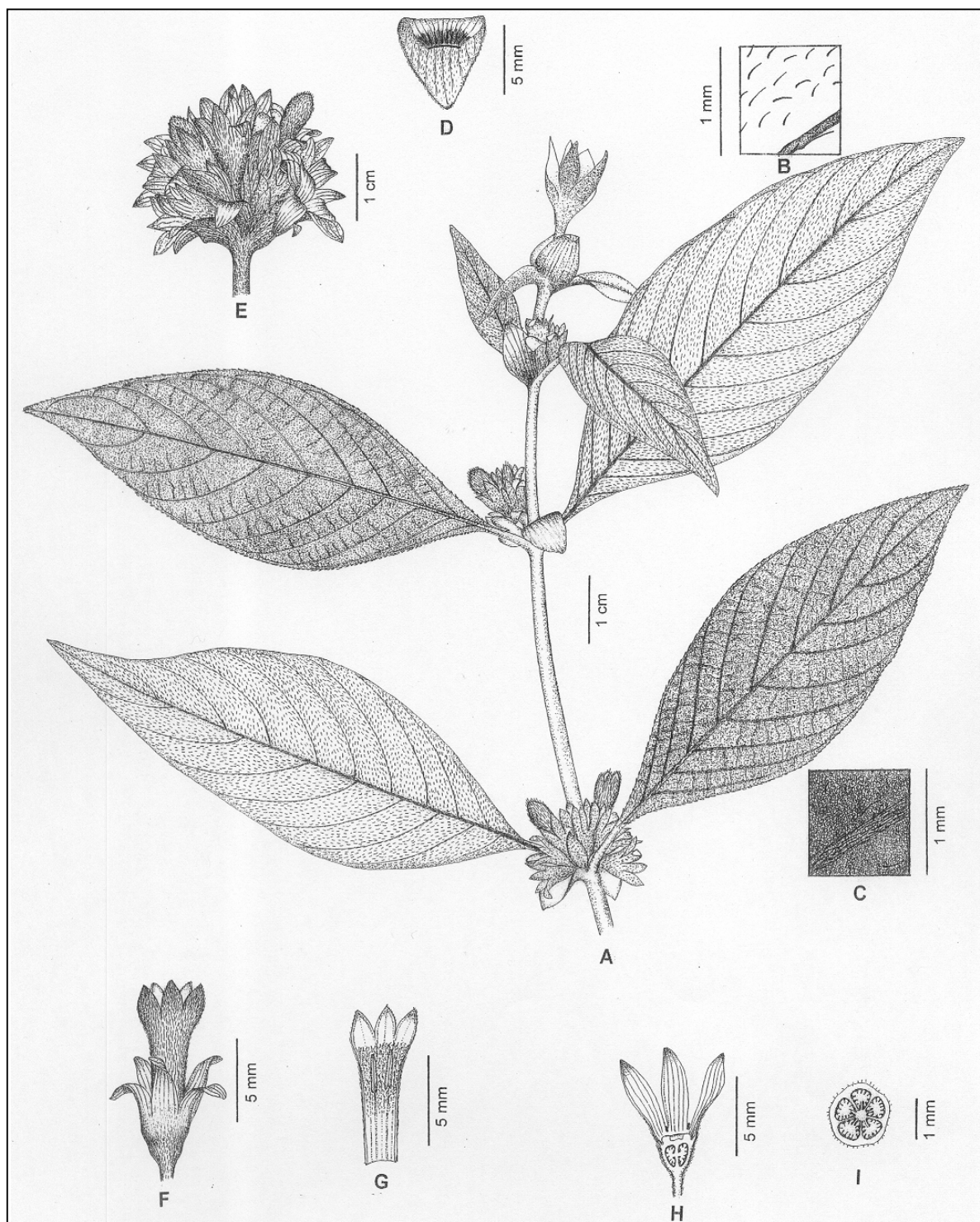


Figure 11. A–I. *Sabicea boyacana*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Part of outer and inner stipule surface. —E. Inflorescence. —F. Flower. —G. Inner corolla surface showing anther's position. —H. Longitudinal section through calyx and ovary. —I. Transversal section through ovary.

adaxially and sunken adaxially, tertiary veins distinct abaxially; *petioles* 3–12 mm long, sparsely to moderately densely hirsutulous to strigulose and lanuginose. *Inflorescences* in one leaf axil of each node, 5–9(–12)-flowered, compact-paniculate, 1–2.5(–3) × 1.5–3 cm; peduncles 1–6 mm long; primary axis (0)3–8 mm long; *bracts* (sub-)exinvolucrate, papyraceous, incompletely isolated into (2–)3–4 parts, isolated parts (3.5–)4.1–9 × 3–5 mm, 1–3-lobed, lobes 0.3–9 × 0.2–3.4 mm, ovate, apically subacute to obtuse, basally obtuse, margins entire, ciliolate with 0.7–0.2(–0.6) mm long cilia, adaxially densely sericeous, at the base, glabrous at rest of the surface, trichomes adaxially 0.4–0.7 mm long, abaxially isolatedly to moderately densely strigulose at the lower part and veins, eventually glabrous near the margins or at rest of the part, trichomes abaxially (0.7–)0.2–0.6 mm long, 5–7(–9)-ribbed, 1–3(–5)-ribbed, bracteoles (2–)4–6(–7) × (0.4–)3–4.1 mm, ovate to lingulate, not lobed, apically acute, base obtuse, margin entire, ciliolate, colleters (2–)4–7, 2–4 at bracteoles, 6 at bracts, (0.2–)0.3–0.9 mm long. *Flowers* white, subsessile or pedicellate, pedicels 1–3.5 mm long; *calyx* widely campanulate, 5-lobed, tubes 0.6–1(–1.5) × 2.2–2.5(–2.7) mm, lobes (2–)2.5–6(–7.1) × (0.5–)1.–2.8(–3.1) mm, antrorse to spreading or gently reflexed, elliptic to lingulate or ovate, apically subacute, margins entire, ciliolate with 0.1–0.2(–0.3) mm long cilia, adaxially, isolatedly to sparsely sericeous only at the base of tubes, eventually glabrous, abaxially indumentum nearly same to those at stipules, (1–)3(–5)-ribbed, with costa, abaxially gently prominulous, adaxially plain, colleters 1 in each sinus, 0.3–0.6 mm long; *corolla* salverform, tubes 7 mm long, lobes 2.4–2.8(–3.5) × 1.4–1.8 mm, ovate, antrorse to slightly reflexed, apically acute, basally truncate, margins entire, lobes adaxially glabrous, the indumentum of orifice extends up to 3.5–3.8 mm inside the tubes, abaxially densely strigulose, trichomes (0.1–)0.4–0.9 mm long, appressed; *stamens* 5 per flower, attached to corolla tube at 5.5–6 mm from the base, anthers 4–5, 1.9–2.5 × 0.4 mm; *style* 3.2 mm long, stigmatic lobes 4–5, linear, 1.8–2.5(–2.8) × 0.3–0.4 mm apices acute to acuminate; *ovaries* 1.4–1.6 × 1.7–1.8 mm, abaxially 5-lobed or uneven, whitish, densely strigulose, appressed to ciliate, 4–5-locular, each locule 1–1.1 × 0.5–0.7 mm. *Fruits* and *seeds* not seen.

*Discussion.* *Sabicea boyacana*, though known only from a single specimen from Colombia (Fig. 12), deserves to be considered as a separate species because it is distinct from its close allies *S. camporum*, *S. trianae*, and *S. burchellii* in a number of characters. None of these three species has indumentum at the adaxial base of calyx tubes and thicker corolla tubes (0.5–0.8 mm in contrast to 0.2–0.3 mm as *Sabicea boyacana* has). The presence of trichomes at the adaxial base of its calyx tubes and its thicker corolla tubes are unusual for other Neotropical *Sabicea* as well. Additionally, this species is distinguishable from *Sabicea camporum* by its compactly paniculate inflorescences including 4–6 colleters (in contrast to 2–4) at the adaxial base of bracts, shortly pedicellate flowers, and longer (7 mm in contrast to usually 4–6 mm long) corolla tubes. Likewise, it is distinct from *Sabicea trianae* by its compact

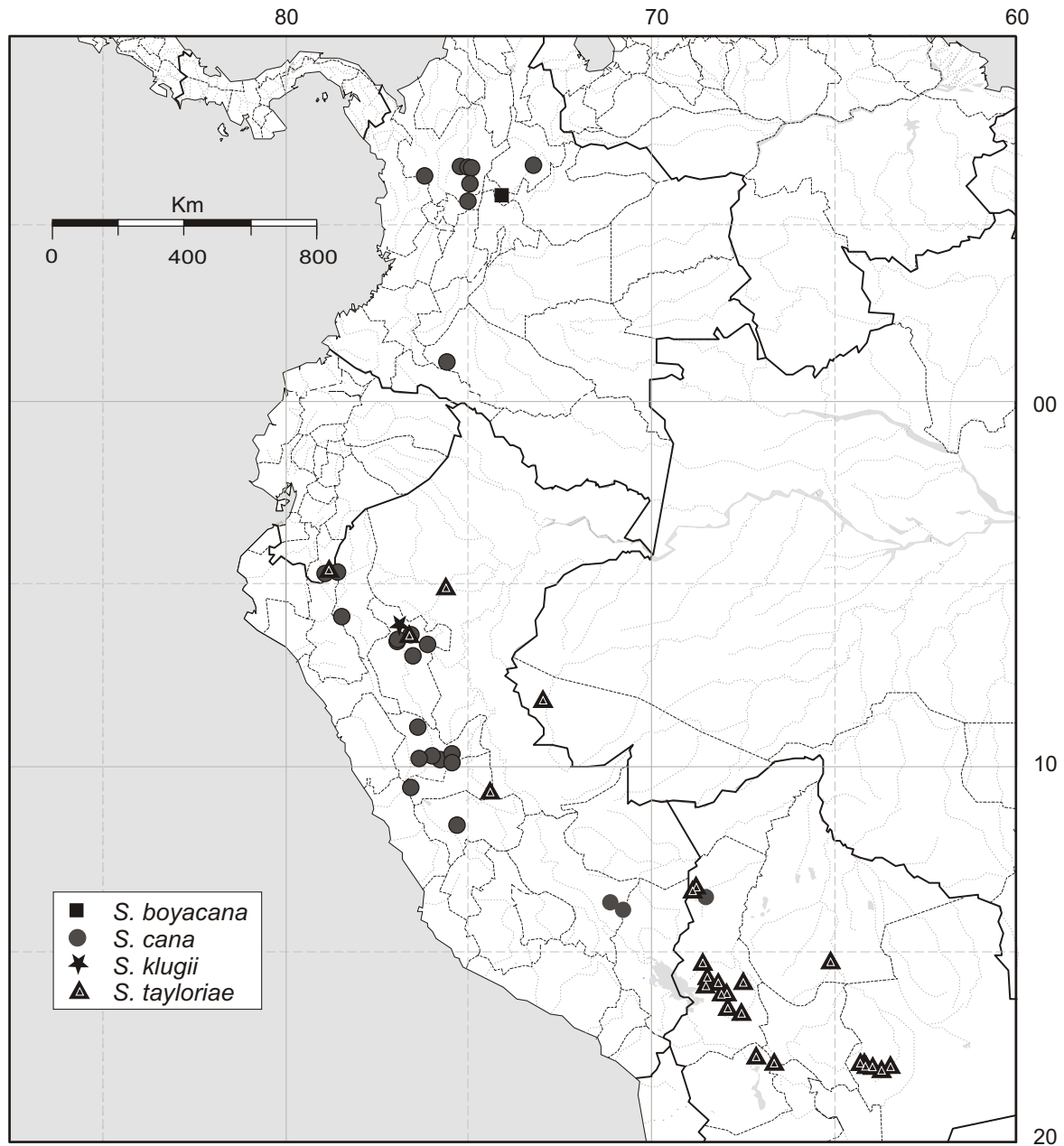


Figure 12. Map of southern Mesoamerica and northwest South America (in part), showing the distribution of *Sabicea boyacana*, *S. cana*, *S. klugii*, and *S. tayloriae*.

-paniculate inflorescences, adaxial surface of its leaves lacking the floccose or arachnose indumentum (Fig. 11B), abaxial surface of bracts, peduncles, pedicels, hypanthium and calyx lobes lacking arachnose indumentum (Fig. 11F), and presence of 4-6 colleters at the adaxial base of its bracts. It is distinguishable from *Sabicea burchellii* by its arachnose indumentum at lower surface of leaves, apically subacute to obtuse bracts, shorter (mostly 2.5-5 mm in contrast to 5-11 mm), and apically subacute to obtuse calyx lobes, distinct or indistinct primary axis (0-8 mm long).

Indumentum at abaxial leaf surface of *Tamberlik s.n.*, (W), collected from Brazil, are not typical as observed in the specimens of this species. Abaxially the leaves of this specimen are mostly

pubescent-strigulose and isolatedly to loosely arachnose all over, instead of densely and compactly arachnose all over and pubescent-strigulose at the costa and secondary veins. But all other characters are very similar to *Sabicea boyacana*, due to which it has been included under this species.

**6. *Sabicea brasiliensis*** Wernham, Monogr. *Sabicea* 51. 1914. TYPE: Brasil. Minas Gerais: Mar. 1839 (fl), *Clausen s.n.* (lectotype, designated here, G [2]!; duplicate, F!). Figure 13A–M.

Erect herbs to suffruticose or (sub-) shrubs, stems 0.4–1.5(–7) m long; terminal flowering branchlets densely arachnose or lanate to lanuginose, trichomes 1–2.5 mm long. *Stipules* widely lanceolate to ovate, reflexed, (2–)4–7(–9) × 3–5(–7) mm, apically subacute to acuminate, papyraceous, ciliolate with usually flexuose to curled cilia, adaxially glabrous excluding the basal part, abaxially sparsely to densely arachnose to or lanate to lanuginose almost all over, 9–12-veined, colleters 3–7, 1.1–1.5 mm long. *Leaf blades* usually elliptic to oblong or ovate, occasionally obovate to (sub-) orbicular to orbicular, rarely obcordiform, (1–)3–15 × (0.8–)3–5.5(–6.5) cm, thickly papyraceous, apically usually acute to acuminate or obtuse, sometimes mucronate, rarely shallowly obcordate, basally usually obtuse to (sub-) acute; adaxially lamina usually canescent to cano-lanuginose, occasionally isolatedly strigulose, costa and lateral veins densely canescent to arachnose, occasionally pilosulous; abaxially grayish-dull brownish white, lanate to lanuginose, secondary veins (5–)9–12(–17) pairs, plain to sunken adaxially and protruding abaxially, tertiary veins distinct and quaternary veins usually distinct or indistinct abaxially; *petioles* 1–4(–7) mm long. *Inflorescences* 1(–2) per node, 5–9-flowered, compact-fascicled, sessile, 1–1.5(–2) × 0.8–1.5(–2) cm; *bracts* exinvolucrate, membranous, incompletely isolated into 2 parts, isolated parts 3.5–5.5 × 3–5 mm, 1–2-lobed, lobes ovate to deltate, 0.5–1.5 × 0.2–1.2 mm, apically (sub-)acute, ciliolate with flexuose to curled cilia, 3–5-ribbed, bracteoles elliptic to lingulate, shallowly cymbiform, 1.4–3.5 × 0.5–1 mm, apically acute, colleters 2(–4), 0.2–0.7 mm long. *Flowers* white, sessile; *calyx* campanulate, 5(–6)-lobed, tubes (0.6–)1–1.5(–2) × 1.5–2.6(–3) mm, lobes 0.8–1.8(–2.1) × 0.8–2 mm, antrorse, deltate to ovate lingulate, apically acute, margins eciliate, adaxially apices usually glabrous, sometimes isolatedly sericeous or lanuginose, abaxially densely or lanate to lanuginose all over with overlapping the margins; *colleters* 1–2(–3), 0.1–0.2 mm below the sinus, 0.2–0.4 mm long; *corolla* white, salverform, tubes (3–)4–7 × 1.7–2(–2.5) mm, 4–5-lobed, lobes (1.5–)2–3(–3.6) × 1.2–1.8(–2.1) mm, ovate, usually antrorse, apically (sub-)acute, adaxially the indumentum of orifice extends up to (2–)2.1–3.2 mm inside the tubes, abaxially (cano-)arachnose to lanuginose, glabrous up to 1.2–3 mm at the base, trichomes (0.2–)0.8–1.4 mm long; *stamens* 4–5 per flower, attached to corolla tubes at (1.8–)2–4.7 mm from the base, anthers 1.5–1.7 × 0.4 mm; *style* 2.8–5.5(–6.5) mm long, stigmatic lobes 4–5,

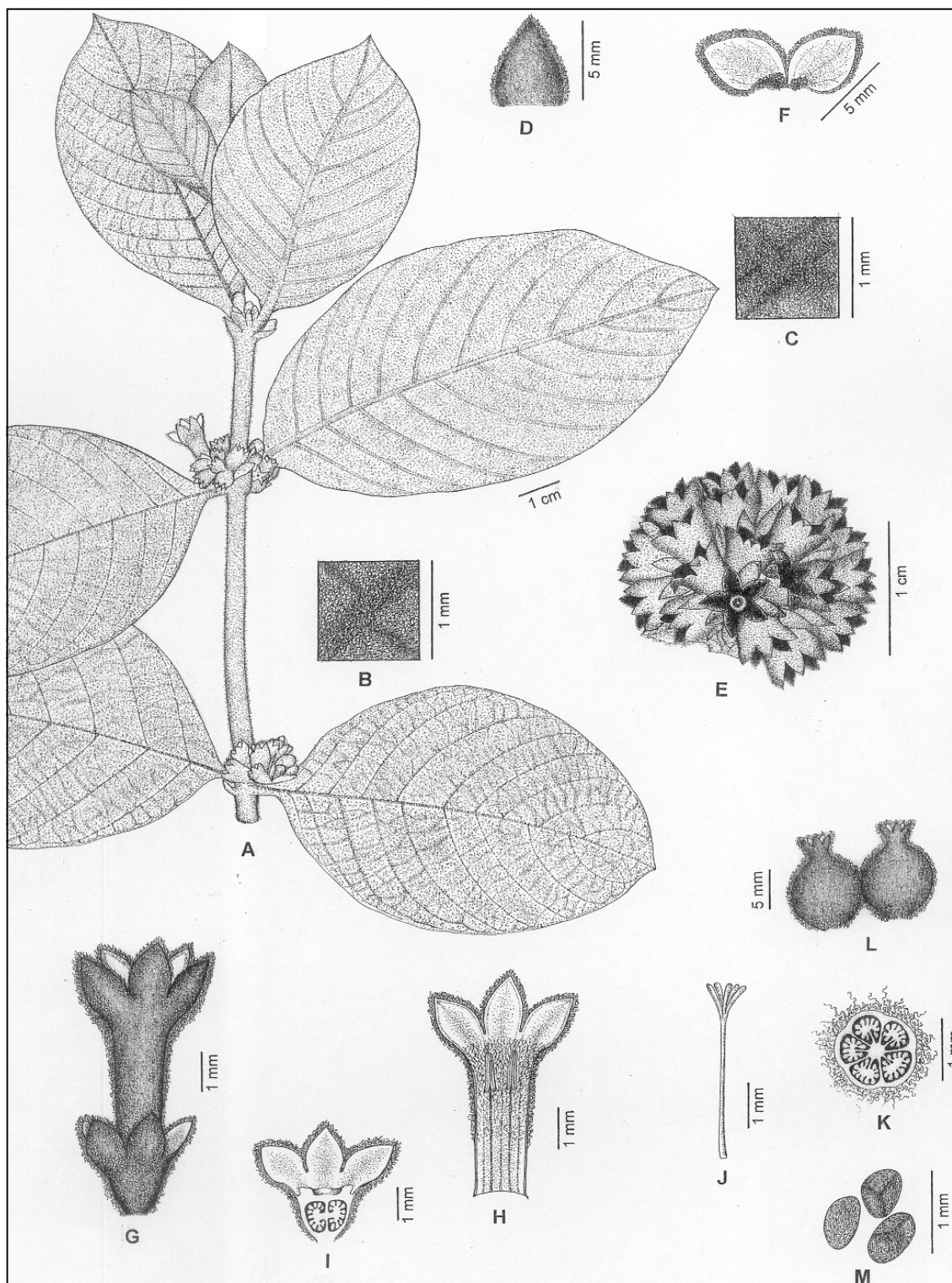


Figure 13. A–M. *Sabicea brasiliensis*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Outer stipule surface. —E. Inflorescence. —F. Inner bract surface. —G. Flower. —H. Inner corolla surface showing anther's position. —I. Longitudinal section through calyx and ovary. —J. Style and stigmas. —K. Transversal section through ovary. —L. Fruits. —M. Seeds.

1.1–2.1 × 0.1–0.3 mm; ovaries abaxially shallowly 5-lobed, (3–)4–5-locular, each locule 0.8–1.2 × 0.5–0.9 mm. Fruits gray-green to pinkish gray or light to grayish dull red or dark red-violet, 8–18 × 8–18 mm, when mature, abaxially sparsely to densely (cano-)arachnose to lanuginose; seeds 0.7–0.9 × 0.5–0.6 mm.

*Phenology, distribution and habitat.* Flowering in October to January, and fruiting January to May. Known from Distrito Federal, Goiás, Mato Grosso, Minas Gerais, Pernambuco and São Paulo of Brazil. Along roads and highways, in open, disturbed arid land in woodland or grassland, or forest or in belt of undisturbed xeromorphic open scrub to steep sandstone slopes, sand shore cliffs or at low hills or rocky hillsides; on red clay soil to low laterite scarp or shallow layer of laterite blocks to white or brown sandy soil enriched with humus, or soil full of quartz stones derived from quartz inclusions in weathered quartzite bedrock; 0.30–1400 m (Fig. 14).

*Discussion.* In the original description of *Sabicea brasiliensis*, Wernham (1914) cited seven characters in which it is distinct from *S. cana*. Four of these characters are contrasting to our observation. In *Sabicea brasiliensis*, neither are the leaves always non-arachnoid above, nor are the leaf bases different from *S. cana*, stamens are not always inserted in the mouth of corolla tubes, and ovary and stigma are not generally 5-merous. Though Wernham mentioned that the petioles of *Sabicea cana* are longer than the inflorescences, but these may be shorter than or equaling the inflorescences. Additionally, this species appears to be native to southeast and western Brazil, not to Bolivia as cited by Wernham (see *Sabicea tayloriae*). *Sabicea brasiliensis* differs from *S. cana* by its erect habit, adaxially always canescent and sometimes in addition lanuginose or arachnose leaf blades (Fig. 13B), short (1–4[–7] mm, in contrast to [8–]10–25[–30]) petioles and usually glabrous styles (Fig. 13J). In *Sabicea brasiliensis*, the isolatedly distributed trichomes are observed only on the upper part of styles but not along the styles as in *S. cana*.

*Sabicea brasiliensis* appears close to *S. tayloriae* from which it is distinct by its erect habit, compact-fascicled and sessile inflorescences (Fig. 13A, E), usually at least partially sunken secondary and tertiary veins, and canescent to cano-lanuginose, in addition occasionally strigulose to pilosulous indumentum at the adaxial surface of leaf blades, short petioles (1–4[–7] mm in contrast to [6–]8–25 mm) and (cano-)arachnose to lanuginose indumentum at abaxial surface of corolla tubes.

*Sabicea brasiliensis* seems close to *S. humilis* due to the similar habit, leaf shapes, presence of arachnoid indumentum at abaxial leaf surface, however, it clearly differs from *S. humilis* by its densely arachnose or lanate to lanuginose branchlets, abaxial stipule surface, and inflorescences, adaxially usually canescent to cano-lanuginose leaf-blades, shorter (usually 0.8–2 mm in contrast to 2.5–7.1 mm), apparently equal, deltate to ovate or oblong, marginally eciliate calyx lobes. Abaxially the leaves of both species contain arachnoid



indumentum. Yet, abaxially the densely arachnose or lanate to lanuginose leaves of *Sabicea brasiliensis* are readily distinguishable from the leaves of *S. humilis* that are covered with shaggy indumentum comprised of long and straight trichomes, almost masking the arachnoid indumentum. Some *Sabicea brasiliensis*, especially of Mato Grosso, seem similar to *S. burchellii* but they are easily distinguishable by their abaxially arachnose calyces and abaxially cano-arachnose to lanuginose corolla. *Irwin et al.* 34959 (WIS), collected from ca. 25 km S of Niquelândia, Goiás seems intermediate between *Sabicea burchellii* and *S. brasiliensis*. Although its indumentum of younger leaves and petiole length indicate its closeness to *Sabicea brasiliensis*, calyx lobes and indumentum of branchlets, older leaves and calices suggest its placement in *S. burchellii*.

Wernham (1914) mentioned thirty syntypes without designating any holotype. Three (*Williams* 173 & 303, and *Rusby* 1905) of these syntypes collected from Apolo, Bolivia, are found to belong to the new species *Sabicea tayloriae*. We have seen fifteen of other twenty seven syntypes: *Claussen* 560 (syntype, G!, F!), 568, 609 (syntypes, G!), *Pohl* 148, 957, *Richard s.n.* (syntypes, not seen) Pernambuco: 1859, *Gardner* 2886 (syntype, HUH!, BM!); Bahia: *Blanchet s.n.* (syntype, not seen), Minas Gerais: no date, *Clausen* 673 (syntype, HUH!, NY [2]!, S!), Mar.01, 1839, *Clausen s.n.* (syntype, G[2]!, F!), 1840, *Clausen* 271 (syntype, BR!), *S. Hilaire* 283, 2281 (syntypes, not seen), Caldas, Mar, 1848, Mar, 1957, Dec 24, 1867, Mar 04, 1868, May 5, 1869, *Regnell* 1016 (syntypes, F!, S[6]!), *Schneck* 3379 (syntype, not seen), *Weddell* 2563 (syntype, not seen); Goiás: 1868, *Burchell* 5136 (syntypes, BR!, HUH!), 1868, 8061 (BR!), no date, 6532 (syntypes, BR!, HUH!), 7035 & 8383 (syntypes, not seen), *Gardner* 3225 (syntype, BM!); Caraca: *Glaziou* 14912 (syntype, not seen), Lagoa Santa, no date, *Warming* 105 (syntype, S!); Andayatuba & Ytú, Feb, 1834, *Riedel* 2065 (syntype, BM!, BR!, F!); Faria: *Glaziou s.n.*, Boro de Campo, *Riedel* 116 (syntype, BR!).

Among these syntypes *Clausen s.n.* (G[2], F.), *Claussen* 560 (G [2], F), *Regnell* 1016 (F, S[6]), and *Warming* 105 (S) are found in good condition with flowers. Only one collection of *Regnell* 1016 was seen with fruit, and it doesn't represent the common shape of leaves. We select *Clausen s.n.* (G) as the lectotype as we have found it in relatively better condition than the others containing flowers.

*Selected specimens examined:* BRASIL. **Bahia.** Espigao Mestre, ca. 10 km N of Rio Roda Velha, ca. 100 km WSW of Barreiras, *Anderson et al.* 36919 (F, NY, WIS). **Distrito Federal:** Brasília, Acampamento do D, V, O, *Belém & Mendes* 80 (NY), University of Brasilia Campus, *Fosberg* 57380 (F, HUH, US, NY, L), Bacia do Rio São Bartolomeu, *Heringer et al.* 2906 (MO), km 16, BR-020 (Road, Brasilia-Fortaleza), Area do CPAC-EMBRAPA, *Kirkbride* 1092 (G[2]), Bacia do Rio São Bartolomeu, 15°0'S, 47°W, *Heringer et al.* 5877 (MO, US), Gama, *Tanaka et al.* 11 (NY); Chapada de Contagem, Steep cerrado hillside, ca. 20 km NE of Brasilia, *Irwin et al.* 9582 (F, HUH, MO), NE Brasilia, about 25 km west of intersection with BR 020, 15°36'S, 48°03'W, *Plowman* 9954 (F, G); Cocheira de Pipiripau, 12 km de Planaltina

Leste, 15°37'S, 47°40'W, *Heringer 14272-A* (MO); near Planatina about 22 km NE of Brasília, *Fosberg 57382* (US); Regiao Burracao, perto de BR 020, 15°35'S, 47°27'W, *Kirkbride Jr. 3962* (BR, F); Corrego Palmeiras, 16°2'S, 47°39'W, *Kirkbride Jr. 4370* (F); Encosta de Morro da Canastra a base da escarpa, 15°35'S, 47°54'W, *Kirkbride Jr. 4590* (BR, F); SW de Corrego Almecegas, 15°33'S, 48°10'W, *Kirkbride Jr. 4827* (BR, F, U); Entre Fazenda São Jose e BR 020 na Regiao Buracao, 15°35'S, 47°27'W, *Kirkbride Jr. 5144* (F); 1,5 km W de Escola Fazedaria, 15°51'S, 47°49'W, *Kirkbride Jr. 5219* (BR, F, US); Bacia do Rio São Bartolomeu, cercanias dos Córregos Forquilha e da Lage, 15°0'S, 47°W, *Heringer et al. 6522* (MO, US); Lago Sul, próximo da barra do córrego do Gama, *Pereira 205* (MO); Basin of Rio São Bartolomeu, 4K from DF-130, north side of DF-260, *Guala & Filgueiras 1447* (US); **Goiás**: Serra dos Pyreneos, Goyaz, *Ule 321* (F-2); BR 7K 655, *Pereira 7355* (F); ca. 33 km S of Caiaponiaon road to Jatai, *Irwin & Soderstrom 7111* (F); Goiás-Goiânia-Alexânia, *Duarte 8307* (US), *Mattos 483* (US); ca. 20 km S of Corumba de Goiás, *Irwin et al. 11022* (F, HUH, MO); Serra Dourada, ca. 20 km SE of Goiás Velho, 14°0'S, 50°00'W, *Irwin et al. 11846* (G, S); serra dos Crist, ca. 8 km S of Cristalina, 17°0'S, 48°00'W, *Irwin et al. 13651* (F, G, HUH, MO, S); Serra Geral de Goiás, Rio da Prata, vicinity of Posse, *Irwin et al. 14525* (G, S); Campo, near Corrego Estrma, ca. 38 km NE of Formosa, *Irwin et al. 15202* (F, HUH), Pirineus, *Harley & Lima 11482* (NY); 15 km north of Corumba de Goiás on road to Niquelândia, Goiás in valley of Rio Corumba, *Irwin et al., 18626* (F, HUH, MO); Pirenopolis, subidapara Serra de Pirineus solo arenoso, *Nelson & Lima, 690* (F); Chapadas dos Veadeiros, ca. 7 km south of Cavalcante, *Irwin et al., 24090* (G), ca. 35 km north of Veadeiros, *Irwin et al. 24286* (F, HUH, MO, S), ca. 10 km S of Alto do Paraiso (formerly Veadeiros) *Irwin et al., 24943* (F, HUH, MO, NY), *Irwin et al. 32934* (MO, WIS), 6–7 km E of Alto Paraiso on road to Nova Roma, region of cerrado with sandstone outcrops, giving way above to grassy campo and below to mesophytic forest, *Anderson 6510* (WIS); Contraforte central, ca. 24 km NE of Catalao, *Irwin et al. 25086* (F, HUH); Serra Geral do Parana, Termite mounds in cerrado, Campo and cerrado, ca. 10 km S of São Jao da Alianca, *Irwin et al. 32011* (WIS); Serra dos Pireneus, Ca. 20 km E of Pirenipolis, *Irwin et al. 34059* (WIS); 8 km by road west of Monte Alerge, *Anderson 6850* (WIS); Caldas Novas, Rio Quente, at foot of west side of the Serra de Caldas, 13 km due WSW of city of Caldas Novas, 17°48'S, 48°45'W, *Heringer & Eiten 14112* (US); Caldas Novas, Pousada do Rio Quente, *Krapovickas et al. 33288*, (F); ca. 3 km NO de Goiás Velho, 15°55'S, 50°09'W, *Kirkbride Jr. 3381* (BR, F); Corumbá de Goiás, Topo do Pico dos Pirineus, serra do Catingueiro 6 km de Cocalzinho, *Noguera et al. 73* (F); Morro do Urubo, Cristalina, 16°45'S, 47°35'W, *Hatschbach 43746* (MO); Morro da Cruz, 16°3'S, 47°48'W, *Kirkbride Jr. 5123* (BR, F); APA Carste de Lagoa Santa, Lagoa Santa e Matozinho, *Brina & Costa s.n.* (MO); Niquelândia, Estrada de chão com entrada no Km 8 da rodovia Niquelândia/Uraucú, Fazenda Traíras, *Fonseca et al. 869* (US). **Mato Grosso**: Xavantina, ca. 6 km S of Xavantina, *Argent et al. 6490* (NY, U); West of Km 245 Xavantina-Cachimbo road, *Philcox et al. 3489* (NY); between Km 256, Xavantina-



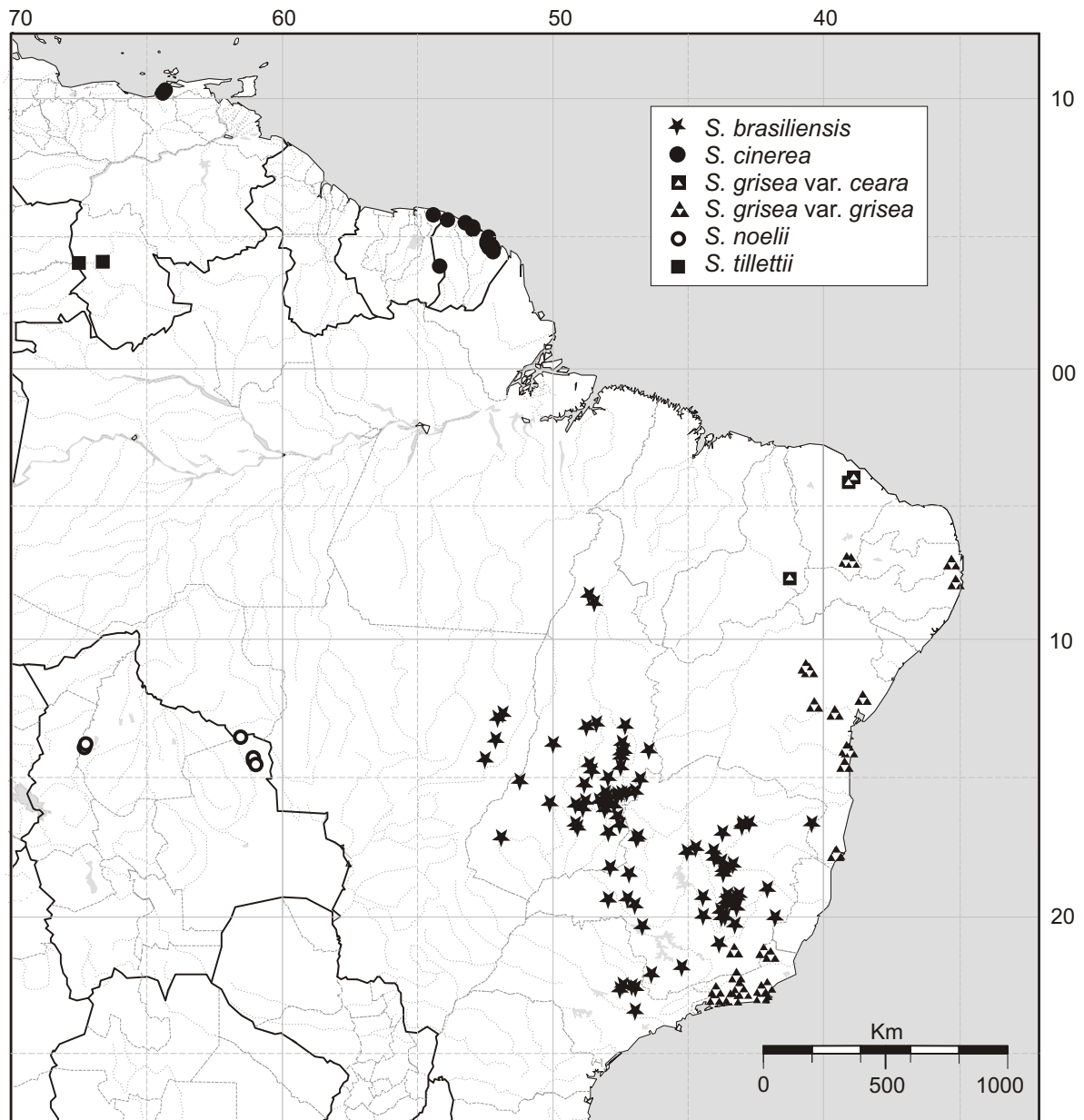


Figure 14. Map of northeast, central, southeast, and eastern South America (in part), showing the distribution of *Sabicea brasiliensis*, *S. cinerea*, *S. grisea* and *S. noelii*, and *S. Tillettii*.

Cachimbo road and Base Camp, 12°49'S, 51°46'W, *Philcox et al.* 3704 (NY); 18,5 km along road S from Base Camp, *Harley et al.* 10877 (NY, U); 8 km NE of the Base Camp of the Expedition, 12°54'S, 51°52'W, *Ratter et al.* 903 (NY, U); Serra do Roncador, Barra do Garcas, 255 km along new road NNE of village of Xavantina, 7,2 km due to SW of Royal Geographic Society Base Camp, 6, east of main road, *Eiten & Eiten* 9749 (MO, NY, US), 260 km along new road NNE of village of Xavantina, at Royal Geographic Society Base Camp, 6 km S of Corrego dos Porcos, *Eiten & Eiten* 9560 (US). **Minas Gerais:** Baguari, *Regnell* 1060 (S), Serra do Curral, Belo Horizonte, *Magalhães* 19189 (U), Belo Horizonte, *Magalhães* 1959 (US); Morro das Pedras, Belo Horizonte, *Williams* 6964 (F, HUH), *Williams* 5988 (F, HUH); Caldas, *Regnell* 1016 (F); Diamantina, Rodovia BR 367, ca. 30 km N de Diamantina, 18°6'41''S, 43°30'07''W, *Pirani et al.*

4004 (G); Serra do Espinhaco, ca. 8 km N of Gouveia on road to Diamantina, *Anderson et al.* 35375 (WIS); Corinto, Fazenda do Diamante, base of Serra do Angico, *Mexia* 5606 (BM, F, G, MO, NY, WIS, S, U); Florestal, *Ucchioni* 44172 (US), Cerrado Horto Florestal, arredores da Cidade, *Brade & Barbosa* 17865 (F); Lagôa Santa, *Pires & Black* 2881 (U); Jaboticatibas, 10 km north of Lagoa Santa, Km 56 on the road from Belo Horizonte to Conceição, *Smith et al.* 6977 (NY), Jaboticatubas, at Km 111 along Almeida-Conceição do Mato Dentro road, *Eiten & Eiten* 10908 (MO, NY, U, US), Cerrado, vicinity of Jaboticatubas, E of Sete Lagoas, 43°45'W, 19°29'S, *Gentry et al.* 49554 (MO), Sua do Cipo, *Ucchioni* 1813 (US); Paraopeba, *Rizzimi* 125722 (F); ; Serra do Esninhaco, Serra do Cipó, ca. Km 112, ca. 135 km N of Belo Horizonte, *Irwin et al.* 20439 (F, G, HUH, MO, NY, S); ca. 18 km West of Grão Mogol, *Irwin et al.* 23649 (F, NY), Grão Mogol-Cristália, 16°42'S, 42°51'W, *Cordeiro et al.* 943 (MO); ca. 20 km SW of Diamantina, *Irwin et al.* 22311 (F, NY), ca. 2 km N, of São Joao da Chapada, *Irwin et al.* 28327 (F[2] HUH, NY, US), ca. 8 km N, of Gouveia on road to Diamantina, *Anderson et al.* 35375 (NY), km 112 ao longo da rodovia Lagoa Santa-Conceição do Mato, *Joly & Gemtchujnicov* 1014 (NY), Curitiba, *Hatschbach et al.* 28668 (US), Corrego Cochoeira (Min, Bocaiúva), *Hatschbach*, 40791 (MO, US), between Veu da Noiva and Alto do Palacio, 19°15'S, 43°40'W, *Landrum* 4216 (NY), Santana do Riacho Co, 100 km of Belo Horizonte, 19°23'S 43°45'W, *Fernandes* 3U2 (NY); 2 km N of São Joao da Chapada, *Irwin et al.* 28327 (F); Immediately E of Joaquim Felicio, *Irwin et al.* 27032 (F, HUH, NY), Morro do Chapéu-Nova Lima, 19°59'S, 43°50'W, *Andrade et al.* 1022 (MO), *Andrade* 4511 (MO); Santana do Riacho, UCAT, Campo Rupestre, *Lopes & Andrade* 8760 (MO), Serra do Cipó próximo ao Chapéu de Sol, 19°9'S, 43°42'W, *Lombardi. & Toledo* 266 (MO); Varzea da Palma a Serra do Cabral, *Hatschbach et al.* 69031 (G); Serra da Anta, ca. 2 km N of Paracatú, *Irwin et al.* 26089 (F, NY); Corações-São Tomé das Letras, *Hatschbach & Ahumada* 31242 (NY, US); Curitiba, ca. 8 km E of the Araxá junction on highways 262 to Belo Horizonte, Ibiá, 19°35'S, 46°53'W, *Devidse & Ramamoorthy* 10873 (MO); São Sebastião das Águas Claras, 17°10'S, 46°50'W, *Martins & Batitucci*, 8504 (MO); 4 km oeste do Rio Preto perto de DF 6, 18°18'S, 47°27'W, *Kirkbride Jrn.*, (F); Indianópolis, Fazenda Bela Tanda and neighbouring fazendas, 6 km NE of Indianópolis, campo cerrado, in the direction of Fazenda tabatinga, 19°13'S, 47°57'W, *Gottsberger* 12–10386 (NY); Perdizes, *Neto & Werneck*, 1754 (MO); Turvo, *Hoehne & Gehrt* 17493 (F, NY). **Pernambuco:** Mouth of Rio Preto, *Gardner* 2886 (BM). **Rio de Janeiro:** Entre Rio das Mortes e Nazare, *Pabst* 6860 (M). **São Paulo:** *Heiner*, s.n. (S); *Burchell* 5136 (BR, HUH); Rio Claro, *Löfgren* 513 (F); Jundiáhy, *Brade* 7057 (F, HUH); Moji-Guacu, Reserva Florestal Fazenda Campininha, proximo de Pauda Sales, E, F, S, *Kuhlmann* 3806 (NY-2); Mogi-Guaçu, *Kuhlmann*, 3806 (F); Pirassununga, cerrado de Emas, 22°02'S, 47°30'W, *Batalha & Mantovani* 28 (F). Santa Luzia, Lagoa Santa, *Mello Barreto* 3598 (F); Fundação Zoobotânica, *Heringer* 8903 (U); Goiânia, terreno firme, *Coêlho* s.n. (MO); O,5 km N of Ministerio Edificios, *Kirkbride Jr.* 1688 (F); BR 414, Prox Dois Irmãos, *Parlo* 017 (F); Campo sujo, cabeça de Veado, 1 km S de Escola Faziendeira por estrada, *Kirkbride* 3169

(BR, F). **Tocantins:** ca. 12 km S of Guará, *Irwin et al.* 21582 (F, G); Presid. Kennedy, Road from highway BR-153 to Itaporã, 12 km west, Fazenda Primavera along Ribeirao Feinho, *Plowman et al.* 8145 (F, MO); Serra do Palmeirópolis, 13°3'44''S, 48°22'1W, *Hatschbach & Guimarães* 56334 (MO).

**7. *Sabicea burchellii*** Wernham, Monogr. *Sabicea* 49. 1914. TYPE: Brazil: Pará, between S. Toao and S. Aña, no date, *Burchell* 9271 (holotype, K!; isotypes, BR!, P, not seen). Figure 15A–N.

Vines; terminal flowering branchlets sparsely-densely pilosulous to pubescent. *Stipules* widely to narrowly ovate, antrorse to reflexed, (3–)10–14 × (3–)7–8(–11) mm, membranous, apically acute, ciliolate with (0.2–)0.4–0.7 mm long cilia, adaxially glabrous excluding the basal part, abaxially sparsely to densely strigulose to pilosulous or puberulous at the lower part, eventually glabrescent at the apices, trichomes (0.2–)0.5–0.9 mm long, 9–11-veined. *Leaf blades* oblong to elliptic or obovate, (1–)7–12(–15.5) × (1–)2–6.5(–8) cm, papyraceous, apically usually acute, rarely acuminate or mucronate, ciliolate with 0.2–0.8 mm long cilia, lamina sparsely, costa and secondary veins sparsely to densely strigulose to hirtellous or pubescent, trichomes 0.2–1.3 mm long; abaxially lamina sparsely, costa and secondary veins densely sericeous to villosulous, trichomes (0.2–)1.5–2.1 mm long, secondary veins 13–14 pairs, obscured or plain adaxially and protruding abaxially, tertiary veins usually prominulous and quaternary veins usually distinct abaxially; *petioles* (2–)9–15 mm long, densely strigulose to pilosulous or hirtellous. *Inflorescences* usually one per node, 5–11-flowered, capitate to compactfascicled, 2–3 × 2–3.5 cm; *peduncles* 0–2 mm long; *bracts* (sub-)exinvolucrate, papyraceous, incompletely isolated into 2 parts, isolated parts, (4–)8–12 × (4–)6–8 mm, 1–3-lobed, lobes usually ovate or widely lanceolate, 1.5–2(–4) × 1–1.5(–3) mm, apically acute to acuminate, ciliolate with (0.1–)0.2–0.6 mm long cilia, adaxially apices isolatedly to sparsely strigulose, densely sericeous at the margin of base, abaxially lower part densely strigulose, trichomes (0.2–)0.5–1.4 mm long, 7–9-ribbed, bracteoles elliptic to narrowly ovate to lanceolate, 2–7(–9) × 1–2(–3.5) mm apically acute, colleters 2. *Flowers* (sub-)sessile, pedicels 0–1.5(–2) mm long, densely pilosulous, trichomes 0.6–1.3 mm long; *calyx* campanulate, 5-lobed, tubes (0.5–)0.8–1.2 × 1.5–2(–2.7) mm, lobes 5–11(–14) × 0.6–2.1 mm, antrorse, rarely spreaded, lanceolate, occasionally narrowly elliptic or widely linear, usually unequal, apically acute to acuminate, ciliolate with 0.5–0.8(–1.1) mm long cilia, adaxially usually glabrous, occasionally isolatedly strigulose to puberulous at apices trichomes 0.2–0.6 mm long, abaxially costa and base densely and rest of the surface isolatedly strigulose to puberulous, trichomes (0.5–)0.0.7–1.1 mm long, colleters 1 in each sinus, 0.3–0.4 mm long; *corolla* white, salverform, tubes 6–8(–11.5) × (1.5–)1.8–2.4 mm, lobes ovate to widely lanceolate, usually antrorse, 2.6–4(–4.6) × (0.8–)1.8–2.4 mm, apically acute, adaxially the indumentum of orifice

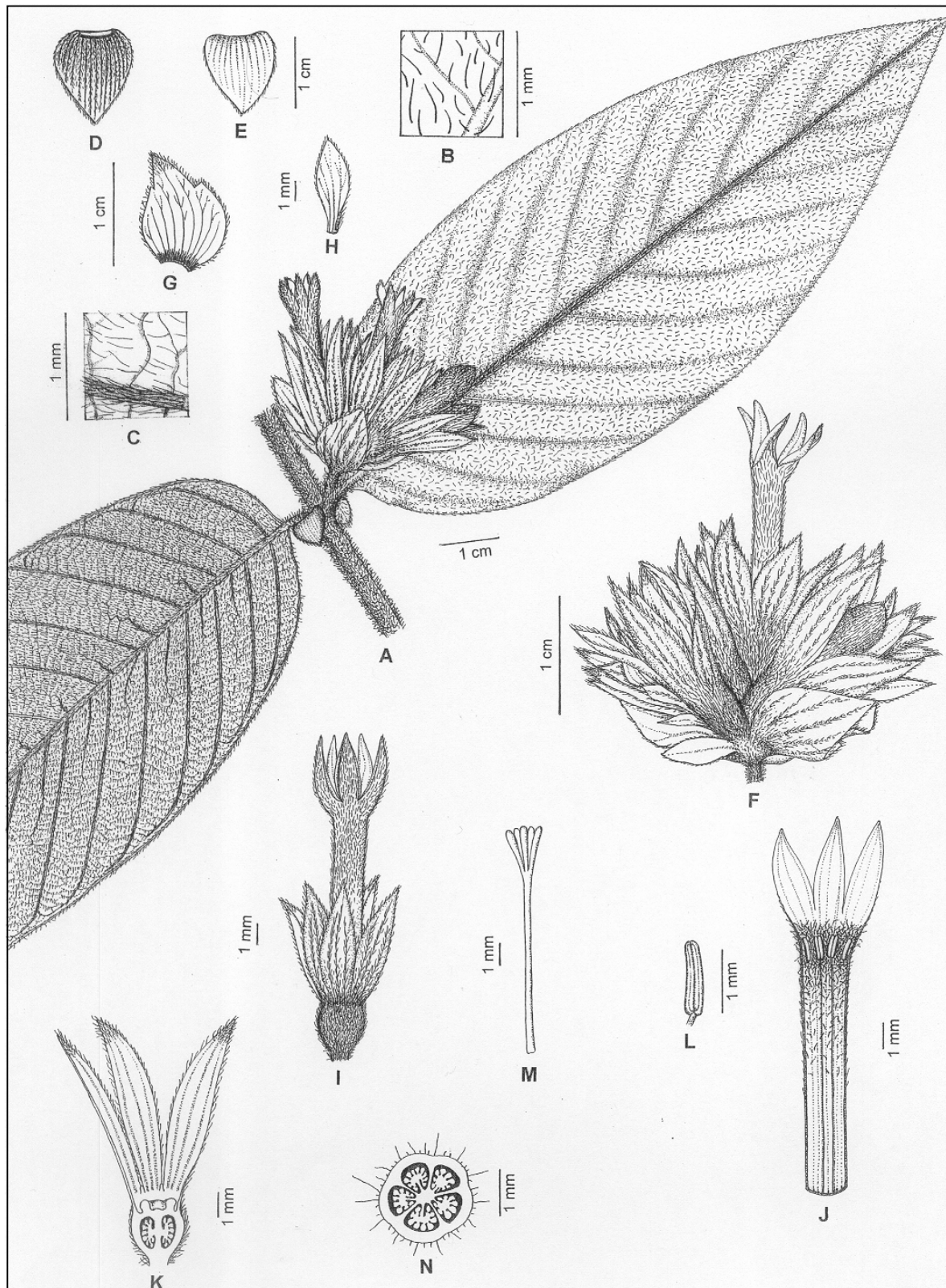


Figure 15. A–N. *Sabicea burchellii*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Outer stipule surface. —E. Inner stipule surface. —F. Inflorescence. —G. Inner bract surface. —H. Inner bracteole surface. —I. Flower. —J. Inner corolla surface showing anther's position. —K. Longitudinal section through calyx and ovary. —L. Face view of Anther. —M. Style and stigmas. —N. Transversal section through ovary.

extends up to 4.1–5 mm inside the tubes, abaxially densely strigulose to pubescent, trichomes (0.5–)0.7–1.1 mm long, (0.8–)1.1–1.5 mm long, or anthers 1.1–1.3 × 0.4 mm; style 8–8.5 mm long, stigmatic lobes 2.4–2.7 × 0.3–0.4 mm; ovaries (1.5–)1.8–2.5 × 1.5–2 mm, abaxially plain or uneven, densely strigulose to pilosulous, trichomes of hypanthium 0.2–1.1 mm long, ovaries 5-locular, each locule 1.4–1.5 × 0.4–0.6 mm. Fruits purple, 8–12 × 8–12, when mature, abaxially strigulose to pilosulous; seeds not seen.

*Phenology, distribution and habitat.* Flowering in October to February, and fruiting in March. Known from Mato Grosso, Pará and Tocantins, Brazil. Found in natural grassland of dried up stream beds, pond's edges, dry open pastures, and roadside thickets along river. Collected from moist and dry soil; 165–460 m (Fig. 9).

*Discussion.* Wernham (1914) recognized *Sabicea burchellii* as a well-defined species nearest to *S. amazonensis*. This species is remarkable basically for its fascicled inflorescences, long and generally lanceolate calyx lobes, indumentum lacking curled to tortuous trichomes, strigulose to hirtellous or pubescent indumentum of upper leaf surface composed of short trichomes and sericeous to villosulous indumentum at the lower surface of leaves comprised of long and fine trichomes (Fig. 15A, I), due to which it seems as barely related to *Sabicea amazonensis*. Rather, apparently it appears close to *Sabicea mexicana*, and then to *S. boyacana*, *S. mattogrossensis*, and *S. noelii*. It differs from *Sabicea mexicana* and *S. mattogrossensis* mainly by its longer trichomes on upper leaf surface, almost indistinct [0–2 mm in contrast to usually (1–)2–6 mm long] peduncles and pedicels and without any primary axis, and longer (2.6–4 mm in contrast to 2–2.4 mm) and lanceolate corolla lobes.

*Sabicea burchellii* is distinct from *S. noelii* by its appressed trichomes at leaves and outer surface of corolla tubes (Fig. 15B), larger stipules, shorter calyx tubes, colleter's location at sinus, longer and shorter trichomes at outer surface of calyx lobes and corolla tubes respectively, and shorter corolla tubes. *Sabicea burchellii* is distinct from *S. boyacana* by its non-arachnoid indumentum at lower surface of leaves, apically acute to acuminate bracts, longer (usually 5–11 mm), and apically acute to acuminate calyx lobes, adaxially glabrous calyx tubes, and absence of any primary axis. Superficially, the inflorescences of *S. burchellii* appear similar to those of *S. grisea*, from which it can be readily distinguished by its non-arachnoid or non-lanuginose indumentum at branchlets, lower surface of leaves, and outer surface of stipules, bracts, and calyces, and appressed external trichomes of corolla tubes.

*Sabicea burchellii* is similar to *S. humilis* in inflorescence structure and calyx lobe size and shape, but can be distinguished by its larger stipules (usually 10–14 × 7–11 in contrast to 4–6 × 4–6 mm), longer petioles [(2–)9–15 mm in contrast to 1–3(–5) mm], non-shaggy indumentum especially of lower surface of leaves and outer surface of inflorescences excluding corolla tubes, absence of arachnoid indumentum at lower surface of leaves, and appressed and shorter (usually 0.7–1.1 mm in contrast to (1.2–1.8) external trichomes of

corolla tubes.

The collections *Eiten & Eiten 9083 & 9090* differ from the type specimen by their short and appressed trichomes on abaxial leaf surface in contrast to long and (sub-)appressed to spreading trichomes. However, any infraspecific categorization was avoided due to the lack of enough representative specimens. The collections *Anderson 9853* (MO, NY, W), *Assumpção & Duarte s.n.* (US), *Plowman et al. 9024* (F, MO, NY) and *Silva et al. 4154* (US) deviate from the original description by Wernham (1914) in their abaxially sparsely to moderately densely arachnoid leaves. However, they differ from *Sabicea grisea* by their adaxially glabrate calyx lobes, and abaxially strigulose corolla tubes. Most probably these collections are hybrids between *Sabicea burchellii* and *S. grisea*, which are found in the adjacent areas and almost similar habitats.

*Additional specimens examined.* BRASIL. **Mato Grosso.** Serra do Roncador, Barra do Garças, At correjo do Gato, a few hundred meters east of main road, 210 km along new road NNE of village of Xavantina, 50 km due S of Royal Geogr. Society Base Camp, *Eiten & Eiten 9083 & 9090* (US, NY).

- 8. *Sabicea calophylla*** Asplund, Svensk Bot. Tidskr. 26(1–2): 195–197, f. 3. 1932. TYPE: Brazil: Amazonas ad flumen Vaupés prope pagum Taraená, 07 Feb. 1924 (fl), *D. Melin 144* (holotype, S!).
- S. grandifolia* J. A. Steyerl., Fl. Venezuela, 9(1): 514. 1974. TYPE: Venezuela: Territories of Federal Amazon, Vicinity of San Simon de Cocuy, 2 km. NE of Piedra de Cocuy, 1°12'N, 66°54'W, alt 100 m, 27 Apr. 1974 (fl), *G. Morillo, B. de Morillo & C. Wood 4070* (holotype, VEN, not seen; isotypes, NY!, US!).

Suffruticose to lianas or vines, scandent and sprawling; terminal flowering branchlets densely strigulose, isolatedly arachnose, trichomes, (0.2–)0.3–0.7 mm. *Stipules* widely oblong to lanceolate or ovate to triangular, usually antrorse and appressed, rarely slightly reflexed, (4–)5–9 (–12) × (3–)4–6 mm, membranous, apically obtuse or subacute, ciliolate with 0.1–0.2(–0.4) mm long cilia, adaxially glabrous excluding the basal part, abaxially densely strigulose, trichomes 0.2–0.7 mm long, 10–12-veined, colleters 15–18, 0.6–1.5 mm long. *Leaf blades* elliptic to oblong, or widely oblanceolate, (7.5–)10–20 × (3–)4–8(–9) cm, membranous, apically (sub-)acute to bluntly acuminate, rarely mucronate or (sub-)obtuse, ciliolate with (0.1–)0.2–0.8 mm long cilia, lamina and secondary veins isolatedly to sparsely and costa usually densely strigulose to puberulous, trichomes 0.07–0.8 mm; abaxially fulvous, lamina isolatedly to sparsely sericeous or strigulose to pilosulous, and densely lanuginose, and costa and secondary veins sparsely to densely strigulose to sericeous, rarely pilosulous, isolatedly to sparsely arachnose or lanuginose, secondary veins 8–12(–13) pairs, slightly elevated or plain adaxially and protruding abaxially, tertiary veins usually plain or prominulous, occasionally

indistinct and quaternary veins usually indistinct, occasionally distinct abaxially; *petioles* 13–36 mm long. *Inflorescences* usually two per node, 21–62(–76)-flowered, moderately lax- to compact-paniculate, (1.5–)2–3(–4.5) × (1.5–)2–3(–4) cm, main lateral axes 2(–4); *peduncles* (2–)3–20 mm long; *bracts* (sub-)exinvolucrate, membranous or papyraceous, incompletely isolated into 2–3 parts, isolated parts 6–9 × 3–4 mm, lobes deltate to ovate or lanceolate, 0.8–4.5 × 0.8–3.5 mm, apically acute, adaxially sparsely to densely sericeous, trichomes 0.6–1.1(–1.5) mm long, abaxially densely strigulose all over, sparsely arachnose to lanuginose at the lower part, trichomes 0.7–0.8 mm long, bracteoles ovate to lanceolate or lingulate to triangular, 1.2–5 × 0.3–3.8 mm, apically acute, colleters 2–6, 0.4–0.5 mm long. *Flowers* subsessile to pedicellate, pedicels (0.5–)1–6(–8) mm long; *calyx* campanulate, (4–)5-lobed, tubes (0.8–)1–2.1 × 1.5–2.3(–2.8) mm, lobes (0.2–)0.6–2.5(–3) × 0.3–1.5(–1.8) mm, gently incurved or antrorse to spreaded or gently reflexed, lingulate to ovate or triangular, apically usually obtuse, sometimes (sub-)acute, margins eciliate, adaxially glabrous, abaxially densely strigulose, trichomes 0.1–0.6 mm long, *colleters* 1–2(–3), slightly below (0.2–0.4 mm) the sinus, 0.1–0.3 mm long; *corolla* salverform, tubes 8–12 × (1–)1.2–2.5 mm, lobes (1.5–)2.2–3.1 × (0.9–)1–1.3 mm, widely lanceolate to narrowly ovate, antrorse to slightly spreaded, apically (sub-)acute, adaxially the indumentum of orifice extends up to 2.4–3.5 mm inside the tubes, trichomes 0.2–0.7 mm long, abaxially densely strigulose, trichomes (0.2–)0.5–1(–1.4) mm long, usually (sub-)appressed, rarely ciliate; *stamens* 4–5 per flower, attached to corolla tubes at 7.6–8 mm from the base, anthers (1.4–)1.6–2.7 × 0.2(–0.4) mm; *style* (3.5–)5–9 mm long, stigmatic lobes 4–5, (1.5–)3–3.6 × 0.1–0.2 mm; *ovaries* 1.1–1.5(–1.8) × 1.1–2(–2.5) mm, abaxially plain or uneven to shallowly (4–)5-lobed, densely strigulose, occasionally isolatedly arachnose or lanuginose, trichomes 0.1–0.9 mm long, 4–5-locular, each locule 0.8–1.3 × 0.5–0.8 mm. *Fruits* purplish to bluish, 4–4.5 × 3.5–4 mm when immature, isolatedly strigulose lanuginose; *seeds* not seen.

*Phenology, distribution and habitat.* Flowering from January to July and fruiting from April to July. *Sabicea calophylla* was reported from the flood plain of Vaupés river in Amazonas of Brazil. According to this study, its distribution is not restricted to Amazonas state of Brazil. It is distributed in the flood plains of Vaupés river covering a part of northern Amazonas of Brazil and the south-east Mitú of Vaupés, Colombia, in the north-west and adjacent areas of Neblina National Park, south-west Amazonas of Venezuela, and Morona Santiago and Zamora Chinchipe of Ecuador. It is found at roadsides, forests, non-inundated areas along riversides and edges of manihot fields, mostly in white sandy soil; 90–3400 m (Fig. 16).

*Discussion.* Steyermark (1974) did not mention the relationship of *Sabicea grandifolia* with *S. calophylla*. It was impossible to find any distinction between *Sabicea calophylla* and *S. grandifolia*, due to which we have merged *S. grandifolia* with *S. calophylla* without any



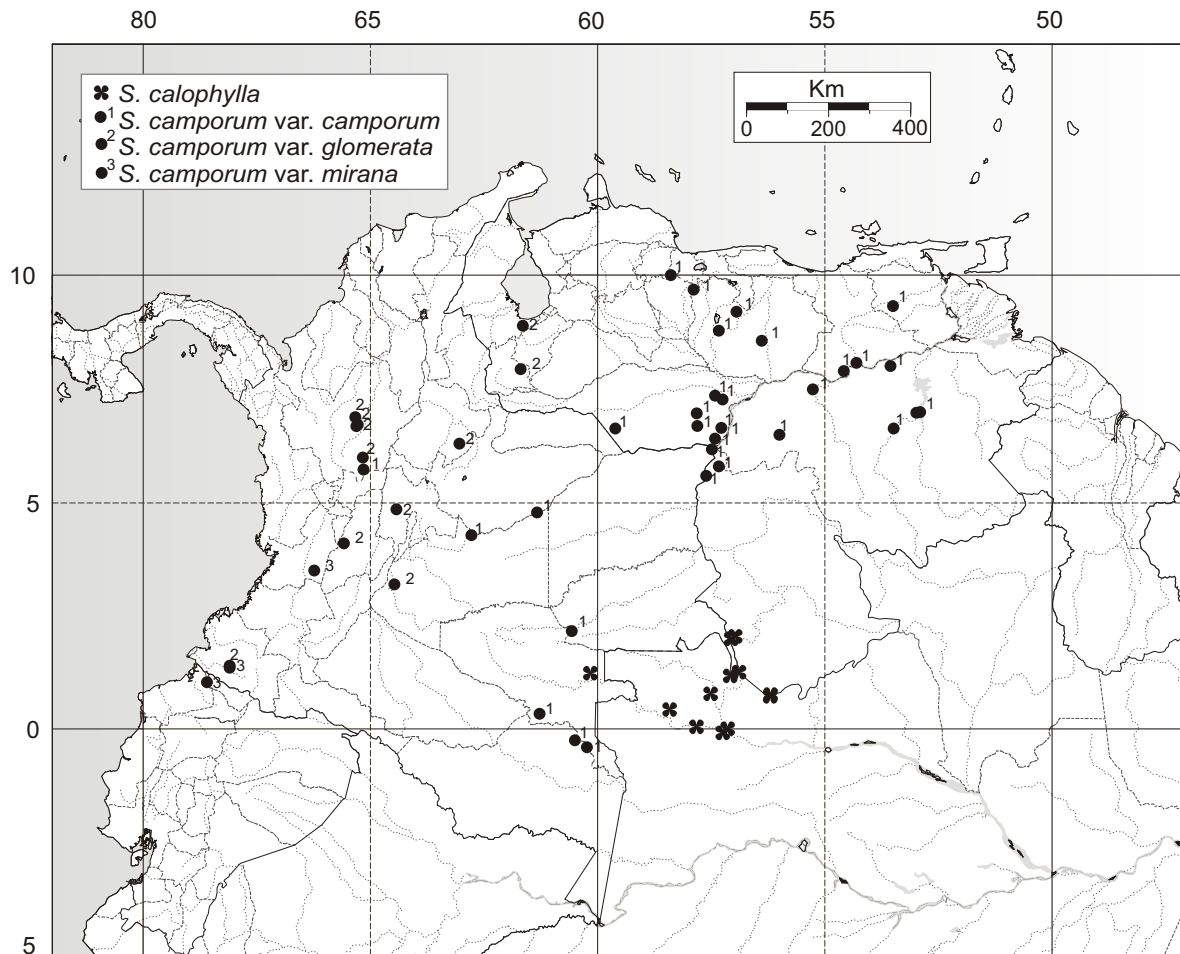


Figure 16. Map of central (in part), northern South America, showing the distribution of *Sabicea calophylla*, and *S. camporum*.

intraspecific circumscription. *Sabicea calophylla* can be distinguished by its moderately lax- to compact-paniculate inflorescences, curled to tortuous trichomes at branchlets, long petioles, abaxial surface of leaves and bracts, and at peduncles and pedicels, adaxially glabrous bracts (excl. base), and smaller, gently incurved to gently reflexed, lingulate to ovate or triangular calyx lobes that are marginally eciliate, adaxially glabrous, abaxially densely strigulose. Asplund (1932) considered *Sabicea calophylla* as the nearest relative of *S. erecta* and *S. acutissima* (synonymized with *S. erecta*). We find this species more closely related to *Sabicea morillorum* and *S. cuneata* than to *S. erecta* due to its similar inflorescences, abaxially arachnose leaf blades, almost similar calyces and corolla. Yet, it is distinct from *Sabicea morillorum* by its longer (13-36 mm in contrast to 5-10 mm) petioles, abaxially densely strigulose stipules, bracts, hypanthium and calyces, antrorse to slightly spread and eciliate calyx lobes, and apically adaxially glabrous bracts and calyces. It differs from *Sabicea morillorum* also by its apically (sub-)acute to bluntly acuminate and adaxially strigulose to puberulous leaf blades, wider stipules ([3-]4-6 mm in contrast to 2.6-3.8 mm).



*Sabicea calophylla* seems close to *S. cuneata* due to its similar inflorescences. It is distinct from *Sabicea cuneata* by its widely lingulate to ovate or triangular to sub-orbicular, eciliate and shorter (generally 0.6–2 mm in contrast to 2.6–3.5 mm) calyx lobes, colleters located at slightly (0.2–0.4 mm) below the sinus of calyces, adaxially (excluding the base) glabrous stipules and bracts, and longer corolla tubes (9–11.5 in contrast to 6–9 mm). *Sabicea calophylla* with larger calyx lobes and sparse arachnose indumentum seems very close to *S. bariensis* from which it is distinct by its usually equal calyx lobes, shorter calyx tubes, and smaller (sub-)globose-inflorescences. *Sabicea calophylla* of Ecuador seems very close to *S. panamensis*, from which it differs by its abaxially arachnose to lanuginose leaf blades, firmly antrorse or appressed stipules and usually triangular calyx lobes. The specimens of Ecuador appear somewhat different from those of Brazil and Venezuela by their hypanthia abaxially isolatedly to sparsely covered with indumentum and glabrous upper part of the calyx lobes. However, based on these marginal differences we avoid the consideration of any infraspecific categories under this species.

*Additional specimens examined.* BRASIL. **Amazonas:** Rio Vaupés, acima de Santa Rosa, *Silva et al. 1563* (US), along BR 307, N from São Gabriel, near Igarapé Freitas and at Equator, roadside secondary growth, 0°0′–0°05′S, 67°00′–67°05′W, *Poole 2026* (HUH, NY), along BR 307 (Perimetral Norte), between São Gabriel and 1°BEC army base (collected along the Rio Negro between Manus and São Gabriel), *Alencar 642* (US); cerca con boca Rio Negro, *Ewel 221* (NY). COLOMBIA. **Vaupés.** Mitú, Camino Yararaca-Santa Cruz, Km 8, Borde del camino, *Cortés 1617* (NY). ECUADOR: **Morona Santiago:** Cordillera de Cutucú, 25 km SE of Logroño, *Madison & Colemon 2579* (HUH, US), Méndez-Morona Road, 53.6 km from Méndez; at the edge of primary forest along road, *Flynn et al. 4080* (F). **Zamora Chinchipe:** Bajo Romerillos, 4°15′S, 78°57′W, ca. *Persson 510* (NY, S). VENEZUELA. **Amazonas:** Between Cana Tremblador and Hauchica. 10 km northeast of San Carlos de Río Negro, 1°57′N, 67°3′W, *Liesner 3625* (MO), Cano 12 km NE of San Carlos de Río Negro 1°56′N, 67°3′W, *Liesner 6636* (MO[2]); Río Negro, lower Cãno Baria, ca. 5 to 10 km above Point of Tambores of Camisioa de Limita and Camp of Comisión de Limite at Boca de Secha going to Brazil, 0°56′N, 66°17′W, *Liesner 17059* (MO, NY, US); upper Río Baria, Río Negro, Selvas pluviales a 8 km al SE de San Carlos de Río Negro, *Aymard et al. 3517* (NY).

**9. *Sabicea camporum*** Sprague, Trans. Proc. Bot. Soc. Edinb. 22: 434. 1904. TYPE: Colombia: Cabuyaro, Río Meta, in the campos, 08 Jan. 1899 (fl), *T. A. Sprague 43* (holotype, BM!). Plate VI, 5–9 (Wernham, 1914), 35A–F (Steyermark, 1967). Figure 17A–N,

Herbs to small shrubs or suffrutices to vines up to about 2 m long, terminal flowering branchlets sparsely to densely hirtellous or hispidulous, puberulous and arachnose, trichomes

0.7–1.6 mm long. *Stipules* ovate to oblong, antrorse to reflexed or recurved, 4–14 × 3–12 mm, apically (sub-)acute to obtuse, basally obtuse to truncate or cuneate, membranous or papyraceous, margins entire, complanate, ciliolate with (0.1–)0.5–0.9 mm long cilia, occasionally eciliate, adaxially glabrous except the basal part, abaxially sparsely to densely strigulose or pilosulous, trichomes 0.1–1.4 mm long, 9–17-veined, veins plain adaxially, slightly raised abaxially, colleters 5–7, 0.2–0.8 mm long. *Leaf blades* elliptic to oblong or lanceolate to ovate, (1–)3–12 × (0.8–)2–6 cm, apically acute to obtuse or acuminate, membranous, ciliolate with 0.4–1.1 mm long cilia, adaxially usually sparsely to densely hirtellous to hispidulous or sometimes strigulose to puberulous at lamina and secondary veins, densely at costa, trichomes 0.9–1.1(1.9) mm long, abaxially sparsely strigulose to pilosulous and densely arachnose to lanuginose at lamina, densely strigulose to villosulous and sparsely to densely arachnose to lanuginose at costa and secondary veins, trichomes 0.7–2.1(–2.3) mm long, secondary veins 9–12 pairs, plain or slightly sunken adaxially, protruding abaxially, tertiary veins obscured to slightly prominulous abaxially; *petioles* (1–)2–16 mm long, densely puberulous to pubescent or pilosulous, sometimes arachnose or lanuginose. *Inflorescences* one per node, (5–)9–36-flowered, verticillate to glomerate, 1–1.8(–2) × 0.7–1.5 cm; *bracts* exinvolucrate, incompletely isolated into 2 parts, isolated parts 3.5–5.9 × 2.9–4.7 mm, ovate to deltate, apically acute to obtuse or acuminate, ciliolate with 0.0–0.4 mm long cilia, 6–9-ribbed, bracteoles, (1.2–)3.5–7.6 × 0.5–2.1(–4) mm, lingulate to lanceolate, or narrowly elliptic, apically usually acute to acuminate or obtuse, adaxially and abaxially the indumenta similar to those of stipules, colleters 2–4, 0.5–0.7 mm long. *Flowers* sessile or subsessile, pedicels 0(–1.8) mm long; *calyx* campanulate, green, (4–)5(–7)-lobed, tubes 0.3–1.8 × 1.5–2.7 mm, lobes (0.8–)2–4(–5.3) × (0.1–)0.8–2(–2.4) mm, usually antrorse to spreaded, occasionally apically slightly reflexed, shortly lanceolate to lingulate, apically (sub-)acute, margins entire, ciliolate with 0.0–0.6(–0.7) mm long cilia, adaxially glabrous, isolatedly to sparsely sericeous to strigulose at the apices, abaxially sparsely to isolatedly strigulose to sericeous or pubescent all over, trichomes (0.1–)0.4–0.8(–1.1) mm long, 3–5-ribbed, plain both abaxially and adaxially, colleters 1–2(–5) in each sinus, (0.2–)0.2–0.5 mm long; *corolla* salverform, tubes 3–6(–7) × 1.1–2 mm, 5–(6)-lobed, lobes 1.8–2.8 × 0.8–1.8 mm, ovate, antrorse to slightly reflexed, adaxially the indumentum of orifice extends up to 1.2–3.8 mm inside the tubes, trichomes 0.5–0.7 mm long, abaxially usually densely strigulose, with or without forming cluster at the apices of lobes, trichomes 0.7–1.4(–1.6) mm long, usually appressed to cliniate or erect; *stamens* 5 per flower, attached to corolla tube at 3.2–3.5 mm from the base, anthers (0.8–)1.4–1.5(–2.2) × (0.1–)0.2–0.4 mm; *style* (2–)3–4 mm long, stigmatic lobes (1–)2–2.1 × 0.1–0.2 mm; *ovaries*, 1.1–1.3 × 1.2–1.6 mm, abaxially uneven to slightly 5-lobed, trichomes 0.2–1.4 mm long, 5-locular, each locule 0.6–1 × 0.3–0.5 mm. *Fruits* red, 3–5 × 3–4 mm when immature, 5–7 × 5–6 mm when mature, abaxially isolatedly to sparsely hirtellous and arachnose; *seeds* 0.5–0.6 × 0.2–0.5 mm.

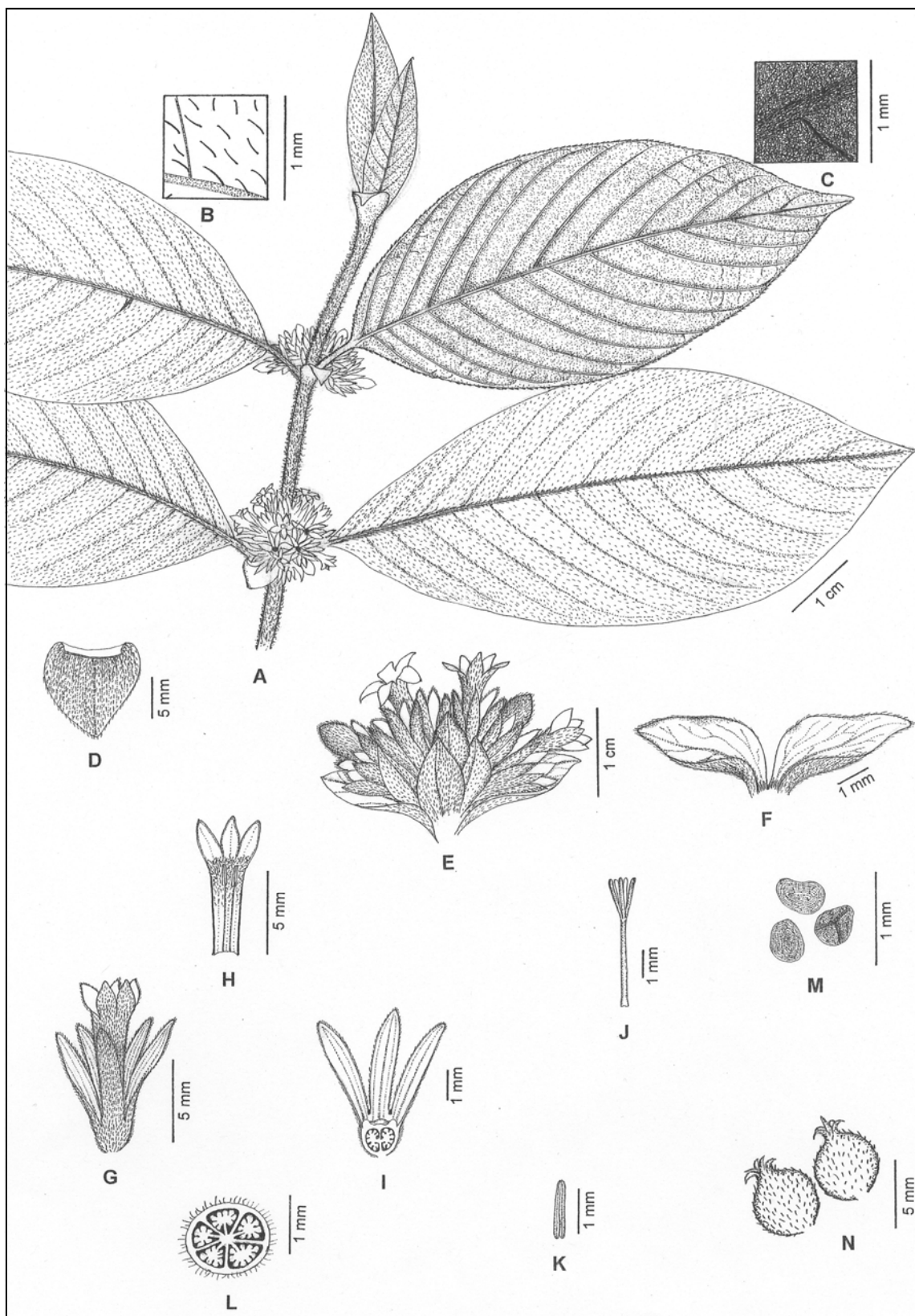


Figure 17. A–N. *Sabicea camporum* var. *camporum*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Outer stipule surface. —E. Inflorescence. —F. Part of outer and inner bract surface. —G. Flower. —H. Inner corolla surface. —I. Longitudinal section through calyx and ovary. —J. Style and stigmas. —K. Face view of Anther. —L. Transversal section through ovary. —M. Seeds. —N. Fruits.

*Phenology, distribution and habitat.* Flowering throughout the year and fruiting in March, July, August and November. *Sabicea camporum* is distributed in the eastern and southern regions of Colombia including southwest Nariño and southeast Valle, most regions of Venezuela, and Esmeraldas Province of Ecuador. It is found in forests, especially tropical wet forests, along or at river slopes, savannah (e.g., *Panicum* or *Trachypogon-Byrsonima* or *Axonopus-Trachypogon* savannah), at pastures, along low-forested streams and in sandstone outcrops to heavy damp soils; 35–2100 m (Fig. 16).

*Discussion.* This species is characterized by arachnose to lanuginose lower leaf surfaces, sessile inflorescences, sessile flowers with patent indumentum, and short calyx lobes and corolla tubes. Its erect growth form mentioned by Wernham (1914) is disputed according to the label information of the specimens examined. The small size of leaves, considered by Wernham (1914) as distinguishing for this species, is labile. *Sabicea camporum* merely differs from *S. glomerata* due to which we consider *S. glomerata* as a variety of *S. camporum*. Characters of *Sabicea camporum* and *S. venezuelensis* are continuous, supporting the here proposed merge of *S. venezuelensis* with *S. camporum*. *Sabicea camporum* seems similar to the new species *S. boyacana* from which it is distinct by its compactly verticillate to glomerulate inflorescences without any distinct axes or pedicels (Fig. A, E), and with 2–4 colleters the adaxial base of bracts, glabrous adaxial base of calyx tubes, and shorter and thinner corolla tubes. *Sabicea camporum* appears as close to *S. grisea* with smaller inflorescences from which it differs by its compactly verticillate to glomerate inflorescences, adaxially glabrous and short calyx lobes (2–4[–5.3]) mm in contrast to usually 5–12 mm) and tubes (0.3–1.5 mm in contrast to 2.5–4 mm), short corolla tubes (3–7) mm in contrast to 9–20 mm) with appressed indumentum on outer surface. *Sabicea camporum* with longer calyx lobes and dense indumentum appears close to some plants of *S. velutina* from which they are distinct by their straight and curled to tortuous trichomes of lower surface of leaves, compactly verticillate to glomerate inflorescences, adaxially apically (sub-)acute to obtuse lobes of bracts and calyces (Fig. 17G, I) with short cilia (0–0.7 mm in contrast to (0.8–1.8 mm), straight trichomes of outer surface of calyces, and short corolla lobes (1.8–2.8 mm in contrast to (2.5–)3–4 mm) and tubes (3–7 mm in contrast to 8–16 mm). *Sabicea camporum* with few-flowered inflorescences can be confused with *S. oblongifolia*, from which it can be set apart by the matted indumentum of its abaxial leaf surfaces, its short-tubed corolla (3–6[–7] mm in contrast to 8–12[–16] mm) with appressed external indumentum, lanceolate to lingulate calyx lobes, apically (sub-)acute to obtuse stipules, and indumentum lacking rusty brown to maroon color.

Plants of *Sabicea camporum* with dense indumentum at the external surface of inflorescences are similar to *S. velutina* from which they can be set apart by their verticillate to glomerulate inflorescences, hirtellous to hispidulous or strigulose to puberulous indument at the adaxial surface of leaf blades comprised of shorter trichomes (0.9–1.1[1.9] mm in contrast

to [1.5–]2–2.3 mm), densely strigulose to pilosulous or villosulous indument at abaxial surface of leaf blades, external surface of stipules and inflorescences lacking a lanuginose to arachnose or floccose indument and adaxially glabrous stipules, bracts and calyx lobes, and shorter cilia (usually 0.5–0.9 mm at stipules and bracts, 0.0–0.6 mm at calyx lobes, in contrast to 0.8–1.7 mm at stipules and bracts, and 1.2–1.8 mm at calyx lobes).

*Dorr 7119* (NY) seems to be an intermediate of *Sabicea camporum* and *S. velutina* with abaxially diffuse to flocculent leaf blades, almost non-arachnose stipules, bracts, calyx lobes and adaxially sericeous apices of calyx lobes.

#### Key to the varieties:

- 1b. Few- to many-flowered inflorescences; calyx lobes usually 2.1–5 mm long with (sub-) acute apices and corolla tubes (3–)3.5–5.5 mm long
  - 2a. Lower surface of leaves compactly arachnose and abaxially the tertiary and quaternary veins are completely covered with indumentum .....9a. *S. camporum* var. *camporum*
  - 2b. Lower surface of leaves flocculent to diffuse arachnose, lower leaf surfaces and abaxially the tertiary and quaternary veins are almost exposed and isolatedly to sparsely covered with indumentum.....9b. *S. camporum* var. *glomerata*
- 1a. Three to few-flowered inflorescences; calyx lobes 1.2–2.1 mm long with obtuse apices and corolla tubes 2.8–3.2 mm long.....9c. *S. camporum* var. *mirana*

#### 9a. *Sabicea camporum* Sprague var. *camporum*,

*S. venezuelensis* Steyerl., Mem. New York Bot. Gard. 17(1): 309, f. 35. 1967. TYPE: Venezuela: Bolívar, Raudal Aguacarita, Río Paragua, 21 Jul. 1943, *F. Cordoana 707*, (holotype, VEN, not seen, photo VEN!).

*Additional specimens examined.* COLOMBIA. **Amazonas-Vaupés:** Río Apaporis, entre el río Pacoa y el Río Kananarí, Soratama, *Schultes & Cabrera 12746* (F, HUH, US, NY), Mouth of Pacoa, *Schultes & Cabrera 12591* (F, HUH); Raudal Yayacopi (La Playa) and vicinity, *Schultes & Cabrera 16949* (US, NY), Jinigojé (at mouth of Río Piraparana) and vicinity, *Schultes & Cabrera 16670* (F), Vaupés, Riberas del Río Inirida, sitio limado Sabanita, *Fernández 2180* (US). **Casanare:** Río Meta, Orocué, *Cutrecasas 4391* (F). **Vichada:** Río Orinoco, Puerto Carreño, *Cutrecasas 4013* (F). VENEZUELA. **Amazonas:** Terreno situado entre la Carretera hacia Samariapo y la pista de aterrizaje del Puerto Ayacucho, *Huber 758* (NY); Estación de Piscicultura de Puerto Ayacucho, Terreno situado entre la Carretera hacia Samariapo y la pista de aterrizaje del Aeropuerto de Puerto Ayacucho, *Huber 894* (NY), 8 km S of Puerto Ayacucho, *Davidse & Huber 14981* (US, NY); Atures, Bosque húmedo del río Cataniapo, Sector Puente, margen izquierdo hacia la desembocadura con el río Orinoco,

*Castillo* 1215 (MO) *Castillo* 3663 (MO). **Anzoátegui**: Morichal de Mapire, *Montes* 1340A (MO), Freites, Morichal Morichalote, 6–7 km al Oeste del río Oritupano, *Fernández et al.* 12742 (MO, US). **Apure**: Pedro Camejo, 4 km NE of El Betun along the banks of Río Capanaparo, *González* 13095 (MO, U), east side of the Galeras de Cinaruco, along Quebrada El Porvenir, ca. 53 airline km northeast of Puerto Páez, *Davise & González* 15564 (MO), ca. 2 km S of Caño La Cochina de La Pica along the main road, south of Paso de San Pablo to the Río Cinaruco, *Davise & González* 15940 (MO), Fundo La Leona, *Rojas & Sánchez* 5350 (MO); Mata Palito, Finca Laguna Redinda, Cunaviche, Camejo, *Martino et al.* 249 (MO). **Bolívar**: Potrerito, Río Paragua, *Cardona* 701 (US), a la cuenca media del río Paragua, a la altura de "Dando y Dando", *Stergios* 10055 (MO, NY); Balnea Río El Bosque, 10 km S of Ciudad Bolívar near Río Orocopiche, *Gentry & Berry* 15104 (MO); San Pedro de las Bocas to 7 km north, *Leisner & González* 5734 (MO), west bank of river, *Liesner & González* 5496 (MO, NY, U); Cedeño, alrededores del caño Villaca, carretera Caicara El Burro, *Stergios & Stergios* 8421 (MO, NY), Morichal El Caballo, ca. 225 km at S de Caicara del Orinoco by road, *Holst & Werff* 2567 (MO, NY); Sucre, *Delgado* 1256 (NY). **Guárico**: Hato San Mauricio, Km 64 carretera Las Mercedes-Cabruta, Infante del, *Rojas* 2762 (F), Morichal San Ramón, *Montes & Davidse* 11456 (MO), Morichal La Babas, Mesa de Becerra Calabozo, *Montes* 1856 (MO). Cano Realito on Via a EL Caballo, *Robertson & Austin* 173 (MO).

**9b. *Sabicea camporum*** Sprague var. ***glomerata*** (Wernham) Liede, Meve & Khan, comb. et stat. nov.

*Sabicea glomerata* Wernham, Monogr. *Sabicea* 50. 1914. TYPE: Colombia: Nariño, Pilcuan, Barbacoas, 891.54 m, 1851–57, *J. Triana* 1756 (holotype, P, not seen, photo F!).

*Additional specimens examined.* COLOMBIA. **Antioquia**: Cordillera Central. Angostura, *Fosberg* 21613 (NY, US); In the middle between Cocorná and Las Alfombras, *Juncosa* 1408 (MO). **Cundinamarca**: Sasaima, San Bernardo, *Schneider* 824 (S); Bogota, *Karsten s.n.* (W). **Meta**: Villavicencio, *Pennel* 1376 (F in part, NY); Cordillera Oriental, Las lagartijas, plateau between Río Papamene and Río Duda, 5–6 km SW of Uribe, *Fosberg* 19500 (US). **Santander**: Cordillera Central, Ridge 3 km northeast of Coromoro, 15 km northeast of Charala, *Fosberg*, 21910 (NY, US).

**9c. *Sabicea camporum*** Sprague var. ***mirana*** Liede, Meve & Khan, var. nov. TYPE: Colombia. Nariño: Tumaco-Tuquerres road, W of Junín, 900 m, 25 Nov. 1981 (fl), *A. Gentry et al.* 34960 (holotype, MO).

*Plantae inflorescentiis tres- ad paucifloris, lobis calycum 1.2-2.1 mm longis, apicibus obtusibus, tubis corollarum 2.8-3.2 mm longis.*

*Additional specimens examined.* COLOMBIA. **Valle Del Cauca:** Hoya del río Anchicaya, cerca del puente de Aguaclara, *Cuatrecasas* 22068 (F, US). Barbacoas, corregimiento de Altaquer, El Sábalo, *Bellow & Parra* 98 (MO). ECUADOR. **Esmeraldas:** San Lorenzo Canton, Reserva Indígena Awa, Canton del río Mira, 10 km a oeste de Alto Tambo, Comunidad La Union, *Rubio et al.* 1175 (F, MO).

**10. *Sabicea cana*** Hook. f., *Hooker's Icon. Pl.* 3: t. 247, f. 1–4, 1840. TYPE: Peru, San Martín: Moyobamba, *Mathews s.n.* (last coll. 1838) (holotype, K!; isotypes F!, HUH!, photo NY!).

Lianas; terminal flowering branchlets sparsely to densely arachnose or lanate to lanuginose, trichomes 1.4–2.3 mm long. *Stipules* ovate to deltate, antrorse, 4–7(–8) × 3–8(–9) mm, apically (sub-)acute to acuminate, papyraceous, eciliate or ciliolate with curled to tortuous cilia, adaxially apically isolatedly lanuginose, abaxially lanate to lanuginose all over, 11–16-veined, colleters 8–12(–14), 1–2 mm long. *Leaf blades* usually ovate to oblong, sometimes elliptic, occasionally widely lanceolate, (3–)6–17.5 × (1.6–)3–10 cm, apically usually (sub-)acute to acuminate, occasionally obtuse, basally attenuate or acute, thickly papyraceous, eciliate or ciliolate with curled to tortuous cilia, adaxially floccose to sparsely arachnose or lanate, eventually and usually partially glabrescent; abaxially densely lanate, secondary veins 11–14(–20) pairs, plain adaxially or protruding abaxially, tertiary veins distinct and quaternary veins obscured or distinct abaxially; *petioles* (8–)10–25(–30) mm long. *Inflorescences* usually two per node, 5–18(–24)-flowered, compact-fascicled to capitate, usually sessile, rarely pedunculate, peduncles 2–18 mm when present, 1–1.5 × 1.5–2 cm; *bracts* (sub-)exinvolucrate, incompletely isolated into 2–3 parts, isolated parts 8–8.5 × 6.5–7.1 mm, 0–3-lobed, lobes ovate to oblong or deltate or widely elliptic, 1.5–5.5 × 1.7–4.5 mm, apically (sub-)acute, margins entire to shallowly wavy, eciliate or ciliolate with curled or tortuous cilia, adaxially apices isolatedly to sparsely lanuginose, trichomes (0.5–)0.8–1.6 mm long abaxially densely lanate to lanuginose, (3–)5–9-ribbed, bracteoles (4–)6–9 × 3–7(–9) mm, usually shallowly cymbiform to elliptic or ovate, apically (sub-)acute or obtuse, colleters 2(–4), (0.4–)0.7–0.9 mm long. *Flowers* usually sessile, rarely subsessile, pedicels 0(–1) mm long; *calyx* campanulate, (4–)5(–6)-lobed, tubes 1–2(–2.5) × 2.3–3(–3.5) mm, lobes (0.5–)1.1–3 × (0.2–)1.5–1.8(–2.1) mm, antrorse, triangular to ovate or widely lingulate or deltate, one lobe per calyx is usually smaller, apically acute to obtuse, margins eciliate, adaxially glabrous or only the apices isolatedly to sparsely lanuginose or sericeous, trichomes 0.07–0.2(–0.4) mm long, abaxially densely lanate to lanuginose, 2–3(–5)-ribbed, plain both abaxially and adaxially, colleters 1(–2) in each sinus, 0.3–0.5 mm long; *corolla* creamy to white, salverform, tubes 3.4–5.5(–6.5) × 1.7–2.1(–2.8) mm, lobes (2–)2.5–3(–3.6) × 1.5–2.5 mm, ovate, antrorse to spreaded, adaxially the indumentum of orifice extends up to 1.5–3 mm inside the tubes, abaxially lobes and tubes usually arachnose to lanuginose and occasionally villosulous at tubes, trichomes (0.6–)1.4–1.8(–2.1) mm long; *stamens* 5 per flower, attached

to corolla tube at 3.5 mm from the base, anthers (1.1–)1.5–1.8(–2.1) × 0.3–0.5 mm; *style* (2.5–)3.5–5.5(–6.2) mm long, usually lanuginose to villosulous at least at upper part, stigmatic lobes 5(–6), 3–2(–2.4) × 0.3–0.4 mm; *ovaries* 1.5–1.8(–2.8) × 1.4–2(–3) mm, abaxially uneven to shallowly 5-lobed, 5(–6)-locular, each locule 1.5–1.8 × 0.5–0.7 mm. *Fruits* pale violet or purple to dark red, 4–5 × 4–5 mm when immature, 7–9 × 7–9 mm when mature, abaxially densely lanuginose to lanate; *seeds* 0.5–0.7 × 0.3–0.6 mm.

*Phenology, distribution, and habitat.* Flowering occurs almost throughout the year (Aug–June), fruiting from April to August. This species is known from Bolivia, Colombia, Ecuador and Peru. It is usually found in primary or secondary, tropical humid, disturbed or virgin, forests, in thickets on gulch, in swampy or open plains, on steep slopes along river; 220–1810 m (Fig. 12).

*Discussion.* *Sabicea cana* is characterized by its floccose to sparsely arachnose or lanate indumentum of upper leaf surfaces, generally compact-fascicled, occasionally capitate inflorescences, lanate to lanuginose indumentum on outer surface of stipules, bracts and calyces, curled to tortuous cilia, small and campanulate calyces, short corolla tubes, and arachnose to lanuginose indumentum on outer surface of corolla tubes. Hooker (1840) and Wernham (1914) described the ovary and stigma of *Sabicea cana* as 4-merous, whereas, Andersson (1999) as 5-merous. We find the ovary and stigma of this species as 5(–6)-merous. *Sabicea cana* differs from *S. tayloriae*, its nearest ally, in its adaxially floccose or sparsely arachnose, eventually and usually partially glabrescent leaf blades, curled to tortuous cilia at the margins of leaves, stipules and bracts, adaxially isolatedly to sparsely lanuginose apices of stipules, bracts, and calyx lobes, longer corolla lobes (usually 2.5–3 mm in contrast to 1.8–2.5 mm), usually arachnose to lanuginose abaxial corolla tube surfaces, and lanuginose to villosulous styles. *Sabicea cana* differs from its close ally *S. brasiliensis* by its lianescent habit, exclusively floccose or isolatedly to sparsely arachnose and eventually glabrescent adaxial leaf surface, longer petioles and usually lanuginose to villosulous styles (at least at upper parts). *Sabicea cana* seems close to *S. cinerea* from which it differs by its short and triangular to ovate or lingulate calyx lobes, short and abaxially usually matted arachnose or lanuginose corolla tubes and isolatedly to sparsely lanuginose to villosulous stigmatic lobes and upper part of style.

Presumably all previous authors, from Hooker (1840) to Andersson (1999), mentioned *Sabicea cana* as a species with sessile inflorescences. However, few collections (*Agular & Castro 822*, *Gentry & Núñez 69504*, and *Beltran & Foster 1594*) contain all characters of *Sabicea cana* but have 2–18 mm long peduncles. These collections deserve to be delimited under a separate variety, due to which we have recognized as a variety. Exceptionally in *Toro 1354* (NY), the corolla lobes and tubes are abaxially lanuginose and villosulous and style and stigmatic lobes glabrate. But, its all other characters support its inclusion under *Sabicea cana*.



*Sabicea cana* var. *pedunculata* contains all characters of *Sabicea cana* var. *cana* but it has 2–18 mm long peduncles.

#### Key to the varieties:

- 1a. Inflorescences sessile..... 10a. *S. cana* var. *cana*  
 1b. Inflorescences pedunculate..... 10b. *S. cana* var. *pedunculata*

#### 10a. *Sabicea cana* Hook. f. var. *cana*

*Sabicea flavida* Krause, Bot. Jahrb. Syst. 40: 323. 1908. TYPE: Peru: Loreto: Habana prope Moyobomba, 800–900 m, no date, *Weberbauer 4568* (holotype, B, not seen, presumably destroyed; isotype, F!).

*Selected Specimens Examined.* BOLIVIA. **La Paz:** Abel Iturralde, Parque Nacional y Area Natural de Manejo Integrado Madidi. Pampas SW Heath, Puerto Moscoso sobre Río Heath, entrando aproximadamente 1 km, *Narel 757* (MO). COLOMBIA. **Antioquia:** between Yolombó and Cancan, *Lehmann 4004* (BM, F, G-2); San Roque, *Toro 1354* (F), vicinity of Medellín, *Toro 1354* (NY); Cocorná, *Daniel 1622* (F, US), vereda La Piñuela, Carretera San Francisco, *Cañas 590* (MO); Comosaria del Caqueta, Florencia, *Cuatrecasas 8804* (F, US); San Luis, *Castaneda 1545* (F); Campamento zona de explotación mina de asbesto, 6°57'N, 75°18'W, *Cogollo & Alzate 2213* (MO), La Aguada, 3–5 km NE del Pueblo, en la vía Campamento-Anorí, *Callejas et al. 8171* (MO); Stanto Domingo, Correg, Santiago, Sector La negra, *Callejas et al. 2307* (MO, NY); Remedios, Sitio Otú, 3 km del Corregimiento santa Isabel, Vereda Los Lagos, Vereda Los Lagos, 11 km de Remedios (S); via Remedios Vegachi, 6°56'N, 74°55'W, *Callejas et al. 4722* (MO, NY). **Santander:** Cordillera Oriental, Quebrada Angulo, 4 km S of Lebrija, *John 20592* (US). ECUADOR. **Zamora Chinchipe:** Nangaraitza Canton, Pachicutza, 04°07'S, 78°37'W, *Palacios & Neil 6444* (MO); along Río Jamboe, ca. Km 30, south of Finca Cruz-Kaya, *Harling & Andersson 13849* (US). PERU. **Amazonas:** Bagua, Montenegro-Abra Muahuajin, 550–950 msm, *Sagaategui et al. 7161* (HUH, MO, US). **Cuzco:** Quispicancha, Manir, *Vargas 14067* (US). **Huánuco:** Chicoplaya, *Tapalla 372* (G), near Monzón, Huamalies, *Tapalla s.n.* (F); Río Monzón at Palo Huimbra, *Hutchinson et al. 5993* (F, G, HUH, M, NY, S); Rondos, *Vigo 5879* (F, US); Cachicoto, *Woytkowski 7863* (HUH, MO); Leoncio Prado, Daniel Alomias Robles, cerca a Delicios, *Vigo 9287* (F, MO, NY). **Junín:** East of Quimiri Bridge, near La Merced, *Kilip & Smith 23925* (F, US, NY). **Loreto:** Vicinity of Aguaytia, on steep slopes along Río Aguaytia, *Croat 20964* (HUH, MO); Balsapuerto, *Klug 2882* (BM, F, G, HUH, NY, S). **San Martín:** South of Uchiza, *Vigo 5779* (F); Tarapoto, Carretera de Tarapoto-Yurimaguas, Km 16 cerca las cataratas de Ahuashiyacu, monte abierto con arena, *Rimachi, 10074* (F, MO, NY). **Ucayali:** Pucallpa,

Aguaytía, Nuñez 2456 (US).

- 10b. *Sabicea cana* Hook. f. var. *pedunculata* Liede, Meve & Khan, var. nov.** TYPE: Peru. Madre De Dios: Tambopata, Pampas de Heath, 12°50'S, 68°50'W, 200 m, 24 Feb 1990 (fl), A. Gentry & P. Núñez 69504 (holotype, MO!).

Differt a varietate typica inflorescentibus pedunculatis.

*Specimens Examined.* **ECUADOR. Zamora-Chinchi:** Along road from Zamora to Romerillos, 13.3 km N of bridge over Río Bombuscaro at Zamora, 0.4 km N of Pituca along river, 4°08'02''S, 78°56'31''W, *Croat and Menke 89773* (MO). **PERU. Amazonas:** Condorcanqui, Cordillera Del Condor, Puesto de Vigilancia Alfonso Ugarte (PV3), cabeceras del río Comainas, *Beltran & Foster 1594* (F). **Madre De Dios:** Santuario Nacional Pampas del Heath, Río Heath, 12°39'23''S, 68°44'13''W, *Agular & Castro 822* (MO).

- 11. *Sabicea chiapensis* Liede, Meve & Khan, sp. nov.** TYPE: Mexico. Veracruz: Jesús Carranza. Lomas, al S del Pob, ± 3 km al S del entronque de la terřacería La Laguna-Boca del Monte con el camino al N. al Pob.2, 17°12'N, 94°39'W, 250 m, 16 Oct 1983 (fl), *T. Wendt 4187* (holotype, MO!). Figure 18A–I.

*Inter species Sabiceae distinguitur inflorescentiis umbellatis ad paniculatis et trichomatibus paginarum foliorum inferiore et tuborum corollarum abaxialium manifesto erecto-patentibus.*

Herbs or vines with slender stem, up to 12 m long; terminal flowering branchlets densely pilosulous to pubescent only or in addition isolatedly to sparsely arachnose, trichomes 0.8–1.5 mm long. *Stipules* widely ovate to suborbicular, erect to recurved, 7–18 × 9–16 mm, apically subacute to obtuse, membranous, margins wavy, ciliolate with (0.2–)0.7–0.1 mm long cilia, adaxially glabrate to isolatedly strigulose or sericeous in addition to the densely basal part, abaxially sparsely pilosulous to pubescent, trichomes (0.4–)0.5–1.2 mm long, 9–15-veined, protruding at both surfaces, colleters 8–14, 1–2.1 mm long. *Leaf blades* oblong, (5.2–)9.5–17.2 × 4.1–8.3 cm, apically acute to acuminate, basally (sub-)acute to obtuse, membranous to papyraceous, margins entire or slightly wavy, ciliolate with (0.2–)0.7–1.3 mm long cilia, adaxially moderately densely pilosulous to pubescent or strigulose at lamina, and densely pilosulous to pubescent at costa and secondary veins, trichomes (0.3–)0.6–1.2(–1.8) mm long, abaxially sparsely to moderately densely pilosulous at lamina, densely pilosulous to pubescent only or in addition sparsely arachnose at costa and secondary veins, trichomes (0.2–)0.5–2 mm long, secondary veins 9–15 pairs, costa and secondary veins protruding abaxially and plain or slightly protruding adaxially, tertiary veins prominulous and quaternary veins distinct or prominulous abaxially; *petioles* 1–3 cm long. *Inflorescences* 2 per node, (4–

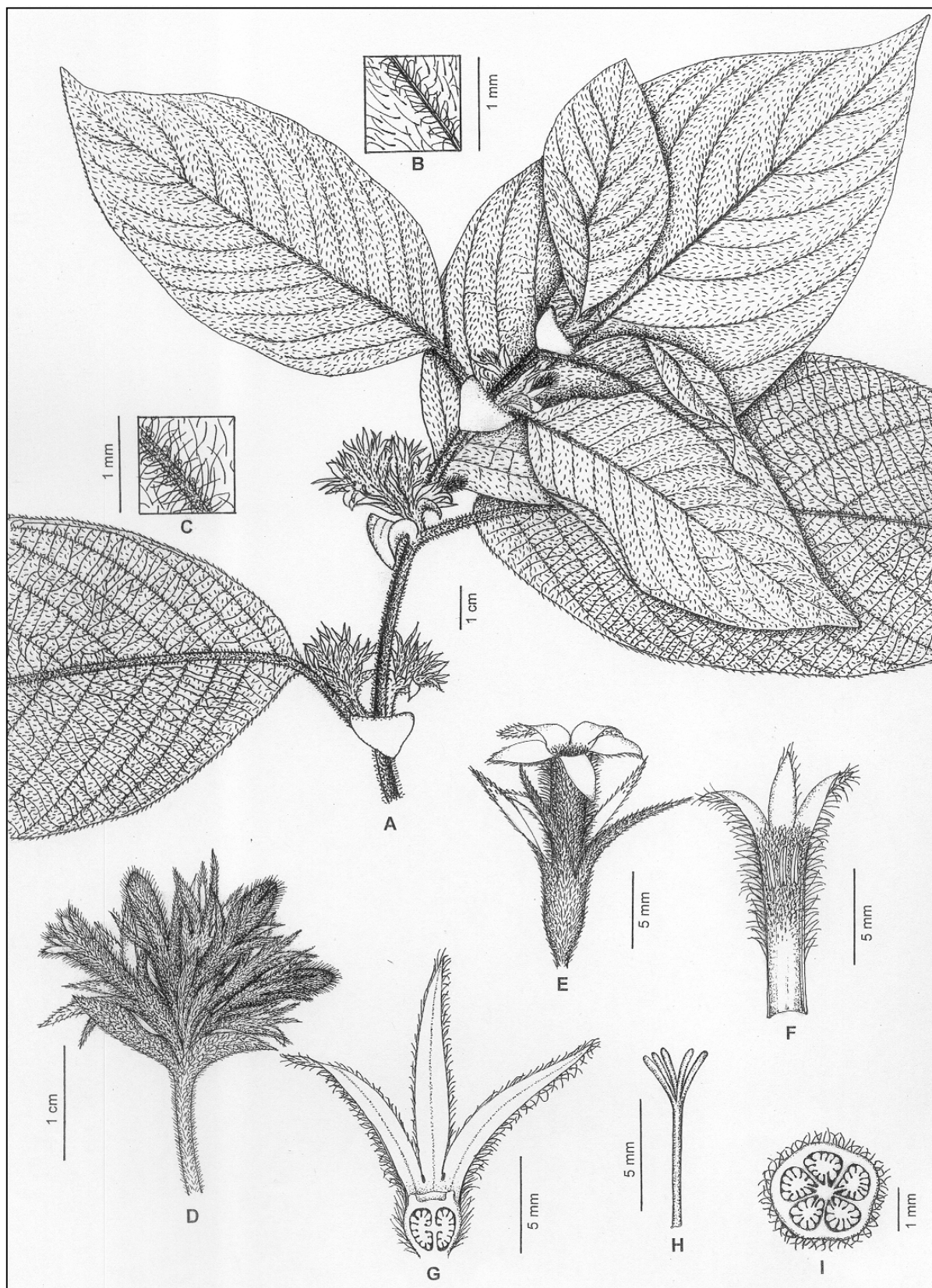


Figure 18. A–I. *Sabicea chiapensis*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Inflorescence. —E. Flower. —F. Inner corolla surface showing anther's position. —G. Longitudinal section through calyx and ovary. —H. Style and stigmas. —I. Transversal section through ovary.

)6–8-flowered, compact-paniculate to umbellate, 1.2–1.8 × 1.5–2 cm, primary axis 0–1.5(–2) mm long, main lateral axes 0–4, 0.5–1.2 mm; *peduncles* 3–6 mm long; *bracts* exinvolucrate, membranous, incompletely isolated into 2–4 parts, isolated parts (5–)6–7 × 3–4 mm, ovate, apically acute, margins entire, ciliolate with 0.6–0.9 mm long cilia, adaxially sparsely pubescent to strigulose in addition to the basal part, abaxially densely pilosulous to pubescent, 5–9-ribbed, bracteoles 2–12 × 2–4 mm, lingulate to elliptic, colleters 4–6 at bracts and 2 at bracteoles (0.2–)0.5 mm long. *Flowers* white, subsessile to pedicellate, pedicels 0.5–6 mm long; *calyx* campanulate, 5-lobed, tubes 0.6–1.2 × 1.7–2.5 mm, lobes 8–15 × (0.8–)1–1.5 mm, antrorse to spreaded, widely linear to narrowly lanceolate, apically acute to acuminate, margins entire, ciliolate with 0.6–1 mm long cilia, adaxially isolatedly to sparsely strigulose at upper part, trichomes 0.2–0.8(–1), abaxially sparsely pilosulous to pubescent, trichomes (0.2–)0.8–1(–1.2) mm long, 3(–5)-ribbed with costa, abaxially prominulous, adaxially plain, colleters (1–)2–3 in each sinus, (0.2–0.4) mm long; *corolla* salverform, tubes (7–)8–11 × 1.6–1.8(–2) mm, lobes 4–4.5 × 1.3–2 mm, widely lanceolate to narrowly ovate, spreaded to slightly recurved, adaxially the indumentum of orifice extends up to 3–4.5 mm inside the tubes, abaxially densely pilosulous, trichomes (0.8–)1.5–1.8 mm long; *stamens* 5 per flower, attached to corolla tube at 5–7 mm from the base, anthers 1.8–2(–2.5) × 0.3–0.4 mm; *style* 6–7 mm long, stigmatic lobes 5, 2.5–3 × 0.2–0.3 mm; *ovaries* 1.5–1.7 × 1.7–1.9 mm, abaxially shallowly 5-lobed or plain, densely strigulose to pubescent and arachnoid, 5-locular, each locule 1.5–1.8 × 0.3–0.4 mm. *Fruits* and *seeds* not seen.

*Phenology, distribution and habitat.* Flowering in July, August and October. Reported from Chiapas, Oaxaca and Veracruz, Mexico. It is found in cutover or disturbed tropical evergreen high forest; 250–350 m (Fig. 19).

*Discussion.* This species is distinguishable by its compact-umbellate to paniculate inflorescences, and manifestly erecto-patent trichomes at lower surface of leaves and outer surface of corolla tubes. It differs from its close ally *Sabicea mexicana* by its pilosulous indumentum at abaxial surface of leaves and corolla tubes (Fig. 18F), and adaxially isolatedly to sparsely strigulose longer (8–15 mm in contrast to 6–7.7 mm) calyx lobes. In both species, arachnoid to lanuginose indumentum absent or present at the lower surface of leaves, yet in this new species this indumentum, when present, is distinct and limited to the abaxial costa and secondary veins (Fig. 18C), whereas, in *Sabicea mexicana* it is spread over lamina also. *Sabicea chiapensis* is close to another Mexican species *S. liedeeae*, from which it differs by its non-arachnoid or non-lanuginose stipules, lamina excluding the costa and secondary veins, peduncles, bracts, pedicels, and hypanthium, pilosulous indumentum of abaxial surface of leaves, especially at the costa and secondary veins and corolla tubes, pilosulous external indumentum of corolla, and straightened and adaxially isolatedly to sparsely strigulose calyx lobes.

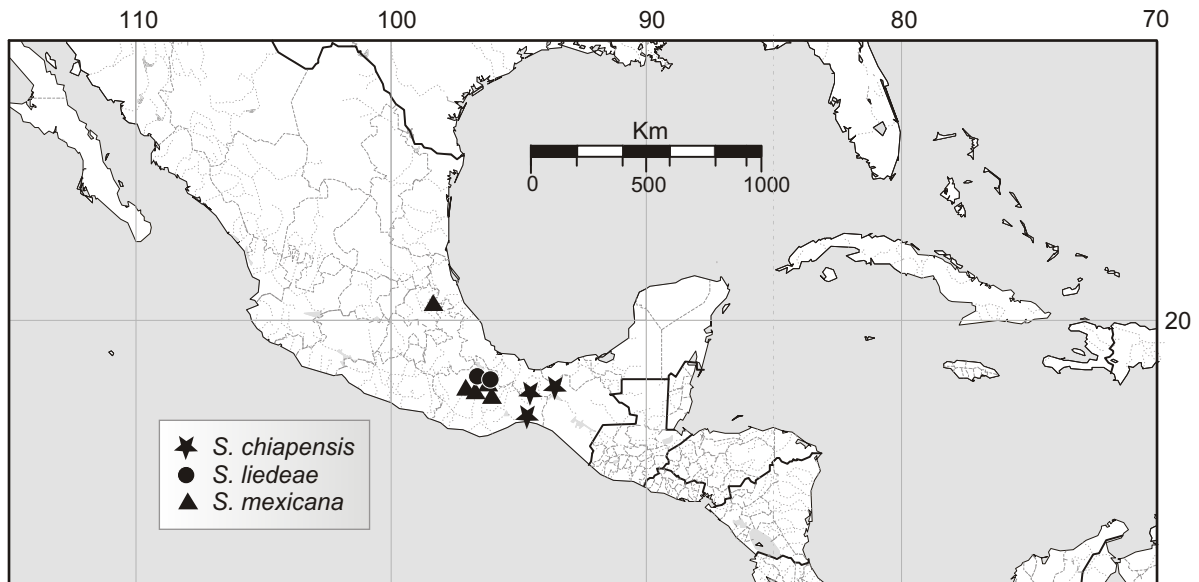


Figure 19. Map of Mesoamerica (in part), showing the distribution of *Sabicea chiapensis*, *S. liedeae*, and *S. mexicana*.

*Sabicea chiapensis* appears close to *S. burchellii*, from which it can be set apart by its compact-umbellate to paniculate inflorescences with distinct peduncles and pedicels, and apparently pilosulous external indumentum of corolla tubes. This new species can not be Wernham's (1914) species *Sabicea flagenioides*, as its are widely oblong ([5.2-]9.5-17.2 x 4.1-8.3 cm) and stipules widely ovate to suborbicular. The other two Mexican species considered in this study are also distinct from *Sabicea flagenioides*.

*Additional specimens examined.* MEXICO. **Chiapas:** Interior lowlands, Km 33 S of Sureste on road to Mal Paso, near Tabasco border, 17°25'N, 93°35'W, *Roe et al.* 1369 (WIS). **Oaxaca.** Sta. Maria Chimalapa, Arroyo Chocolate, junto al camino en pequeña cañada, Acahual en area de selva, suelo café cascajoso, 16°52'N, 94°44'W, *Heriberto Hernández* 1333 (MO).

**12. *Sabicea chocoana*** C. M. Taylor, *Novon* 12 (2): 284285, f. 1A-B. 2002. TYPE: Colombia. Antioquia-Choco border: zona de Urabá, Cerro El Cuchillo, Finca Cidon a la Cumbre, 20100 m, 9 Oct 1987, *D. Cárdenas* 584 (holotype, JAUM, not seen; isotype, MO!).

Twining suffrutex or vine, stems 1-2 m long; terminal flowering branchlets densely and usually uniformly hirtellous, sometimes strigulose, trichomes (0.7-)0.1-0.8 mm long. *Stipules* oblong to deltate, reflexed, (2-)3-7 x (2.6-)3.5-6(-8) mm, apically obtuse to rounded, papyraceous, ciliolate with cilia 0.1-0.6 mm long cilia, adaxially sparsely to moderately densely strigulose almost all over, abaxially usually sparsely to densely hirtellous all over, occasionally strigulose at the lower part, trichomes (0.7-)0.1-0.7 mm long, 9-12-veined, colleters 6-19, 0.5-0.9 mm long. *Leaf blades* elliptic to

widely oblong or ovate, (3–)5.5–12(–15.5) × (1.9–)4–8.2 cm, apically gently acuminate to obtuse, basally acute to cuneate, obtuse or rounded, papyraceous, cilia (0.1–)0.2–0.7 mm long; adaxially usually sparsely to moderately densely hirtellous, occasionally strigulose at lamina, densely hirtellous at costa, trichomes (0.07–)0.1–0.8 mm long; abaxially sparsely to densely hirtellous at lamina, densely at costa and secondary veins, trichomes(0.1–)0.2–0.7 mm long, secondary veins 7–11 pairs, plain adaxially and protruding abaxially, tertiary veins indistinct or distinct abaxially; *petioles* (5–)7–25 mm long, densely hirtellous. *Inflorescences* in one and both axes of each node, 5–10-flowered, and usually shortly pyramidal to sometimes subglobose- and lax-paniculate, (1.5–)2–5.5 × (1.5–)3–5.5 cm, primary axis 0.2–3(–4.5) mm long, main lateral axes 2–4, (0–6 mm long); *peduncles* (0.2–)0.5–35(–45) mm long; *bract* (sub-)exinvolucrate, (1–)2–5 × 1–2 mm, papyraceous, 3–5-lobed, lobes 0.4–1.5 × 0.5–1.2 mm, lingulate to narrowly elliptic or lanceolate, apically obtuse or acute, margins entire, ciliolate with (0.1–)0.2–0.5 mm long cilia, adaxially sparsely to moderately densely sericeous to strigulose almost all over or at the basal part, abaxially sparsely to moderately densely hirtellous all over, bracteoles (0.5–)1–2(–3) × 0.3–1(–1.5) mm, triangular to deltate or lanceolate, apically (sub-)acute to obtuse, margins entire to serrulate, colleters 2–4, 0.2–0.6 mm long; *Flowers* pedicellate, pedicels (1–)3–9 mm long; *calyx* campanulate, 5-lobed, tubes (1–)1.5–1.8 × 1.7–2 mm, lobes (0.3–)1.2–2.2 × (0.3–)1.1–1.2 mm, reflexed, usually narrowly lingulate to ovate or occasionally narrowly triangular, apically (sub-)acute, margins entire, ciliolate with 0.2–0.3 mm long cilia, adaxially sparsely strigulose at the apices or upper part, eventually glabrescent, always glabrous at lower part, trichomes 0.07–0.2(–0.4) mm long, abaxially densely hirtellous at lobes and tubes, trichomes 0.1–0.6 mm long, colleters 1(–3) in each sinus; *corolla* salverform, tubes (6–)8–9.5 × 1.5–1.8 mm, lobes 2–3.5 × 1.1–1.8 mm, lobes ovate, antrorse, adaxially the indumentum of orifice extends up to 4.5–5.3 mm along the tube surface, glabrous at lower part, trichomes (0.07–)0.2–0.6 mm long, abaxially usually densely hirtellous, occasionally strigulose, trichomes (0.07–)0.2–0.8 mm long; *stamens* 5 per flower, attached to corolla tube at 6.5–7 mm from the base, anthers 1.3–1.7 × 0.3–0.4 mm, free part of filament 0.2–0.3 mm long; *style* 5.5–6 mm long, stigmatic lobes 1.2–1.7 × 0.2–0.3 mm; *ovaries* 1.5–1.8 × 1.6–1.8 mm, abaxially shallowly 5-lobed or uneven, densely and uniformly hirtellous, 5-locular, each locule 1.1–1.2 × 0.4–0.7 mm; *Fruits* purple or black, (2–)3–4 × (2–)3–4 mm when immature, 9–12 × 9–12 mm when mature, abaxially isolatedly to sparsely hirtellous; *seeds* 0.3–0.5 × 0.3–0.5 mm.

*Phenology, distribution and habitat.* *Sabicea chocona* is collected mostly with corolla-less flowers in May–November and with fruits in July and October. Fruiting occurs also in May, and September through November (Taylor 2002). This species is mainly collected from Chocó, where this is supposed to be centered (Taylor, 2002), but also found in Antiqua, and Santandar Departments of Colombia. Taylor (2002) described this species as distributed in

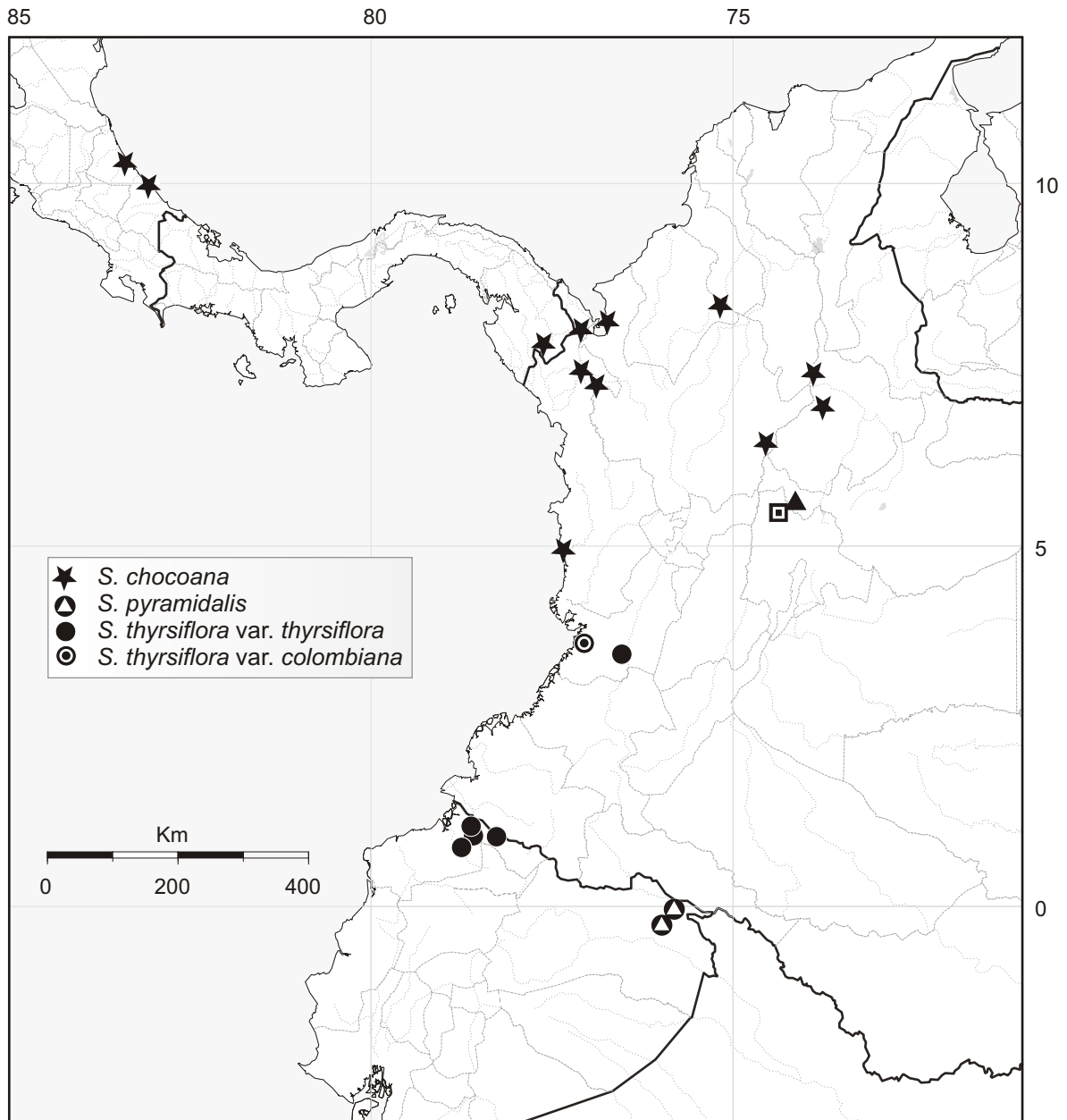


Figure 20. Map of southern Mesoamerica and northwest South America (in part), showing the distribution of *Sabicea chocoana*, *S. pyramidalis*, and *S. thysiflora*.

eastern Panama to northwestern and central Colombia; 10-600 m (Fig. 20).

*Discussion.* *Sabicea chocoana*, *S. panamensis*, *S. pyramidalis*, *S. thysiflora*, and *S. cochabambensis* with medium sized inflorescences superficially seem alike because of their similar inflorescence type including distinct peduncles, inflorescence axes, and pedicels. The size of leaves, stipules, and bracts, and size and orientation of calyces of this species fall within the variation range of *Sabicea panamensis*. However, *Sabicea chocoana* is a distinct species, which can easily be set apart from *Sabicea panamensis*, *S. pyramidalis*, and *S. thysiflora* by its erect and uniformly hirtellous indumentum of branchlets, lower surface of leaves, and outer surface of



inflorescences including corolla tubes, and presence of indumentum at the adaxial upper part or apices of stipules, bracts and calices, as mentioned by Taylor (2002). Additionally it differs from *Sabicea panamensis* and *S. pyramidalis* by its apically obtuse stipules, whereas, from *S. thyrsoiflora* by its shorter ([0.3–]1.2–2.2 mm in contrast to 2.4–3.8 mm long), narrower (usually 1.1–1.2 mm in contrast to 1.3–1.9 mm wide) and reflexed (in contrast to antrorse) calyx lobes. Both *Sabicea chocoana* and *S. cochabambensis* are notable for their erecto-patent trichomes. Yet, *Sabicea chocoana* is distinct from *S. cochabambensis* by its apparently mostly uniform hirtellous indumentum, shorter cilia (0.1–0.7 mm in contrast to 0.7–3.5 mm), apically obtuse to rounded stipules, and fewer flowers per inflorescence (5–10 flowers in contrast to (12–)30–46(–56) flowers), presence of indumentum at the adaxial upper part or apices of stipules, bracts and calices, elliptic to lingulate or narrowly ovate, shorter (usually 1.2–2.2 mm in contrast to 3–7 mm) calyx lobes, and longer (6–9.5 mm in contrast to 3–4.5 mm long) corolla tubes externally covered with usually hirtellous, sometimes strigulose indumentum, comprised of shorter (0.2–0.8 mm in contrast to 0.9–2.5 mm) trichomes. The indumenta of *Sabicea chocoana* and the new species *S. noelii* are almost identical. But *Sabicea chocoana* markedly differs from *S. noelii* by its lax inflorescences, reflexed and shorter ([0.3–]1.2–2.2 mm in contrast to (1.8–)5–11 mm] calyx lobes, and colleter's location in the sinus. Of the paratypes cited by Taylor (2002) from Bolívar (Colombia), and Darién (Panama), only *Sullivan*, 715 (MO) from Darién could be studied here. It constitutes an intermediate of *Sabicea chocoana* and *S. panamensis*, as well as *Castañeda*, 4870 (US), collected from Santander of Colombia. The collections *Kuntze* 2012 (NY), and *Shank & Molina* 4165 (F, HUH) of Costa Rica seem mostly similar to *Sabicea chocoana* instead of *S. panamensis*, commonly found in Costa Rica, due to which we have included these with *S. chocoana*.

*Selected specimens examined.* COLOMBIA. **Antioquia:** Turbo, Carretera Tapón del Darién, sector Río Leon-Lomas Aisladas, Km 37, *Brand & González* 680 (MO); Cauca, Along road to Nechí ca. 19 km E from Cauca-Plainta Rica road, 8°2'N, 75°10'W, *Brant & Escobar* 1185 (NY); Puerto Berrio, corregimiento Calera, Planta Hidroeléctrica Calera, margen izquierda, de la quebrada Malena, *Fonnegra et al.* 6992 (MO). **Choco:** Logging road ca. 2–4 km NW of Teresita, *Duke* 11039 (MO, NY), 11054 (MO); Trail from Río Tigre base camp up Serranía del Darién W of Unguía, *Gentry & Aguirre* 15236 (MO, NY); Río Sucio, Parque Natural Nacional Los Katyos, Salto de Tilupo, *León* 137 (MO), Por el camino que conduce de la Cabana de Peyé a la quebrada 'del camino', *Barbose* 1045 (HUH), Region de Urabá, cerro del Cuchillo, *Cárdenas* 2240 (MO), *Cárdenas* 254 (MO), *Cárdenas* 363 (MO), *Cárdenas* 787 (MO), Camino entre Cuchillo Negro y Punta de las Flores, *Cárdenas* 1944 (MO); Nuqui, Camino desde el aeropuerto por la loma, *Delprete* 6339 (NY), *Delprete*, 6342 (NY). **Santandar:** Magdanella Valley, Campo Capote, 30 km E of Carare, *Gentry & Renteria* 20079 (MO); Vicinity of Barranca Bermeja (El Centro), *Haught* 2210 (HUH, NY). COSTA RICA: Puerto Limón, 10°0'N, 83°02'W, *Kuntze* 2012 (NY), Suerre y Dos Bocas, Drenajes de los Ríos Parismina y Reventaz, *Shank & Molina* 4165 (F, HUH).



**13. *Sabicea cinerea*** Aubl., Hist. Pl. Guian. 1: 193, t. 75. 1775. *Schwenkfelda cinerea* (Aubl.) Sw., Fl. Ind. Occ. I. 452. 1797. TYPE: Mufeo Banks, in fepibus Cayennae, Guanae, *Aublet von Rohr*. (BM!). Figure 21A–O.

Spreading shrubs or lianas; terminal flowering branchlets densely lanate to lanuginose or arachnose, trichomes 0.9–1.2 mm long. *Stipules* widely lanceolate to ovate or triangular or oblong, erect and appressed, 4–7(–8) × 2–5.5 mm, occasionally bifided, apically acute to obtuse, basally obtuse or truncate, papyraceous, margins entire, complanate, eciliate, adaxially glabrous excluding the basal part, sometimes sparsely puberulous-floccose near apices, abaxially usually densely lanate to lanuginose or arachnose, 5-veined, colleters 5–7, (0.8–)1–1.8 mm long. *Leaf blades* usually elliptic to oblong or obovate to oblanceolate to widely lanceolate or ovate, (2–)5–12.5 × (1–)2.5–5.5(–6.2) cm, apically (sub-)acute or acuminate, rarely mucronate to obtuse, basally acute to obtuse or cuneate, membranous or papyraceous, usually eciliate, occasionally ciliolate, adaxially floccose or isolatedly to moderately densely arachnose or lanate at lamina, usually almost all over when immature and partially when mature, eventually glabrous, usually densely floccose to sparsely arachnose or lanate at costa, rarely isolatedly puberulous, trichomes 0.6–1.2 mm long; abaxially densely lanate to lanuginose all over, sometimes sparsely arachnose and rarely strigulose or villosulous at costa and secondary veins, trichomes 0.8–1.5 mm long, secondary veins (9–)12–15(–17) pairs, costa and secondary veins usually distinct or plain adaxially and protruding abaxially, tertiary veins usually distinct, sometimes prominulous abaxially; *petioles* (5–)7–15(–25) mm long, usually densely arachnose and rarely strigulose or tomentose, trichomes 0.9–1.5 mm long. *Inflorescences* usually one, rarely two per node, 3–8(–10)-flowered, compact-fascicled, 2–2.5(–3) × 1.5–2.5(–3) cm; *peduncles* 0(–3) mm long; *bracts* (sub-)exinvolucrate, papyraceous incompletely isolated into 2–5 parts, isolated parts 7–12 × 5–9 mm, 2–3-lobed, lobes (1–)2–10 × 2–7 mm, ovate to deltate or lanceolate or lingulate, apically acute or obtuse, margins entire or denticulate, eciliate, adaxially glabrous to strigulose or sericeous at upper part, and densely sericeous at base, trichomes adaxially (0.2–)0.5–1.1 mm long, abaxially densely lanate to lanuginose or arachnose usually all over, trichomes 0.8–1.2(–1.7) mm long, 3–5-ribbed, bracteoles (0.7–)4–9(–11) × 1–3(–5) mm, elliptic to lingulate, colleters 2–4, 0.5–0.6 mm long. *Flowers* usually sessile, rarely subsessile, pedicels 0(–2.1) mm long; *calyx* campanulate, 5(–7)-lobed, tubes 1.2–3(–4) × 2.5–3.5(–4) mm, lobes (1.8–)5–11 × (0.6–)1.5–2.5(–4) mm, antrorse or spreaded, usually lingulate to lanceolate, occasionally narrowly very elliptic, apically (sub-)acute to obtuse, basally truncate, margins entire, ciliolate at upper part or eciliate, ciliolate with (0.2–)0.4–0.6(–0.8) mm long cilia, adaxially usually isolatedly to sparsely strigulose and arachnose only at the upper part, always glabrous at lower part, trichomes (0.2–)0.4–0.6(–0.9) mm long, abaxially usually densely lanate to lanuginose or arachnose with covering the margins, occasionally isolatedly sericeous to strigulose all over

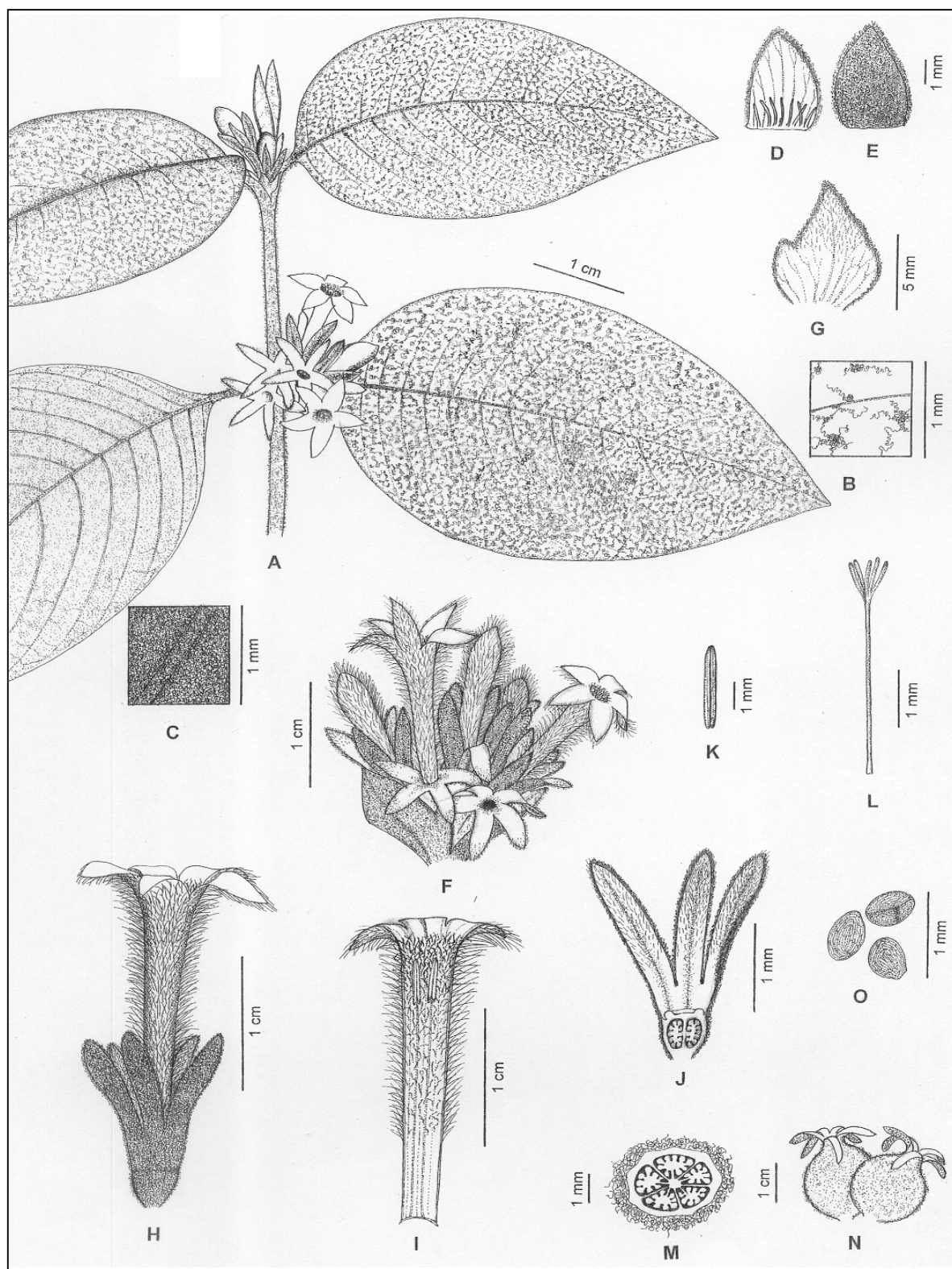


Figure 21. A–O. *Sabicea cinerea*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Inner stipule surface showing the arrangement of colleters. —E. Outer stipule surface. —F. Inflorescence. —G. Inner bract surface. —H. Flower. —I. Inner corolla surface showing anther's position. —J. Longitudinal section through calyx and ovary. —K. Face view of Anther. —L. Style and stigmas. —M. Transversal section through ovary. —N. Fruit. —O. Seeds.

the lobes or tubes, 3(–5)-veined, colleters 1–3 in each sinus, (0.2–)0.4–0.8 mm long; *corolla* white, salverform to hypocrateriform, tubes 9–21(–23) × 1.3–2(–3.5) mm, lobes 4–7 × 1–2 mm, widely lanceolate to narrowly ovate, antrorse or spreaded, adaxially the indumentum of orifice extends up to 4.1–6.5(–7.6) mm inside the tubes, abaxially pilosulous to pubescent, (1–)1.8–2.4(–3.5) mm long; *stamens* 5 per flower, attached to corolla tube at 12–16.5 mm from the base, anthers (2–)3–3.2 × 0.4–0.6 mm; *style* 11–14(–20) mm long, stigmatic lobes (2–)3–3.5 × 0.2 mm; *ovaries* (2.3–)2.5–3 × (2.5–)3–3.5 mm, abaxially uneven or shallowly 4–5-lobed, usually densely arachnose, (4–)5(–6)-locular, each locule 1.1–1.8 × 0.5–0.6 mm. *Fruits* red to pink, 4–6 × 4–6 mm when immature, 9–11(–15) × 9–10(–15) mm when mature, abaxially sparsely arachnose to lanuginose; *seeds* 0.5–0.7 × 0.3–0.4(–0.6) mm.

*Phenology, distribution and habitat.* Flowering occurs almost all over the year and fruiting in April, June and November. This species is centered in French Guiana, and extends to Suriname, Brazil, and Venezuela. It is found in lowland wet forest, weedy and waterlogged savanna vegetation, roadside, open places and on lateritic to clayey soil; 2–600 m (Fig. 22).

*Discussion.* *Sabicea cinerea* is distinguishable by its floccose or isolatedly to moderately densely arachnose or lanate indumentum at upper surface of lamina (Fig. 21B), densely lanate to lanuginose all over the abaxial surfaces of lamina, and stipules, bracts, hypanthia and calyx lobes, 3–8(–10)-flowered compact-fascicled, usually 5–11 mm long, oblong to lanceolate or narrowly elliptic calyx lobes, 9–21(–23) mm long corolla tubes, with 4–7 mm long lobes, and external erecto-patent trichomes (Fig. 21I). Aublet (1975) recognized *Sabicea cinerea* by its twining habit, ovate and apically acute leaves, and long corolla. Wernham (1914) keyed out this species by its subentire stipules, sessile inflorescences, long calyx, adaxially arachnoid, otherwise glabrous leaves. *Sabicea cinerea* seems very similar to *S. grisea*, from which it differs by its generally exclusively floccose to arachnose adaxial surface of lamina, eciliate stipules and bracts, and lanate to lanuginose or arachnose indumentum of abaxial surface of bracts and calices that usually overlap the margins.

*Sabicea cinerea* seems superficially close to *S. amazonensis* and *S. mollissima* from which it differs by its floccose to arachnose and eventually glabrous adaxial leaf blades, shorter (usually 1.2–3 mm in contrast to 5–11 mm [*S. amazonensis*] or 4–9 mm [*S. mollissima*]) and adaxially glabrous calyx tubes, thick, lingulate to widely linear and abaxially densely arachnose to lanate calyx lobes with eciliate or only apically ciliolate margins and location of colleters in the sinus. Due to the similar indumentum at leaves, and outer surface of stipules and inflorescences (excluding corolla), *Sabicea cinerea* appears close to *S. cana* and *S. tillettii*. It is distinct from *Sabicea cana* by its longer, narrowly lingulate to lanceolate, narrowly elliptic calyx lobes, abaxially pilosulous to pubescent and longer corolla tubes, and glabrous style and stigmas. It can be set apart from *Sabicea tillettii* by its lingulate to lanceolate, occasionally narrowly elliptic and apically (sub-)acute to obtuse calyx lobes, longer corolla

lobes, and external pilosulous to pubescent indumentum of corolla tubes.

*Sabicea cinerea* seems close to some *S. velutina* with oblong leaves from which it can be set apart by its floccose, arachnose or lanate indumentum at upper surface of leaf blades, eciliate stipules and bracts and mostly longer (5–11 mm in contrast to usually 3–6 mm long), usually lingulate to lanceolate, occasionally narrowly very elliptic, apically (sub-)acute to obtuse calyx lobes that are marginally eciliate or ciliolate with shorter cilia ([0.2–]0.4–0.6[–0.8] mm in contrast to [0.8–]1.2–1.8 mm).

Steyermark (1974) mentioned the indumentum of adaxial leaf surface of *Sabicea cinerea* of Venezuela as “arachnoideo-o flocoso-pubescente”. Pubescent indumentum or straight trichomes are totally absent at the adaxial surface of lamina of *Sabicea cinerea* of French Guiana and Suriname. We observed one (Steyermark *et al.* 107750, NY) of the two collections cited by Steyermark (1974) and additionally another collection (Steyermark *et al.* 108427 (MO) from Sucre, Venezuela). The presence of pubescent or puberulous indumentum at adaxial lamina of these collections is not very distinct at all leaves. Its constant presence with floccose to arachnose indumentum might support a new infraspecific delimitation, however, the material studied is insufficient to arrive at a new subspecific delimitation based on this character. In *Kalle 443* (US) the free parts of filaments are unusually long (up to 3.5–5 mm in contrast to usually less than 1 mm long).

*Selected specimens examined.* BRASIL. *Martii 82* (BR). FRENCH GUIANA. **Cayenne:** Karouany, *Sagot 309* (BM, G[2], HUH, S); Vicinity of Cayenne, *Broadway 210* (HUH, NY, US), Bord de route entre Cayenne et Rochambeau, *Kallé 443* (US, U); Basse Approuague, près de Régin, *Oldeman B-501* (NY, U); Savane bordelaise, rout du tour de l’fle, sud-ouest Cayenne, *Veyret & Cremers 4408* (US); Savane Macrabo, *Hoff 5455* (G, MO, NY, U); Ile de Cayenne, Mont de Bourda, 5 km à l’E de la ville, *Raynal-Roques 20023* (NY, US, U), Mont Baduel, *Cremers & Hoff 12922* (MO), Mont Grand Matoury, *Granville et al. 12865* (MO), *Cremers et al. 13830* (MO, US); Plaine de Kaw, Crique Anjelique Marais, *Granville 6811* (BR), Montage de Kaw, Environ du camp Caiman, *Granville 6662* (MO), Piste du Village Eskol, Bord de route et de Piste, *Hoff & Hoff 226* (MO), along road, ca. 4 km W of Camp Caimans, *Andersson et al. 1926* (S), Piste de Kaw, 8 km apres le pont sur le Mahuri, *Billiet & Jadin 6364* (BM, BR, G, MO[2]); Montagnes des Cheveaux, South of Cayenne (32 km along road), *Leeuwenberg 11621* (NY); Riviere Comte, á proximeté de la route N2, *Billiet & Jadin 1261* (U); Comté, Rivière Comté, á proximité de la route N2, *Billiet & Jadin 1261* (BM, BR, NY, U); Piste de St. Elie, S from Sinnamary, 5–15 km S of coastal highway, *Zentry, & Zardini 50339* (MO[2]); St. Laurent region, along Route D9 to Mana, *Skog et al. 7457* (NY); RN 2 pres du pont sur La Comte, *Billiet & Jadin 4303* (BM, BR); Ile Corossony-Région Littorale, Bord de crique, *Toriola-Marbot & Hoff 175* (MO); Crique Canceler, Région littorale, *Toriola-Marbot & Hoff 212* (MO); Route RN2, Cayenne-Regina, pk 67, Crique Tibourou, *Billiet & Jadin 5744* (BR, MO); By old airstrip at Le Gallion, ca. 10 km SW of Rochambeau airport along Route N2,

*Andersson et al.* 903 (MO, NY, S); Layon Montage Prise d'eau-Basin de l'Approague, *Hequet* 356 (MO, U); Route Cayenne-Brazil, Bridge over the Orapu River, near Auberge des Orapailleurs, *Delprete & Croizer* 7158 (MO). SURINAME. Mariwijne, Moengo, *Hekking* 1044 (NY, U); Cottica. *Kock, s.n.* (MO, U). VENEZUELA. **Sucre:** Entre La Sabana, Los Altos y La Silleta, hacia Zurita, *Steyermark et al.* 107750 (NY), Montaña de Mochima, quebrada bosqueada, al Sur de Mochima, 20 kms al Sureste de Cumaná, *Steyermark et al.* 108427 (MO).

**14. *Sabicea cochabambensis*** Liede, Meve & Khan, sp. nov. TYPE: Bolivia. Cochabamba: Chapare, Pie de la cordillera de Mosestenes, comunidad de Villa Fátima, 16°33'36''S, 65°57'36''W, 15 May 2002 (fl), *M. Zárate, B. Agular, S. Altamirano, D. Méndez & N. Altamirano*, MZ 1334 (holotype, MO!). Figure 22A–I.

*Sabicea pearcei similis, sed differt pedunculis multo longioribus et foliis magnioribus.*

Vines or lianas; terminal flowering branchlets sparsely to densely pilosulous, isolatedly puberulous, eventually glabrescent, trichomes (0.2–)0.4–3 mm long. *Stipules* widely ovate or deltate, reflexed, 8–13 × (7–)8–15 mm, apically (sub-)acute to acuminate, membranous, ciliolate to ciliate with 0.7–1.8(–3) mm long cilia, adaxially glabrous excluding the basal part, abaxially sparsely to densely pilosulous, at the middle, lower part or all over, trichomes 0.7–1.8 mm long, 12–14-veined, colleters 5–9, 0.8–1.8 mm long. *Leaf blades* elliptic to widely elliptic or ovate, 13–17.5 × (2–)5–9 cm, apically acute to acuminate, basally attenuate, papyraceous, ciliate with (0.3–)1–3.5 mm long cilia, adaxially usually sparsely pilosulous at lamina and secondary veins, densely at costa, trichomes (0.1–)0.3–3 mm long, abaxially sparsely to densely pilosulous, occasionally isolatedly puberulous, trichomes (0.07–)0.3–3 mm long, secondary veins 11–14 pairs, slightly protruding or plain adaxially and protruding abaxially, tertiary veins prominulous and quaternary veins distinct, sometimes prominulous abaxially; *petioles* 20–40 mm long, densely pilosulous to hirtellous. *Inflorescences* two per node, (12–)30–46(–56)-flowered, elongated- and moderately lax-, widely pyramidal- to cylindrical-thyrsoid or ovoid- to subglobose-paniculate, 3–6 × 2–4(–6) cm, primary axis (5–)10–35 mm long, main lateral axes 4(–6), usually compound dichasia; *peduncles* 12–45 mm long; *bracts* usually subinvolucrate, membranous, (8–)10–15 × (8–)10–15 mm, (3–)5–6-lobed, lobes (2–)3–14 × 2–12 mm, ovate to triangular or lanceolate, apically acute to acuminate, margins serrulate, ciliolate to ciliate with 0.7–1.8(–3) mm long cilia, adaxially usually glabrous, rarely isolatedly to sparsely pilosulous at apices or upper part, sericeous at the base, trichomes 0.6–2.1 mm long, abaxially isolatedly to sparsely pilosulous all over or at the lower part, and middle of upper part, trichomes 0.7–2.4(–3) mm long, (5–)9–12-ribbed, bracteoles (3–)8–12 × 2–6 mm, lanceolate to ovate, colleters 2. *Flowers* usually pedicellate, occasionally sessile, pedicels (0.5–)1.5–6 mm long, densely pilosulous; *calyx* campanulate, 5-lobed,

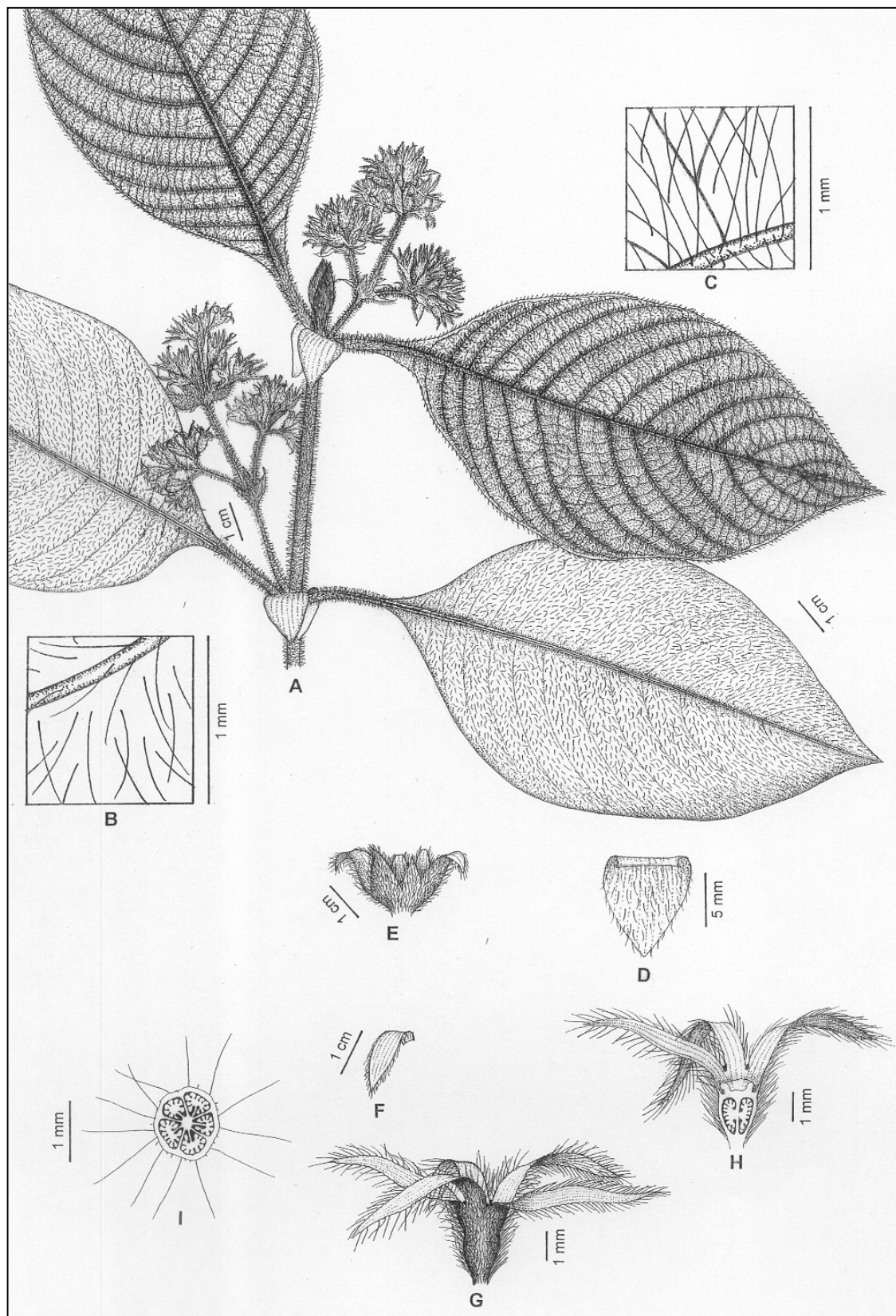


Figure 22. A–I. *Sabicea cochabambensis*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Outer stipule surface. —E. Side view of bract. —F. Inner bracteole surface. —G. Side view of calyx. —H. Longitudinal section through calyx and ovary. —I. Transversal section through ovary.

tubes 0.9–1.3 × 1.5–1.8 mm, lobes (2–)3–7 × (0.5–)0.8–1.3 mm, lanceolate to lingulate, usually antrorse to spreaded, rarely recurved, apically acute to acuminate, margins entire to serrulate, ciliolate to ciliate with with 0.7–1.8(–3) mm long cilia, adaxially glabrous, abaxially isolatedly to sparsely pilosulous all over the lobes and tube, trichomes 0.7–2.4(–3) mm long, (3–5)-veined, colleters 1 in each sinus, 0.2–0.3 mm long; *corolla* salverform, tubes 3–4(–4.5) × 1.8–2.7 mm, lobes 1.7–2.1 × 1.2–1.5 mm, ovate, antrorse, adaxially the indumentum extends up to 1.8–2.1 mm along the tube surface and orifice, glabrous the base and lower part of tube, trichomes 0.3–0.5 mm long, abaxially pilosulous, all over the lobes and tubes, glabrous at the base, trichomes 0.9–2.5 mm long; *stamens* 5 per flower, attached to corolla tube at 2.3–2.6 mm from the base, anthers 2–2.2 × 0.3–0.4 mm; *style* (1–)1.5–1.8 mm long, stigmatic lobes 5, 1.1–1.2 × 0.1–0.1 mm; *ovaries* (1.1–)1.3–1.6 × 1.2–1.5 mm, abaxially uneven, pilosulous, 5-locular, each locule 1.2–1.5 × 0.4–0.6 mm.

*Phenology, distribution and habitat.* Flowering in January to March, May to June, and November to December. Tropical evergreen or semi-evergreen or tropical humid forest, on remnants of evergreen forest subjected to agricultural uses; sandy to clayey soil along rivers, on slopes or beside stream; 260–1600 m (Fig. 10).

*Discussion.* *Sabicea cochabambensis* is characterized by its thyrsoid to lax-paniculate inflorescences, usually subinvolute bracts and antrorse to spread calyces, acute to acuminate apices of stipules, bracts and calyx lobes, long petioles and peduncles, 3–4.5 mm long corolla tubes, pilosulous indumentum of branchlets, leaves, and outer surface of inflorescences including corolla tubes comprised of apparently longer erecto-patent trichomes, and longer erecto-patent cilia of stipules, leaves, bracts and calyces.

*Sabicea cochabambensis* superficially seems an extreme form of *S. pearcei* due to some common qualitative characters, yet, it is distinct from *S. pearcei* by its longer petioles (2–4 cm in contrast to 0.4–0.7 cm; Fig. 22A), larger lamina (13–17.5 × [2–]5–9 cm in contrast to 7–12 × 2.5–4.3 cm), longer peduncles [(1.2–)1.5–4.5 cm in contrast to 0.4–0.7 cm), larger (3–6 × 2–6 cm] in contrast to 2–2.5 × 2 cm) inflorescences with usually subinvolute bracts and longer primary axes (0.5–3.5 cm long in contrast to 0.2–0.4 cm), and lanceolate to lingulate calyx lobes. It seems also close to *Sabicea chochoana* due to its almost similar inflorescence types and erecto-patent trichomes. However, it is distinct from *Sabicea chochoana* by its mostly differentiated and pilosulous indumentum, longer cilia (0.7–3.5 mm in contrast to 0.1–0.7 mm; Fig. 22G, H), apically (sub-)acute to acuminate stipules, many-flowered ([12–]30–46[–56] flowers in contrast to 5–10 flowers) inflorescences, adaxially glabrous apices of stipules, bracts and calyces, lanceolate to lingulate, usually antrorse to spread and longer calyx lobes, shorter (3–4.5 mm in contrast to 6–9.5 mm long) corolla tubes, externally covered with pilosulous indumentum, comprised of longer trichomes. Its inflorescence is reminiscent of



*Sabicea panamensis*, *S. pyramidalis* and *S. thyrsoiflora*, but it differs from these species by its pilosulous indumentum of branchlets, leaves, and outer surface of inflorescences including corolla tubes, mostly comprised of apparently longer erecto-patent trichomes, and its erecto-patent and longer (0.7–3 mm in contrast to 0.4–0.5 mm) cilia at the margins of stipules, leaves, bracts and calyces.

*Additional specimens examined.* BOLIVIA. **Beni:** Ballivian, Serrania del Pilon Lajas, vertiente oriental, 14–15 km de Yucumo, 15°13'S, 67°03'W, *Smith et al. 13260* (MO), carretera Caranavi-San Borja, ca. 14–15 km de Yucumo, 15°9'S, 67°31'W, *Smith et al. 13967* (MO). **Santa Cruz:** Ichilo, Parque Nacional Amboró. Río Sagwayo, *Paz 121* (syntype, MO); Del Sara, Buena Vista, *Steinbach 1813* (HUH); Ichilo, 4 km WSW of El Hondo Poterillo, 17°40'20''S, 63°28'W, *Nee & Vargas 44951* (NY), Parque Nacional Amboró, along Río Sagwayo, near mouth of Quebrada Yapojé, 17°34'S, 63°44'W, *Nee 40958* (NY), Río Sagwayo, Choza de don Alberto, 10.5 km SW de Huaytú, 17°39'S, 63°43'W, *Salcias 501* (F, NY), 0–2 km, SW of EL Carmen, 17°32'S, 63°42'W, *Nee 39835* (NY), ca. 12 km. SW of main highway at Villa Germán Busch, 17°30'S, 63°56'W, *Nee 46511* (NY). PERU. **Junin:** Pichis Trail, Yapas, *Killip & Smith 25548* (F, NY). **Madre De Dios:** Tambopata, Río Tambopata, Comunidad Nativa de Infierno, 12°50'S, 69°17'W, 20 Feb. 1991, *V. P. Baca 98* (syntypes, MO, NY).

**15. *Sabicea cuneata*** Rusby, Mem.Torrey Bot. Club, 6: 47.1896. TYPE: Bolivia. Between Guanai and Tipuani, Apr-June 1892 (fl & fr), *M. Bang 1380* (holotype, F, not seen; isotypes, BM!, G!, HUH!, K!, M!, MO!, NY[2]!, US!, W!). Figure 23A–K,

Woody vines; terminal flowering branchlets usually sparsely-densely strigulose to occasionally hirtellous and sparsely to densely arachnose to lanuginose, trichomes (0.07–)0.2–1.1 mm long. *Stipules* ovate to deltate or oblong, usually reflexed or antrorse, 3.2–7 × 2.5–8 mm, apically (sub-)acute, margins entire, complanate, eciliate or ciliolate, ciliolate with (0.07–)0.1–0.4 mm long cilia, adaxially densely sericeous at the base, isolatedly to densely at rest of the surface, eventually glabrate towards the apices, abaxially densely strigulose to pubescent all over, sometimes arachnose or floccose at the base or at the lower part, trichomes (0.1–)0.4–1.1 mm long, 12–14-veined, colleters 8–12, 0.4–0.9 mm long. *Leaf blades* elliptic to ovate or lanceolate, (2–)5.5–12(–16) × 2.4–6.6(–8) cm, apically acute to acuminate, basally acute to moderately cuneate, membranous, usually eciliate, occasionally isolatedly to sparsely ciliolate, ciliolate with (0.1–)0.2–0.6 mm long cilia, adaxially sparsely to densely strigulose to pubescent or puberulous all over, occasionally costa and secondary veins arachnose to floccose, trichomes usually 0.5–1.1 mm long; abaxially isolatedly to sparsely strigulose and densely lanuginose at lamina, densely strigulose and usually sparsely arachnose to lanuginose at costa and secondary veins, secondary veins (8–)10–12(–14) pairs



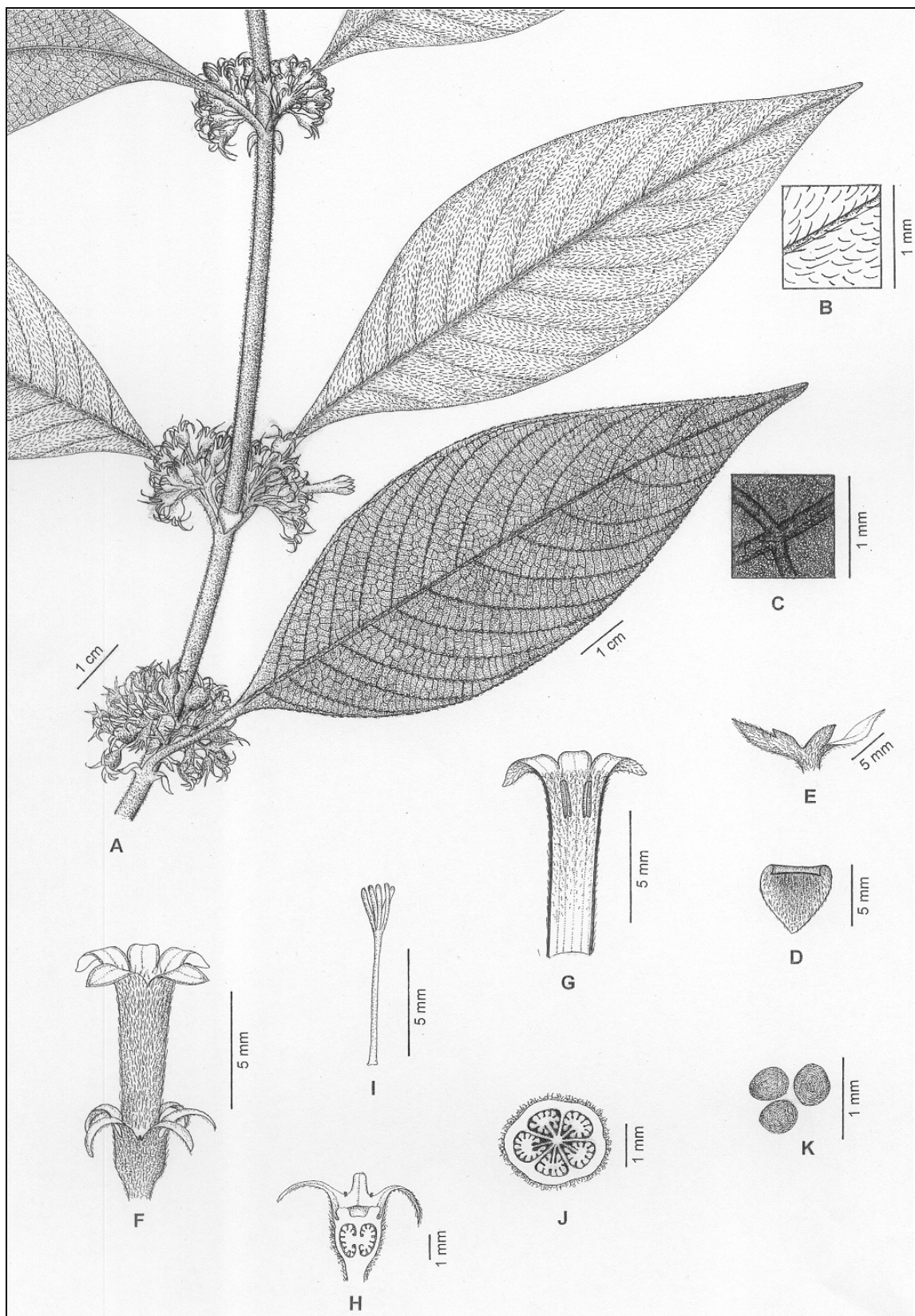


Figure 23. A–K. *Sabicea cuneata*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Outer stipule surface. —E. Side view of bract. —F. Flower. —G. Inner corolla surface showing anther's position. —H. Longitudinal section through calyx and ovary. —I. Style and stigma. —J. Transversal section through ovary. —K. Seeds of immature fruit.

, plain adaxially or protruding abaxially, tertiary veins distinct or prominulous and quaternary veins indistinct, sometimes distinct abaxially; *petioles* (5–)7–20 mm long, densely pubescent to strigulose and lanuginose. *Inflorescences* usually two, sometimes one per node, (6–)12–26-flowered, moderately lax-paniculate, 1.5–2.5 × 2–3.5 cm, primary axis 1–5 mm long, main lateral axes 2–4, 1–2.4 mm long, simple-reduced dichasia; *peduncles* (1–)2–7(–9) mm long; *bracts* exinvolucrate, membranous, incompletely isolated into 2 parts, isolated parts 3.5–6(–8.2) × 1–3(–4.8) mm, 2–3-lobed, lobes 1–2 × 0.5–1.2 mm, elliptic to lanceolate or ovate, apically acute to acuminate, margins entire, ciliolate with (0.07–)0.2–0.9 mm long cilia, adaxially densely sericeous from the base towards upper part usually along the costa, glabrescent at rest of the surface, abaxially densely sericeous to pubescent at the lower part, sparsely towards the upper part, trichomes (0.07–)0.1–0.9 mm long, 3–5-ribbed, bracteoles 1.5–3.5(–4.4) × 0.5–1.5 mm, lanceolate to linear or lingulate, colleters 2, 0.2–0.4 mm long. *Flowers* pedicellate, pedicels 2–7 mm long, trichomes (0.1–)0.2–0.9 mm long; *calyx* campanulate, 5-lobed, tubes 0.4–1.2 × 1.5–2.6 mm, lobes (1.8–)2.6–3.5(–6) × 0.4–1 mm, antrorse or spreaded to inflexed, narrowly linear to narrowly lanceolate, apically acute to acuminate, margins entire, ciliolate with 0.1–0.6 mm long cilia, adaxially usually glabrous, rarely isolatedly pubescent at apices, abaxially sparsely-densely strigulose or puberulous all over, sometimes arachnose at lower part of tubes, trichomes 0.4–0.8 mm long, colleters 1(–2) in each sinus, 0.2 mm long; *corolla* white, salverform, tubes (6–)7–9 × (1.8–)2.1–3 mm, lobes 2–3(–3.6) × 1–1.5 mm, widely lanceolate to narrowly ovate, antrorse to spreaded, adaxially the indumentum extends up to 2.5–3.5 mm inside the tubes, abaxially densely strigulose with forming cluster near the apices of lobes, glabrous up to 1.5–1.8 mm at base, trichomes 0.2–1.2(–1.4) mm long; *stamens* 5 per flower, attached to corolla tube at 7–7.4 mm from the base, anthers 1.5–2.4 × 0.2–0.4 mm; *style* 5.5–6.2 mm long, stigmatic lobes 1.7–2 × 0.2–0.3 mm; *ovaries* 1.5–2.2 × 1.5–2.5 mm, abaxially shallowly 5-lobed to plain or uneven, 5-locular, each locule 1.4–1.5 × 0.6–0.7 mm. *Fruits* color unknown, 5–6 × 5–6 mm when immature, (6–)8–10 × (5–)6–9 mm when mature, abaxially sparsely strigulose to pubescent and floccose to sparsely arachnose; *seeds* 0.40–0.6 × 0.12–0.5 mm.

*Phenology, distribution and habitat.* Flowering in January, May and December, and fruiting in December. *Sabicea cuneata* var. *cuneata* is known only from La Paz, Bolivia and *S. cuneata* var. *setiloba* from Santa Cruz, Colombia. It occurs in humid montane forest or disturbed moist forest with primary forest trees; 1100–1500 m (Fig. 10).

*Discussion.* *Sabicea cuneata* can be distinguished by its abaxially dense and matted arachnose to lanuginose lamina (Fig. 23C); moderately lax-paniculate inflorescences, narrowly linear to lanceolate, apically acute to acuminate and adaxially glabrous calyx lobes, and erecto-patent trichomes of corolla tubes. Rusby described *Sabicea cuneata* with gray-

tomentose indumentum throughout except the strigose upper leaf surface. The upper leaf surface is in fact strigulose to pubescent or puberulous. Rusby mentioned that this species appears to be erect, which cannot be confirmed. The distinction of *Sabicea cuneata* and *S. boliviensis* as mentioned by Wernham (1914) is not clear-cut (see *S. boliviensis*). Yet, it can be set apart from *Sabicea boliviensis* by its appressed trichomes at adaxial surface of lamina, secondary veins of abaxial surface of leaves and abaxial surface of corolla tubes (Fig. 23F), marginally usually eciliate, and mostly elliptic to narrowly ovate leaves, moderately lax-paniculate inflorescences, and adaxially apically glabrate calyx lobes. This species appears close to *Sabicea erecta* and *S. calophylla* due to the almost similar inflorescence types and presence of curled to tortuous trichomes. It can be set apart from *Sabicea erecta* by its compressed and matted lanuginose and strigulose indumentum on the lower leaf surfaces, stipules apically covered with indumentum inside and longer corolla tubes (6–9 mm in contrast to 2.7–4.5 mm long). It can be distinguished from *Sabicea calophylla* by its indumentum at the upper part inside the stipules and bracts, narrowly linear to lanceolate, apically acute to acuminate, and generally longer (2.6–3.5 in contrast to 0.6–2 mm long) calyx lobes, colleter's location in sinus, inflorescences usually comprised of fewer (6–26 in contrast to 21–76 per inflorescence) flowers, and shorter (6–9 mm in contrast to 9–11.5 mm long) corolla tubes.

*Sabicea setiloba* is known only from its holotype (K) which was collected almost in fruiting stage. Only one corolla in mature stage and few in bud were observed. *Sabicea setiloba* seems very close to *S. boliviensis* and *S. cuneata*. It differs from *Sabicea boliviensis* by its (sub-)appressed trichomes at secondary veins of abaxial surface of leaves and abaxial surface of corolla tubes, whereas, from *S. cuneata* only by its pedicel's lengths. In Neotropical *Sabicea*, no species could be defined solely on the basis of pedicel length. On the other hand, in Neotropical *Sabicea*, variation in trichome types at abaxial surface of leaves and corolla tubes appears by far more consistent than pedicel length. Based on these facts, we consider *Sabicea setiloba* as a variety of *S. cuneata* with shorter pedicels.

#### Key to the varieties:

- 1a. Pedicels (2–)4–6(–8) mm long, with dense, curled or tortuous trichomes at peduncles, pedicels and hypanthia .....15a. *S. cuneata* var. *cuneata*  
 1b. Pedicels 0–2.5 mm long, with isolated curled or tortuous trichomes at peduncles, pedicels and hypanthia.....15b. *S. cuneata* var. *setiloba*

#### 15a. *Sabicea cuneata* Rusby var. *cuneata*

*Additional specimens examined.* BOLIVIA. **La Paz:** Morillo, 44,3 km N of dam at Lago Zongo, *Solomon 9196* (MO, M, NY, U); Nor Yungas, 13.7 km NW of San Pedro on road

through Incahuara-Mejillones, Trail to 12 de Octubre, *Solomon 14874* (MO, NY, U), 21.1 km al noroeste del camino entre Yolosa y Caranavi por el camino a Suapi, ca. 2.5 km al oeste de Suapi, cerca del puente sobre el Río Suapi, *Solomon 18431* (MO), Larecaja 13,8 km al SO de Guanay por el camino a Tipuani, *Solomon 17654* (G, NY).

**15b. *Sabicea cuneata* Rusby var. *setiloba* (Wernham) Liede, Meve & Khan, comb. et stat. nov.**

*Sabicea setiloba* Wernham, Monogr. *Sabicea* 37. 1914. TYPE: Colombia: Santa Cruz, in woods, Feb 1885 (fl), *R. Pearce s.n.* (holotype, BM!).

Known only from the holotype (BM).

**16. *Sabicea erecta* Rusby, Bull. New York Bot. Gard. 8 (28): 120.1912. TYPE: Bolivia: Tumapasa, 548.64 m, 13 Dec. 1901, *R. S. Williams, 446*, (holotype, NY!; isotypes, BM!, US!). Figure 24A–L.**

*Sabicea acutissima* Rusby, Mem. New York Bot. Gard. 7: 371. 1927. TYPE: Bolivia. Rurrenabaque, 304.8 m, 25 Nov 1921, *D. Cárdenas 1185* (holotype, NY!, photo F!, photo S!; isotype, F[fragments, leaf & flower!]).

Suffruticose or vine; terminal flowering branchlets sparsely to densely pilosulous to hirtellous and lanuginose, 0.4–1.1 mm long, internodes 4–9 cm long. *Stipules* ovate to deltate, reflexed, 5–8 × 4–6 mm, apically acute, ciliolate with 0.1–0.7 mm long cilia, adaxially sericeous at the base, trichomes (0.1–)0.4–1.1 mm long, abaxially densely pilosulous all over, trichomes 0.2–1 mm long, 9–14 veins, colleters 12–18, 0.5–0.9 mm long. *Leaf blades* elliptic to oblong or ovate, (3–)5–11(–13.5) × (1.8–)3–5.8 cm, apically acute to acuminate, basally acute, papyraceous, ciliolate with (0.1–)0.2–1 mm long cilia, adaxially sparsely hirtellous or pilosulous at lamina and lateral veins, densely at costa, trichomes 0.1–0.8 mm long; abaxially isolatedly to sparsely pilosulous to pubescent and sparsely lanuginose to arachnose at lamina, densely pubescent and lanuginose to arachnose, at costa and secondary veins, 0.2–1.3) mm long, secondary veins 9–12 pairs, plain adaxially or protruding abaxially, tertiary veins obscured or distinct abaxially; *petioles* (6–)8–20 mm long, densely hirtellous to pilosulous, and lanuginose. *Inflorescences* two per node, (16–)46–60-flowered, compact-paniculate to umbellate, 1.5–2.5 × (1.5–)2–3 cm, primary axis 0–7 mm long, main lateral axes 3–4, 0–3 mm long, simple to compound dichasia; *peduncles* (5–)8–30 mm long; *bracts* (sub-)exinvolucrate, papyraceous, incompletely isolated into 2 parts, isolated parts 5–7 × 4–6 mm, lobes 2–3.5 × (1–)1.3–6 mm, ovate to deltate, apically acute to acuminate, margins entire, ciliolate with 0.4–0.8 mm long cilia, adaxially glabrate to isolatedly strigulose at upper part, densely sericeous at the base, trichomes (0.5–)0.7–1.1 mm long, abaxially sparsely to

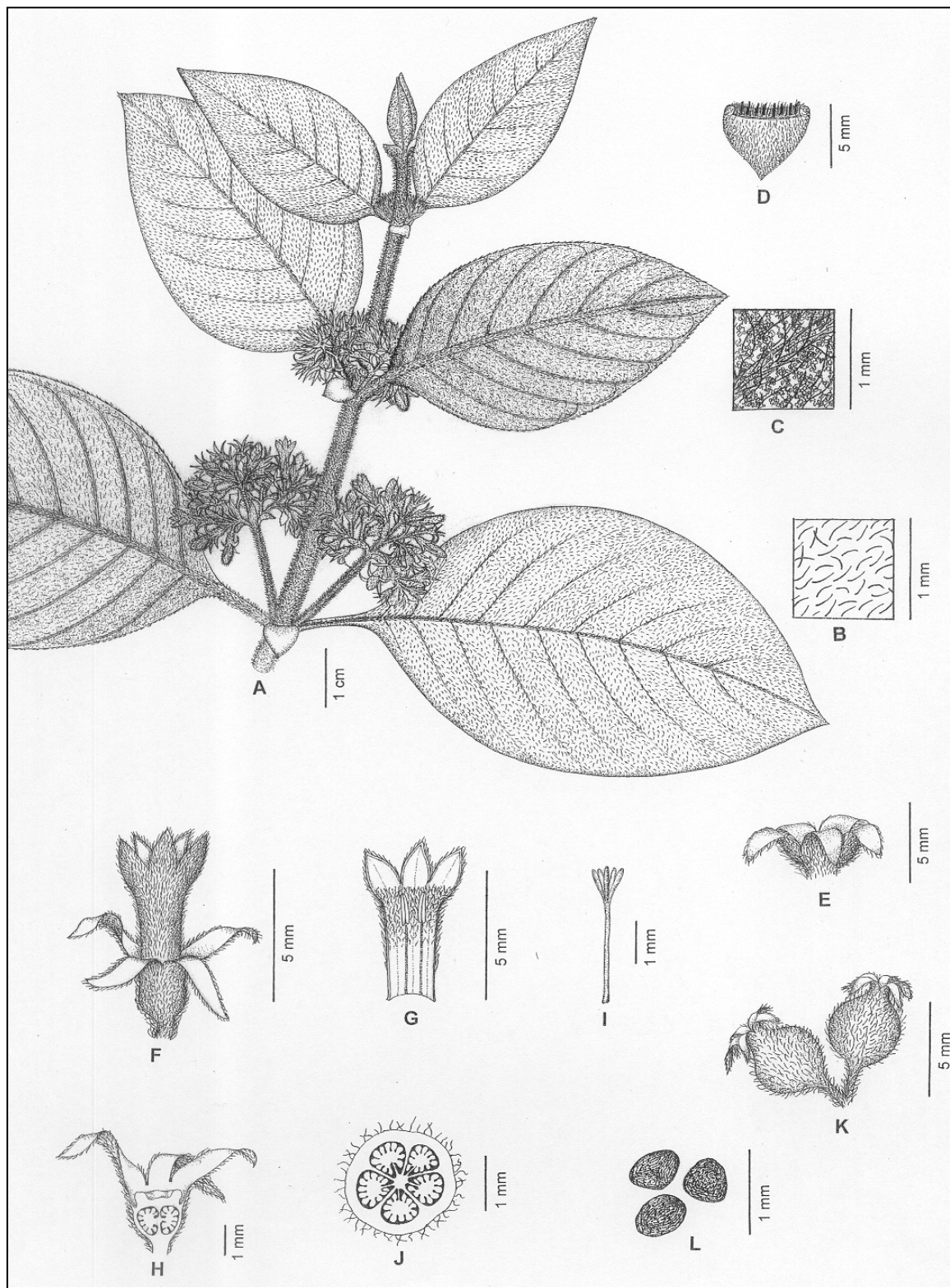


Figure 24. A–L. *Sabicea erecta*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Outer stipule surface and colleters at the base of inner stipule surface. —E. Side view of bract. —F. Flower. —G. Inner corolla surface showing anther's position. —H. Longitudinal section through calyx and ovary. —I. Style and stigmas. —J. Transversal section through ovary. —K. Immature fruit. —L. Seeds.

densely strigulose to pilosulous, occasionally isolatedly to sparsely lanuginose almost all over, trichomes 0.5–1.1 mm long, bracteoles 1.5–6 × 0.1–4.5 mm, colleters 2, 0.2–0.9 mm long. *Flowers* usually pedicillate, pedicels 1–5 mm long; *calyx* campanulate, 5(–6)-lobed, tubes (0.5–)1–1.2 × 1.5–2(–3) mm, lobes (1.5–)1.8–4.5 × (0.5–)0.7–1.3 mm, spreaded to moderately reflexed, narrowly elliptic to lanceolate, apically acute to acuminate, margins entire and serrulate, ciliolate with 0.1–0.3 mm long cilia, adaxially completely glabrous or isolatedly to sparsely strigulose at the apices, abaxially sparsely to moderately densely pilosulous, trichomes (0.2–)0.4–0.8 mm long, 3–4(–5)-ribbed, colleters 1(–2) in each sinus, 0.4 mm long; *corolla* salverform, tubes (2.7–)3–4.5 × 1.8–2.4 mm, lobes (1.8–)2–2.5(–2.7) × 0.8–0.9 mm, widely lanceolate to narrowly ovate, antrorse, adaxially the indumentum of orifice extends up to 1.5–2.1 mm inside the tubes, abaxially densely strigulose to pubescent; *stamens* 5 per flower, attached to corolla tube at 1.8–2.4 mm from the base, anthers 1.3–1.5 × 0.2 mm; *style* 1.8–2.4(–2.7) mm long, stigmatic lobes 0.8–0.9 × 0.1–0.1 mm; *ovaries* 1–1.5 × 1–1.5 mm, abaxially plain or uneven, trichomes (0.2–)0.4–0.9 mm long, 5-locular, each locule 0.9–1.2 × 0.4–0.6 mm. *Fruits* color unknown, 3.5–4.5 × 4–4.5 mm when immature; *seeds* unseen.

*Phenology, distribution and habitat.* Flowering and fruiting in May and December. Found in Savanna, secondary forests and disturbed secondary bush and woods; 290–320 m (Fig. 38).

*Discussion.* *Sabicea erecta* is distinguishable by the combination of its erect habit, smaller stipules, 9–16-flowered (sub-)globose-paniculate or umbellate inflorescences, exinvolucrate bracts (Fig. 24A) with short lobes, adaxial surface of leaves lacking a floccose or lanuginose indumentum but covered with short straight trichomes (Fig. 24B), isolatedly to sparsely and diffuse lanuginose to arachnose indumentum at abaxial surface of lamina, short cilia at the margins of stipules, bracts, and calyx lobes, and short calyx and corolla lobes. Rusby described this species as an erect shrub, gray-tomentose or hirsute throughout, and with sub-hemispherical dense cymes with long peduncles and distinct pedicels. *Sabicea erecta* seems very similar to *Sabicea subinvolucrata* due to their nearly same indumentum types, stipules and inflorescence structure. However, *Sabicea erecta* can be distinguished from *S. subinvolucrata* by the combination its smaller stipules (5–8 × 4–6 mm in contrast to 7–10 × 6–11 mm), (sub-)globose-paniculate or umbellate inflorescences lacking cylindrical and pyramidal thyrsoid type, and exinvolucrate bracts with short lobes (2–3.5 mm long in contrast to 3.5–16 mm long).

*Sabicea erecta* appeared as a very close ally of *S. klugii*, from which it is distinct by its adaxial surface of leaves lacking the floccose or lanuginose indumentum and covered with hirtellous or pilosulous indumentum comprised of shorter trichomes (0.1–0.8 mm in contrast to usually 0.8–1.8 mm), shorter cilia at the margins of stipules, bracts, and calyx lobes (e.g., 0.1–

0.7 mm in contrast to 1.–1.5 mm long at the margins of stipules), (16–)46–60-flowered (in contrast to 9–16-flowered) compact-paniculate to umbellate inflorescences, narrowly elliptic to lanceolate calyx lobes, and strigulose to pubescent external indumentum of corolla. *Sabicea erecta* seems close to *S. cuneata* and *S. boliviensis*, from which it is distinguishable by its isolatedly to sparsely and diffused lanuginose to arachnose indumentum at abaxial surface of lamina, shorter corolla lobes (3–4.5 mm in contrast to  $\geq 6$  mm long), adaxially glabrous upper part of stipules. In *Nee & Vargas 43237*(MO, NY), adaxially apically calyx lobes are isolatedly to sparsely strigulose in contrast to the adaxially glabrous calyx lobes of rest of the specimens. Presence of indumentum at the upper part of adaxial surface is a useful key character in some other *Sabicea* species. The consistency of this character in *Sabicea erecta*, however, could not be confirmed.

*Additional specimens examined.* BOLIVIA. **La Paz:** Tumapasa, *Williams 590* (BM, F, NY); Ixiamas, Abel Iturralde, 68°46'W, 13°35'S, *Gentry et al. 70813* (MO). **Beni:** Río Beni, Rurrenabaque, 1 km upstream, 14°28'S, 67°31'W, *Daly et al. 6476* (NY). Santa Cruz: Ichilo, flood plain of Río Ichilo, downstream (N) of highway bridge, 17°16'S, 64°20'W, 23 Dec 1992, *Nee & Vargas 43237* (MO, NY).

**17. *Sabicea grisea*** Cham. & Schtdl., *Linnaea* 4: 192–193. 1829. TYPE: Brazil: no date, *Sello 328* (holotype, B, not seen, presumably destroyed, photo G!). Figure 25A–K.

Terminal flowering branchlets isolatedly to densely pubescent, isolatedly to densely lanuginose to arachnose. *Stipules* oblong to ovate, occasionally widely lanceolate or deltate, usually erect and appressed, occasionally slightly reflexed, 4–7(–10)  $\times$  2–6(–10) mm, usually not fided, apically acute to obtuse, rarely minutely bifid, papyraceous, margins entire, complanate, eciliate or ciliolate, adaxially glabrate, sometimes strigulose to sericeous near apices in addition to the basal part, abaxially densely arachnose or lanuginose, occasionally isolatedly to sparsely strigulose, 5–9-veined, colleters 5–7. *Leaf blades* usually elliptic to oblong or lanceolate, (2.5–)5–13  $\times$  (1.4–)2.5–6 cm, apically acute or acuminate, basally acute or attenuate to obtuse, herbaceous or membranous, eciliate or ciliolate, adaxially usually hirtellous to strigulose or pubescent at lamina, usually strigulose to hirtellous or pubescent and occasionally lanuginose at costa, trichomes 0.1–1.1 mm long; abaxially usually densely lanate to lanuginose all over, isolatedly to densely villosulous or pilosulous to strigulose at costa and secondary veins, secondary veins (9–)11–16 pairs, plain adaxially or protruding abaxially, tertiary veins prominulous, obscured or distinct abaxially; *petioles* (5–)7–18 mm long. *Inflorescences* one per node, 3–7(–9)-flowered, compact-fascicled, 2–2.5(–3)  $\times$  1.5–2.5(–4) cm; *peduncles* 0(–2) mm long; *bracts* exinvolucrate, papyraceous, incompletely isolated into 2–5 parts, isolated parts 7–11  $\times$  (5–)7–12 mm, 2–3-lobed, lobes (1–)2–9(–10)  $\times$  (0.6–)1.5–6 mm, ovate to deltate or lanceolate or oblong to elliptic, apically (sub-)acute or



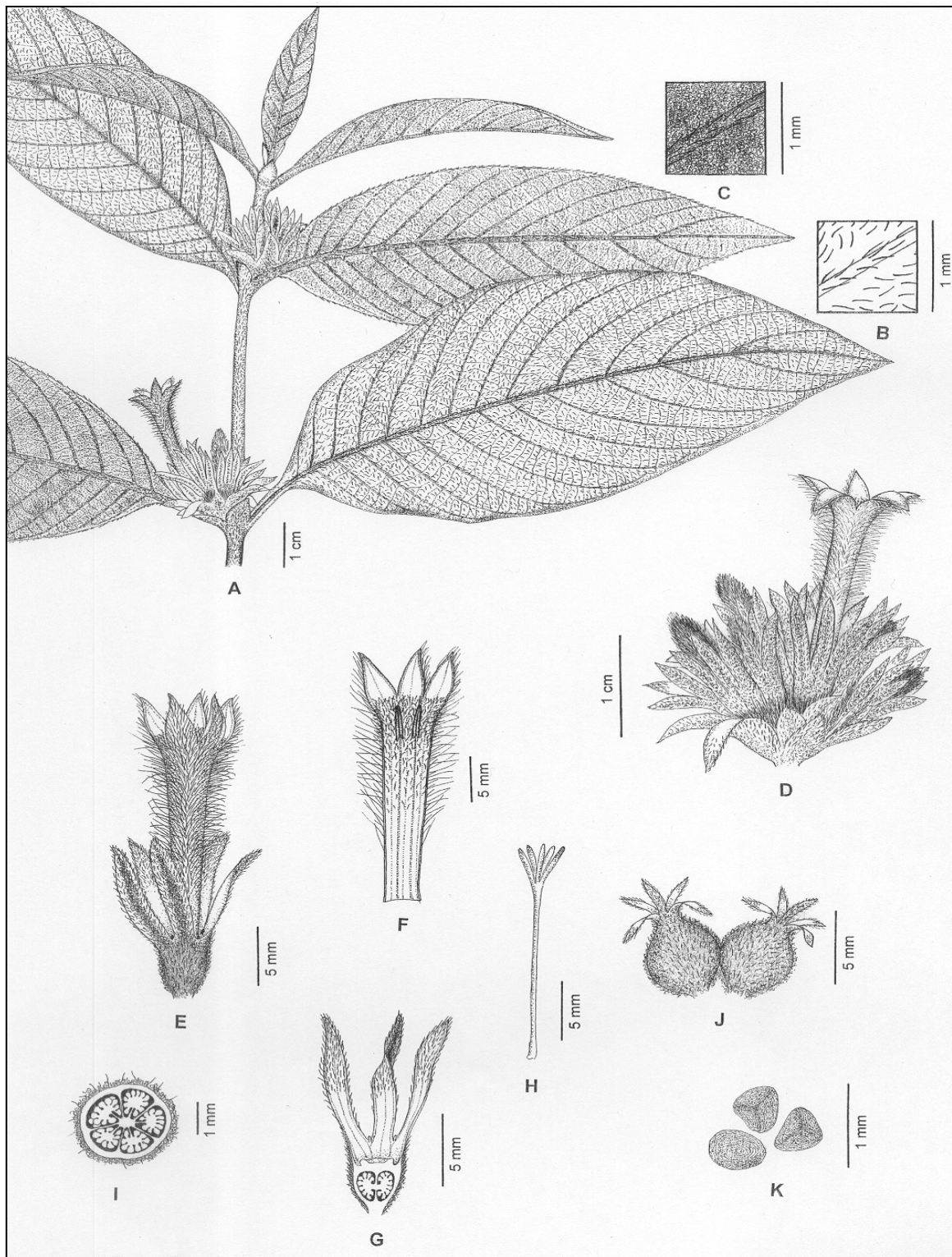


Figure 25. A–K. *Sabicea grisea* var. *grisea*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Inflorescence. —E. Flower. —F. Inner corolla surface showing anther's position. —G. Longitudinal section through calyx and ovary. —H. Style and stigmas. —I. Transversal section through ovary. —J. Fruit. —K. Seeds.



obtuse, margins entire, eciliate or ciliolate, ciliolate with cilia 0.2–0.8 mm long cilia, adaxially isolatedly to densely strigulose to sericeous all over or only at the upper part in addition to the densely serious base, abaxially isolatedly to densely strigulose to sericeous and arachnose all over, sometimes non-arachnose or arachnose only at the middle and lower part, 3–5(–7)-ribbed, bracteoles 2.5–9 × 0.6–2 mm, colleters 2, 0.5–0.7 mm long. *Flowers* usually sessile, rarely subsessile, pedicels 0(–1.5) mm long, densely pilosulous; *calyx* campanulate, tubes 1–3 × 2.5–3.5(–4) mm, lobes (2–)5–12 × (0.6–)1.5–2.5(–3) mm, antrorse or spreaded, usually linear to narrowly lingulate, narrowly elliptic or lanceolate, apically (sub-)acute to obtuse, margins entire, usually ciliolate, cilia 0.2–0.8 mm long, adaxially usually sparsely strigulose to sericeous all over or at the upper part, glabrous at lower part, abaxially sparsely to densely strigulose to pubescent, sometimes isolatedly to densely arachnose or lanuginose all over or up to the lower part or middle of lobes, 3(–5)-ribbed with costa, plain adaxially, colleters 1(–2) in each sinus, 0.4–0.6 mm long; corolla salverform or hypocrateriform, tubes (9–)12–20 × 1.3–2(–3) mm, lobes 2.5–4(–6) × 1.5–2.5 mm, ovate, antrorse or spreaded, adaxially the indumentum of orifice extends up to 4.5–8 mm inside the tubes, abaxially pilosulous to pubescent, (0.8–)1.8–2.1 mm long; *stamens* 5 per flower, attached to corolla tube at (9–)12–14.5 mm from the base, anthers, 2–3 × 0.3–0.4 mm; *style* 11–14(–16.5) mm long, stigmatic lobes 2–3(–3.4) × (0.2–)0.2–0.3 mm; *ovaries* 2.1–3 × 2.4–3.5 mm, abaxially uneven or shallowly 5-lobed, densely arachnose to villosulous, trichomes 0.7–0.9 mm long, 5-locular, each locule 1.1–1.8 × 0.5–0.9 mm. *Fruits* red, 4–5 × 4–5 mm when immature, 9–14 × 9–14 mm when mature, abaxially isolatedly to sparsely arachnose to villosulous; *seeds* 0.5–0.7 × 0.4–0.7 mm.

*Phenology, distribution and habitat.* Flowering of *Sabicea grisea* var. *grisea* occurs in January to May, June, August, October to December and fruiting only in June. Flowering of *S. grisea* var. *ceara* in April, fruiting unknown. *Sabicea grisea* var. *grisea* is mostly distributed in Bahia and Rio de Janeiro. It extends to Alagoas, Pernambuco, and São Paulo. Wernham (1914) mentioned that *Sabicea grisea* is distributed also in Paraguay, as the only representative of the genus. We could not observe any specimens of *Sabicea* from Paraguay. *Sabicea grisea* var. *ceara* is found only in Ceará. The habitat of this species is unknown; 587–2000 m (Fig. 14).

*Discussion.* Wernham (1914) described *Sabicea grisea* as close to his two distinct species- *S. lindmaniana* and *S. pannosa*). Comparing the original and relevant specimens of these species, it was impossible to distinguish *Sabicea lindmaniana* and *S. pannosa* as distinctly different from *S. grisea*, due to which we synonymize these under *S. grisea*. *Sabicea grisea* is characterized by the combination of compact-fascicled inflorescences, adaxially puberulous to hirtellous or strigulose and abaxially usually densely lanate to lanuginose leaf blades, linear or

lingulate to narrowly elliptic or lanceolate, abaxially and adaxially sparsely to densely strigulose to pubescent, sometimes isolatedly to densely arachnose or lanuginose calyx lobes, and abaxially pilosulous to pubescent corolla. Information on the habit of this species was not available. Schlechtendal (1829) described this species as “volubilis”. Wernham (1914) recognized it as “scandent” and “a hedge and thicket scrambler”. In the original description, the stipules are mentioned as “subcordata”. We have not found this unusual shape in the studied specimens.

*Sabicea grisea* is confusable with *S. cinerea* from which it is easily distinguishable by its generally hirtellous to strigulose adaxial surface of lamina (Fig. 25B), ciliolate stipules and bracts, and only strigulose to sericeous or pubescent or in addition arachnose to lanuginose abaxial surface of bracts and calices. Schlechtendal (1829) mentioned that this species differs from *Sabicea cinerea* also by its leaves, stipules and corolla, which is inconsistent to our observation. In *Sabicea grisea*, the arachnose or lanuginose indumentum of stipules, bracts and calices usually do not overlap the margins, as in *S. cinerea*. Straight trichomes are commonly present at the branchlets and outer surface of the hypanthia of *S. grisea* that are rarely present in case of *S. cinerea*. Some *Sabicea grisea* seem very close to *S. camporum*, from which these differ by their fascicled inflorescences, adaxially sparsely strigulose to sericeous and longer calyx lobes (Fig. 25G), longer calyx tubes, and longer corolla tubes with erecto-patent trichomes on outer surface (see *S. camporum*). Due to the superficially similar inflorescences, *Sabicea grisea* seems close to *S. burchellii* from which it differs by its manifestly arachnoid indumentum at branchlets, lower surface of leaves, and outer surface of stipules, bracts, and calyces, and apparently erecto trichomes of corolla tubes. *Moraes 2173* (HUH, NY, U) and *Silva & Sobral 2173* (US, NY) seem to very similar to *Sabicea burchellii* but these have been included under *S. grisea* due *S. grisea* than to *S. burchellii*. Some *Sabicea grisea* with narrow calyx lobes appears as near to *S. oblongifolia* from which they are distinct by their fascicled inflorescences, indumentum lacking rusty-brown to maroon color, *Sabicea grisea* appears as near to *S. velutina* with elliptic or oblong leaves from which it is distinct by its hirtellous to strigulose, or pubescent indumentum of leaf blades comprised of apparently shorter (0.1–1.1 mm in contrast to [1.5–]2–2.3) trichomes, villosulous or pilosulous to strigulose indumentum at the costa and secondary veins of abaxial surface of leaf blades, shorter (usually 3–6 mm in contrast to 5–12 mm), abaxially sparsely to densely strigulose to pubescent, sometimes arachnose or lanuginose, and linear to narrowly lingulate, narrowly elliptic or lanceolate calyx lobes marginally covered with shorter cilia (cilia 0.2–0.8 mm in contrast to 0.8–1.8 mm). Some *Sabicea grisea* with narrower and longer calyx lobes appear as close to *S. liedae*, from which they are distinguishable by their compact-fascicled inflorescences, usually straight, entire and adaxially strigulose to sericeous calyx lobes, and abaxially pilosulous to pubescent and longer ([9–]12–20 mm in contrast to 6.5–9 mm) corolla tubes.

The collections from Ceará [*Gardner 1697* (F, G, HUH, NY), *Ducke 2002* (G), and *Albuías*

24018 (F)] are remarkable for the presence of arachnose indumentum at the adaxial surface of leaf blades in addition to the pubescent to hirtellous indumentum, which is unusual for this species and warrants the creation of a separate variety. Superficially this new variety appears indistinguishable from the included specimens of *Sabicea cinerea* of Sucre, Venezuela. However, it can be set apart from *S. cinerea* of Sucre by their manifestly strigulose indumentum at the abaxial surface of bracts and calyces and predominant pubescent to hirtellous indumentum at the adaxial surface of leaf blades. No holotype is cited for *S. lindmaniana* except two syntypes (Brazil: no date, *Glaziou 8740*, G & S; Porto d'Estrella, no date, *Warming s.n.*, P, not seen, photo F!). We have selected *Glaziou 8740* (G), seen with flower, as the lectotype.

#### Key to the varieties:

- 1a. Leaf blades adaxially hirtellous to strigulose or pubescent, and occasionally arachnose only at costa.....17a. *S. grisea* var. *grisea*  
 1b. Leaf blades adaxially hirtellous to pubescent, and arachnose all over .....17.b *S. grisea* var. *ceara*

#### 17a. *Sabicea grisea* Cham. & Schltld. var. *grisea*

*S. eriantha* DC., Prodr. 4: 439. 1830, TYPE: Brazil: Bahia, *P. Salzmänn s.n.* (holotype, G!; isotypes, BM!, BR!). *Schwenkfeldia eriantha* Dietr. Syn. Pl. (D. Dietrich), i. 173.1839.

*S. pannosa* Wernham, Monogr. *Sabicea* 48. 1914. TYPE: Brazil: Pernambuco, Caxanga, 06 June 1887, *H. Schenk 4279* (holotype, B, not seen, presumably destroyed; isotypes, BR!, G!).

*S. lindmaniana* Wernham, Monogr. *Sabicea* 50. t. 12. 1914. TYPE: Brazil: no date, *A. F. M. Glaziou 8740* (lectotype, designated here, G!; duplicate, S!).

*Selected specimens examined.* BRASIL. **Alagoas:** Murici, fazenda Amora margem de riacho, Mata Atlântica em serra, *Lemos et al. 6936* (NY), Fazenda Boa Vista, proximo a torre, *Barbosa et al. 2484* (NY). **Bahia:** In Sepibun, *Salzmänn s.n.* (BR, G, BM, HUH, M); Jacobina, *Blanchet s.n.* (G); Near the city of Alagoas, *Gardner 1338* (BM); Meta Costeira, Camamu, *Belém & Pinheiro 3355* (F, US); Lamarão do Passé, *Noblick et al. 2218* (MO); Maraú, Ubaítaba, Entroncamento que liga a estrada a Maraú, Mata umida, perturbada, *Carvalho & Plowman 1453* (F); Ilhéus, Fazenda Theobroma, próximo á margem do Rio Santana, Ramal com entrada 2 km antes da Vila do Rio Engenho, *Silva & Sobral 2173* (US, NY); Itacaré-Bahia, Itacaré/Taboquinhas entrada a 6 km de Itacaré. Loteamento da Marambaia, *Jardim et al. 653* (MO), *Amorim et al. 894* (MO); Jacobina, Itaitu, Cochoeira do Véu Noiva, *Forzza et al. 1333* (NY). **Pernambuco:** Entre Recife e Cabo, Km 28 da BR-11, A margem de um cana,

*Tavares 597* (US). **Paraíba:** Paraíba, Terrenos altos e incultos, *Moraes 2173* (HUH, NY, U). **Rio De Janeiro:** Carcovado, *Guillemín 129* (G); Pegnena, *Brade 24* (HUH); Porto das Caixas, *Brade 14987* (F); Rio Teresipole, *Cluluini, 5397* (US); Silva Jardim, Rio São Joao, *Vianna & Cacaúta 12428* (US). **São Paulo:** Cidade de Ubatuba, Bairro de Parqueacu, *Mizoguchi 2589* (MO).

**17b. *Sabicea grisea*** Cham. & Schltld. var. **ceara** Liède, Meve & Khan, var. nov. TYPE: Brasil. Ceará: C. G. *Gardner 1697* (holotype, BM!; isotypes, FI, GI, HUH[2]!, NY!).

*Differt a varietate typica paginarum foliorum inferiore pubescentis arachnoideisque.* Leaf blades adaxially hirtellous to pubescent, and arachnose all over

*Additional specimens examined.* BRASIL. **Ceará:** Serra de Baturite, Guaramiranga, *Ducke 2002* (G). Rio De Janeiro: *Albuías 24018* (F).

**18. *Sabicea hirta*** Sw., Prodr. 46.1788. TYPE: Jamaica: no date, *Swartz s.n.* (holotype, GI, isotype, MI). *Schwenkfelda hirta* Sw., Fl. Ind. Occid. 1: 450. 1797. Figure 26A–K.

Scrambling to straggling or trailing vines; terminal flowering branchlets sparsely to moderately densely pilosulous, trichomes 1–2.1 mm long. *Stipules* deltate to cordiform or reniform, antrorse to reflexed, 6–9 × (6–)8–14 mm, apically usually obtuse to rounded, occasionally (sub-)acute, membranous, ciliolate with 0.2–0.8 mm long cilia, adaxially sericeous at the base, abaxially isolatedly to sparsely sericeous to pilosulous almost all over, eventually sometimes glabrous at the upper part and near the margins, trichomes 0.6–0.9 mm long, (14–)18–24-veined, eventually reticulate, plain adaxially, slightly raised abaxially, colleters 18–24, (0.6–)1 mm long. *Leaf blades* elliptic to oblong or ovate, (5.5–)6.5–14(–18) × (2–)2.5–5.5(–6.2) cm, apically bluntly acuminate, papyraceous, ciliolate with 0.6–1.1 mm long cilia, usually isolatedly to sparsely pilosulous or villosulous to puberulous at secondary veins and lamina, sparsely to moderately densely at costa, trichomes (0.2–)0.7–1.7 mm long; abaxially usually sparsely pilosulous, occasionally sericeous at lamina, and sparsely to moderately densely pilosulous and puberulous at costa and secondary veins, (0.2–)0.6–1.1(–1.7) mm long, secondary veins (9–)11–14 pairs, plain or slightly protruding adaxially and protruding abaxially, tertiary veins slightly prominulous and quaternary veins distinct abaxially; *petioles* (3–)5–12(–26) mm long. *Inflorescences* one to two per node, (1–)3–9-flowered, moderately lax-umbellate, 1.5–2(–2.5) × (1.5–)2.5–3 cm; *peduncles* (2–)5–15(–17) mm long; *bracts* (sub-)involucrate, membranous, (4–)7–12(–16) × (5–)7–10(–14) mm, (3–)5–7-lobed, lobes (0.5–)1.5–11 × (1–)1.5–4.2 mm, ovate to lingulate, apically obtuse to subacute, margins entire, ciliolate with (0.1–)0.4–0.9 mm long cilia, adaxially glabrous to isolatedly or sparsely sericeous, at upper part in addition to the densely basal part, trichomes (0.2–)0.8–1.6 mm

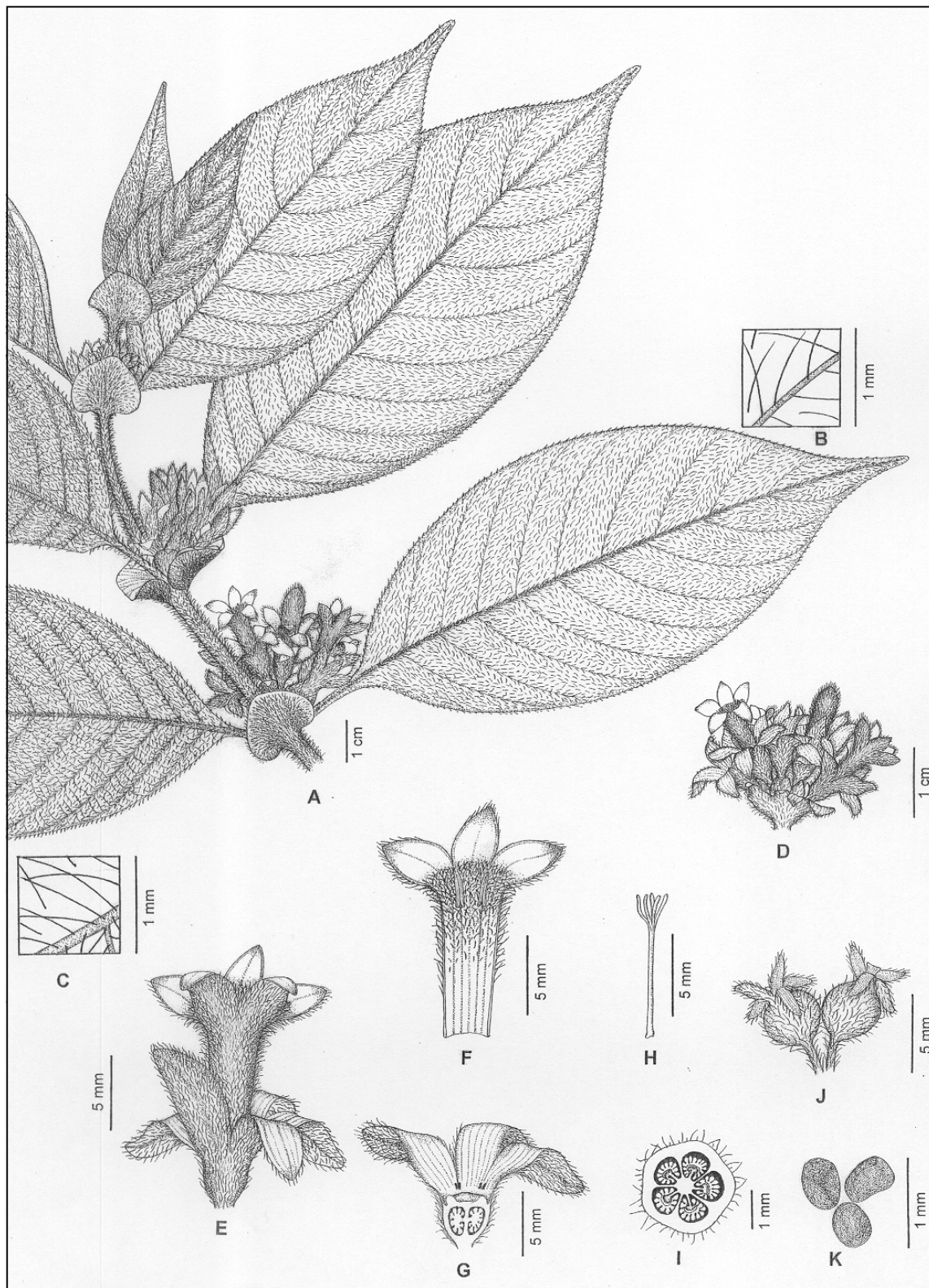


Figure 26. A–K. *Sabicea hirta*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Inflorescence. —E. Flower. —F. Inner corolla surface showing anther's position. —G. Longitudinal section through calyx and ovary. —H. Style and stigma. —I. Transversal section through ovary. —J. Fruit. —K. Seeds.

long, abaxially sericeous to pilosulous, usually along the veins and at the lower part, eventually glabrate near the margins and upper part, trichomes (0.2–)0.6–0.9 mm long, involucre 18–24-ribbed, lobes (1–)3–6-ribbed, bracteoles 1.8–6 × 0.8–4.5 mm, deltate to ovate or lingulate, colleters (12–)18–30 at the at adaxial base of bracts, 6–15 at bracteoles, 0.2–0.7(–0.9) mm long. *Flowers* pedicellate, pedicels 4–14 mm long, isolatedly to sparsely pilosulous, trichomes 0.3–1.2 mm long; *calyx* widely campanulate, 5-lobed, tubes (0.3–)0.6–1.8 × (2.1–)2.5–3(–3.2) mm, lobes (4–)4.5–7.6 × (1.5–)2–3.5 mm, antrorse to spreaded or moderately reflexed, lingulate to narrowly ovate or elliptic, apically obtuse to rounded, basally truncate, margins entire to sparsely denticulate, ciliate with 0.1–0.6 mm long cilia, adaxially glabrous, rarely isolatedly sericeous at the upper part, trichomes 0.07–0.4 mm long, abaxially isolatedly to sparsely pilosulous, trichomes 0.2–1.1 mm long, 3–7-ribbed with costa, colleters 2–4 in each sinus, (0.2–)0.5–0.7 mm long; *corolla* salverform, tubes 7–9(–9.4) × 2.5–3(–3.2) mm, (6–)5-lobed, lobes 3–4.4 × (1.5–)1.8–2.5(–3) mm, ovate, antrorse to spreaded, apically (sub-)acute, adaxially the indumentum of orifice extends up to 3–3.8 mm inside the tubes, trichomes 0.2–0.9 mm long, abaxially densely sericeous to pilosulous at lobes, usually pilosulous at tubes, trichomes (0.4–)0.8–1.5 mm long; *stamens* 5 per flower, attached to corolla tube at (5.9–)6–7.1 mm from the base, anthers 1.5–1.8 × 0.2–0.3 mm; *style* 4.4–6.8(–7.1) mm long, stigmatic lobes 2–2.5(–3.1) × 0.2–0.3 mm; *ovaries* 2.4–2.7 × 2.4–2.7 mm, abaxially usually shallowly 5-lobed, isolatedly to sparsely sericeous to pilosulous, trichomes 0.3–1.2 mm long, 5-locular, each locule 1.5–1.8 × 0.6–0.7 mm. *Fruits* 3–4 × 3–4 mm when immature, 9–11 × 9–11 mm when mature, color unknown, abaxially usually isolatedly sericeous to pilosulous; *seeds* 0.5–0.7 × 0.3–0.5 mm.

*Discussion.* *Sabicea hirta*, endemic to Jamaica (Fig. 27), is distinct by its usually few-flowered ([1–]3–9) moderately lax-umbellate inflorescences with ample peduncles and pedicels, stipules wider than long and basally gently cordate at least at the apical part of branchlets, (sub-)involucrate bracts with numerous colleters along the base inside, 2–4 colleters in each sinus of calyces, and lingulate to narrowly ovate or elliptic calyx lobes that are apically obtuse to rounded and marginally entire to sparsely denticulate. Candolle (1830) described the leaves of *Sabicea hirta* as ovate to lanceolate and apically acuminate and the inflorescences as pedunculate. We haven't seen any specimen with lanceolate leaves, but found the elliptic shape as common in the examined specimens. The presence of numerous colleters along the base inside the bracts appears as unique, and so are the 2–4 colleters in each calyx sinus.

*Sabicea hirta* seems to be close to *S. mattogrossensis* and *S. novo-granatensis* due to the almost similar inflorescences and ample calyx lobes. Superficially, this species appears as closely allied to *Sabicea mexicana* due to its few-flowered inflorescences and antrorse calyx lobes. However, none of these species has the stipules that are wider than long and basally

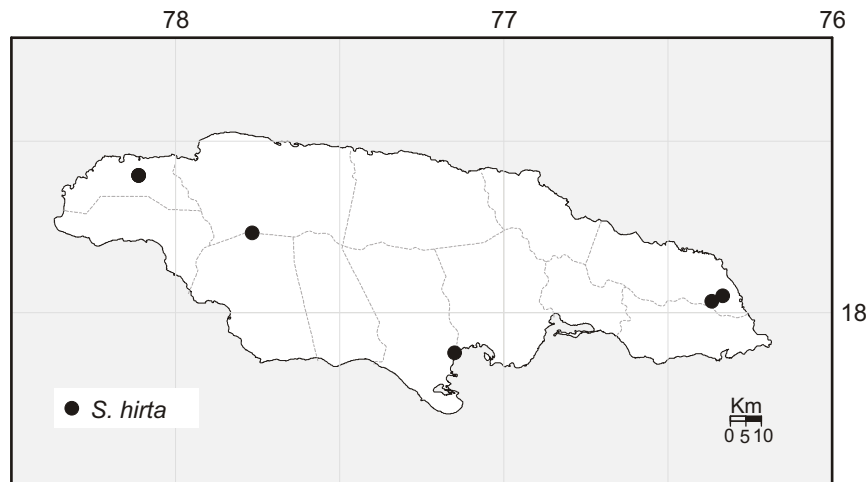


Figure 27. Map of Jamaica, showing the distribution of *Sabicea hirta*.

gently cordate (Fig. 26A), numerous colleters along the base inside the bracts, and 2-4 colleters in each sinus of calyces (Fig. 26G), as *Sabicea hirta* has. In *Stearn 1014* (BM), the base or lower part inside the calyx lobes around the colleters, and outside the hypanthia are irregularly densely covered with few (3-9) celled, (0.1-)0.07-0.5 mm long papillae-like hairs with rounded tips that have not been found in other specimens of *Sabicea hirta*. These papillae-like hairs are absent in other collections of *Sabicea hirta*, as well as in other species we have seen, although trichomes are present inside the calyx lobes and around the colleters in *S. amazonensis*, and *S. mollissima*.

*Additional specimens examined.* JAMAICA. **Clarendon:** Cockpit Country, *Britton, 555* (NY). **Hanover:** Road from Askenish to Dolphin Head, *Harris 9246* (BM, F, NY); Askenish to Dolphin Head, *Harris 10278* (BM, F, NY). **Saint Elizabeth:** Near Accompong, *Stearn 1014* (BM, HUH). **Portland:** Northside of Cuna Cuna Pass, *Harris & Britton 10561* (BM, F, NY, US); Vicinity of Thomsons Gap, *Maxon & Killip 752* (F, HUH, NY); The John Crow Mts, 1,52,5 mile SW of Ecclesdown, *Howard & Proctor, 14864* (F, HUH, US); Ecclesdown, *Adams, 9110* (BM).

**19. *Sabicea humilis*** S. Moore, Trans. Linn. Soc. London, Bot. ser. 2, 4: 369. 1895. TYPE: Brazil: Mato Grosso, ad Santa Cruz, no date (fl), *S. Moore 472* (holotype, BM!, photo F!, GI!, NY [2]!; isotype, NY!). Figure Plate IV14 (Wernham, 1914).

*S. humilis* S. Moore var. *lanceolata* S. Moore, Trans. Linn. Soc. London, Bot. ser. 2, 4: 370. 1895. TYPE: Brazil: Mato Grosso, Santa Cruz, no date (fl), *S. Moore 794* (holotype, BM!, photo NY!).

*S. moorei* Wernham, Monogr. *Sabicea* 39. t. 4, f. 14. 1914. TYPE: Brazil: Mato Grosso: Santa Ana de Chapada, 02 Nov 1902, *A. Robert 687* (holotype, BM!; isotype, K, not seen).

Erect herb or suffruticose; terminal flowering branchlets densely hirsutulous or hispidulous to pubescent, (0.1-)0.2-2.3 mm long. *Stipules* narrowly ovate to deltate or oblong, antrorse, 4-6(-8) x (3.2-)4-6(-8) mm, usually undivided, apically occasionally minutely bifid, usually (sub-)acute to acuminate, rarely obtuse, papyraceous, margins entire to widely denticulate,

complanate, ciliolate with (0.07–)0.2–0.7 mm long cilia, adaxially glabrous excluding the basal part, abaxially densely strigulose at the lower part, eventually sparsely towards at the apices, trichomes (0.2–)0.4–1.3 mm long, 7–9-veined, eventually reticulate, adaxially plain and raised abaxially, colleters 6, (0.2–)0.3–0.5 mm long. *Leaf blades* usually elliptic-oblong, occasionally obovate or ovate to suborbicular, (0.7–)1.5–8(–20) × (0.5–)1.2–4(–5.5) cm, apically usually (sub-)acute, occasionally obtuse to acuminate or mucronate, ciliolate with (0.4–)0.7–1.1(–1.4) mm long cilia, adaxially moderately densely hirsutulous or hispidulous at secondary veins and lamina, densely hirsutulous or hispidulous and isolatedly to sparsely pubescent at costa, (0.2–)0.7–2.1(–2.6) mm long; abaxially moderately densely pilosulous to villosulous, isolatedly to sparsely arachnose, isolatedly pubescent at lamina, and densely at costa and secondary veins, trichomes (0.2–)0.8–2.3(–2.7) mm long, secondary veins (6–)9–12(–14) pairs, usually plain, occasionally prominulous or protruding abaxially, tertiary veins indistinct, sometimes prominulous abaxially, quaternary veins indistinct or distinct abaxially; *petioles* 1–3(–5) mm long. *Inflorescences* two per node, (3–)5–7(–9)-flowered, loose fascicled, 1–1.5 × 1–2 cm, main inflorescence branches 0(–3), main axes when present 1.8 mm long; *peduncles* (0–)1–6 mm long; *bracts* (sub-)exvolucrate, papyraceous, incompletely isolated into 2 parts, isolated parts 5.5–7.6 × 6–7 mm, usually 3–5-lobed, 4.5–7.6 × 3–4.7 mm, 1–3-lobed, lobes 0.2–4.5 × 0.5–3.5 mm, ovate to widely lanceolate or triangular, apically subacute to acuminate, margins entire to widely denticulate, ciliolate with 0.2–1.5 mm long cilia, adaxially isolatedly to sparsely sericeous or pilosulous at apices or upper part in addition to the basal part, trichomes (0.1–)0.5–1.5 mm long, abaxially densely pilosulous at the lower part, sparsely to densely at upper part, trichomes (0.2–)0.7–1.9(–2.4) mm long, bracteoles (2.4–)3.5–6.5(–8.2) × 0.5–1.2 mm, lingulate, colleters 2, 0.1–0.2 mm long. *Flowers* usually sessile, pedicels (0–)0.5–1.8 mm long; *calyx* shallowly campanulate, (4–)5–6(–7)-lobed, tubes 0.2–1(–1.5) × 2.3–2.6(–2.9) mm, lobes (0.8–)2.5–7.1 × (0.2–)0.8–2.4 mm, antrorse, unequal, usually narrowly elliptic to lingulate, occasionally linear to lanceolate, apically (sub-)acute, basally truncate, margins denticulate, straight or erecto-patent, sparsely sericeous almost all over, ciliolate to ciliate with (0.6–)0.9–1.8(–2.1) mm long cilia, abaxially densely pilosulous all over, trichomes (0.12–)0.2–0.9 mm long, erecto-patent, 3(–5)-ribbed, with costa, abaxially gently prominulous, adaxially plain, colleters 1 in each sinus, 0.1–0.4 mm long; *corolla* salverform, tubes 5–6.5(–8) × 1.5–2.1 mm, 5-lobed, lobes 3–3.3(–4.1) × 1.2–1.5 mm, widely lanceolate to narrowly ovate, antrorse, apically (sub-)acute, adaxially the indumentum of orifice extends up to 3–3.5(–4.4) mm inside the tubes, abaxially densely pilosulous all over the lobes and upper part of lobes, trichomes (0.2–)1.2–1.8(–2.1) mm long; *stamens* 5 per flower, attached to corolla tube at 3.5–4.2 mm from the base, anthers 1.4–1.8(–2.1) × 0.4–0.5 mm; *style* (3–)5.5–6.5(–7.1) mm long, stigmatic lobes (0.9–)1.1–1.5 × 0.2–0.3 mm; *ovaries* 1.2–1.5 mm long, 1.1–1.8(–2.2) mm, trichomes of hypanthium (0.8–)1.2–2.2(–2.) mm long, 4–5-locular, each locule 0.7–1.1 × 0.4 × 0.7 mm. *Fruits* and *seeds* not seen.



*Phenology, distribution and habitat.* Flowering in August and October to December. The distribution of this species in Brazil seems limited to Mato Grosso and southern Amazonas of Brazil and in Bolivia in Santa Cruz and southeast Beni. It found in grassy Savanna and in forests; 0.7–900 m (Fig. 9).

*Discussion.* Moore (1895) described *Sabicea humilis* var. *lanceolata* by its adaxially villosulous to pilose leaves, lanceolate stipules, 6 mm long bracts, and 8 mm long corolla tubes. Wernham (1914) distinguished *Sabicea humilis* var. *lanceolata* as distinct by its leaf shape and size, pilose indumentum and little flowers, whereas *S. moorei* by its leaf-shape, and the shape and size of its corolla. We have not found any distinct supporting character to distinguish *S. humilis* var. *lanceolata* as a variety of *S. humilis* and *S. moorei* as separate species, due to which we merged these under *S. humilis*.

*Sabicea humilis* seems closely allied to *S. brasiliensis* due to the similar habit, leaf shapes, and presence of arachnoid indumentum at abaxial leaf surface. It is distinct from *Sabicea brasiliensis* by its non-arachnoid branchlets, abaxial surface of inflorescences, and shaggy indumentum of branchlets, leaves, and outer surface of inflorescences comprised of long and erecto-patent trichomes, longer, apparently unequal, usually narrowly elliptic to lingulate, occasionally linear to lanceolate and marginally ciliolate calyx lobes. This species appears close to *Sabicea burchellii* from which it is distinguishable by smaller stipules, shorter petioles, shaggy indumentum of leaves including the arachnoid indumentum of abaxial surface and outer surface of inflorescences excluding corolla tubes, and longer erecto-patent external trichomes of corolla tubes.

*Additional specimens examined.* BRASIL. **Amazonas:** Humatia, 500 m ao Norte da BR 230, 7°31'S, 63°10'W, *Janssen & Gemtchunjanicov 505* (M), Road Humaitá to Labrea Km 20, *Prance et al. 3371* (F, HUH, NY, S). **Mato Grosso:** Santa Anna da Chapada, *Malme 2071* (S); Guyaba, *Malme 2684* (S); Vicinity of Veú de Noiva, Chapada dos Guimaraes, *Prance et al. 18968* (NY). Near the base camp of the expedition, ca. 270 km N of Xavantina, 12°54'S, 51°52'W, *Ramos & Sousa 74* (NY, U); Barra do Garcas, 250 km along the road NNE of village Xavantina, 11,4 km due to SW of Royal Geographic Society Base Camp, *Eiten & Eiten 9260* (US); Rib. da Motuca (Cuiaba), *Hatschbach 37520* (US); Sararé, Radambaasil, 16°10'S, 59°25'W, *Pires & Santos 16601* (MO). BOLIVIA. **Beni:** Gral. Ballivián, Estancia Villa Camba, 39 km al N del río Yata, lado E de la carretera a Riberalta, 4 km hacia el río Benicito, *Hanagarth & Rosales 35A* (MO). **Santa Cruz:** Velasco, Parque Nacional Noel Kempff Mercado, Los Fierros, 14°36'S, 60°52'W, *Killeen et al. 5909* (MO), Las Gamas, Al borde de un bosque de galaria, 14°48'11''S, 60°23'33''W, *Killeen 7739* (F, NY), 6 km NE del campamento Las gamas, Borde de quebrada, con aguas lóxicas estacionales, 13°53'41''S, 60°48'46''W, *Rodriguez & Surubí, 550* (NY), Estación Flor de Oro, 13°33'S, 61°00'W, *Israel,*

*et al.* 3782 (MO), a 10 km del campamento Los Fierros, 4°36'39''S, 60°51'35''W, Jiménez, *et al.*, 1165 (MO).

**20. *Sabicea klugii*** Standl., Field Mus. Nat. Hist., Bot. Ser.13 (6): 88. 1936. TYPE: Peru. San Martín, Zepelacio, near Moyobamba, clearing in mountain forest, 1200–1600 m, Dec 1933 (fl), G. Klug 3425 (holotype, F!; isotypes, K!, G!, HUH!, MO!, NY!, SI!, US!, WIS!). Figure 28A–L.

Scandent; sparsely to densely pilosulous to sericeous, and arachnose to lanuginose, trichomes 1.1–1.8 mm long. *Stipules* ovate, antrorse to (sub-)reflexed, 5–9 × 6–7 mm, apically acuminate, membranous, ciliate with (0.7–)1.–1.5 mm long cilia, adaxially glabrate to isolatedly sericeous at upper part, densely at the lower part or base, abaxially sericeous and lanuginose almost all over, trichomes 1–1.8 mm long, 12–14-veined, adaxially and abaxially usually plain, colleters 5–7. *Leaf blades* ovate to elliptic or oblong, 6–12 × 3.2–5.8 cm, apically acute to acuminate, thinly papyraceous; adaxially isolatedly to sparsely pilosulous and floccose or isolatedly lanuginose at lamina, densely pilosulous to sericeous, sparsely to densely lanuginose or floccose at costa, trichomes (0.6–)0.8–1.8 mm long; abaxially isolatedly sericeous to pilosulous, sparsely to densely lanuginose to arachnose at lamina and densely sericeous to villosulous or pilosulous and sparsely to densely lanuginose to arachnose at costa and secondary veins, secondary veins 11–14 pairs, plain adaxially, protruding abaxially, tertiary veins prominulous abaxially; *petioles* 5–10 mm long. *Inflorescences* two per node, 9–16-flowered, umbellate, 2–2.5 cm × 2–2.5 cm, main inflorescence branches 4–5, fascicled, main axes 0.5–2 mm long; *peduncles* 4–24 mm long; *bracts* exinvolucrate, membranous or papyraceous, completely isolated into 2–3 parts, isolated parts 7–9 × 4–6 mm, ovate to deltate, apically acuminate, margins entire to denticulate and ciliolate with 0.6–1.1 mm long cilia, adaxially glabrate to isolatedly sericeous at upper part, trichomes (0.1–)0.4–1.4(–1.7) mm long, abaxially densely sericeous to pilosulous and lanuginose at costa, isolatedly to densely at rest of the part, (3–)5-ribbed, bracteoles 2.5–8.5 × 0.4–3 mm, elliptic to ovate or lingulate or linear, colleters 2, 0.2–0.4 mm long. *Flowers* pedicellate or (sub-)sessile, pedicels (0–)1–2 mm long; *calyx* campanulate, (4–)5-lobed, tubes 0.8–1.2 × 1.5–1.8 mm, lobes (1.5–)2.5–5 × 0.4–1.2 mm, spreaded to slightly reflexed, narrowly lanceolate, apically acuminate to acute, margins denticulate, ciliolate with (0.4–)0.8–1.4 mm long cilia, adaxially glabrous to isolatedly sericeous at apices, trichomes 0.1–0.4 mm long, abaxially densely pilosulous to sericeous and lanuginose, trichomes 0.4–1.6 mm long, usually 3 ribbed with costa, ribs plain both abaxially and adaxially, colleters 1(–3) in each sinus, 0.07–0.2 mm long; *corolla* white, salverform, tubes 4–5 × 1.2–1.8 mm, lobes 1.8–2.1 × 1.1–1.5 mm, ovate, antrorse to spreaded, apically (sub-)acute, adaxially the indumentum of orifice extends up to 2–2.7 mm inside the tubes, abaxially densely pilosulous to pubescent, at lobes and almost all over the

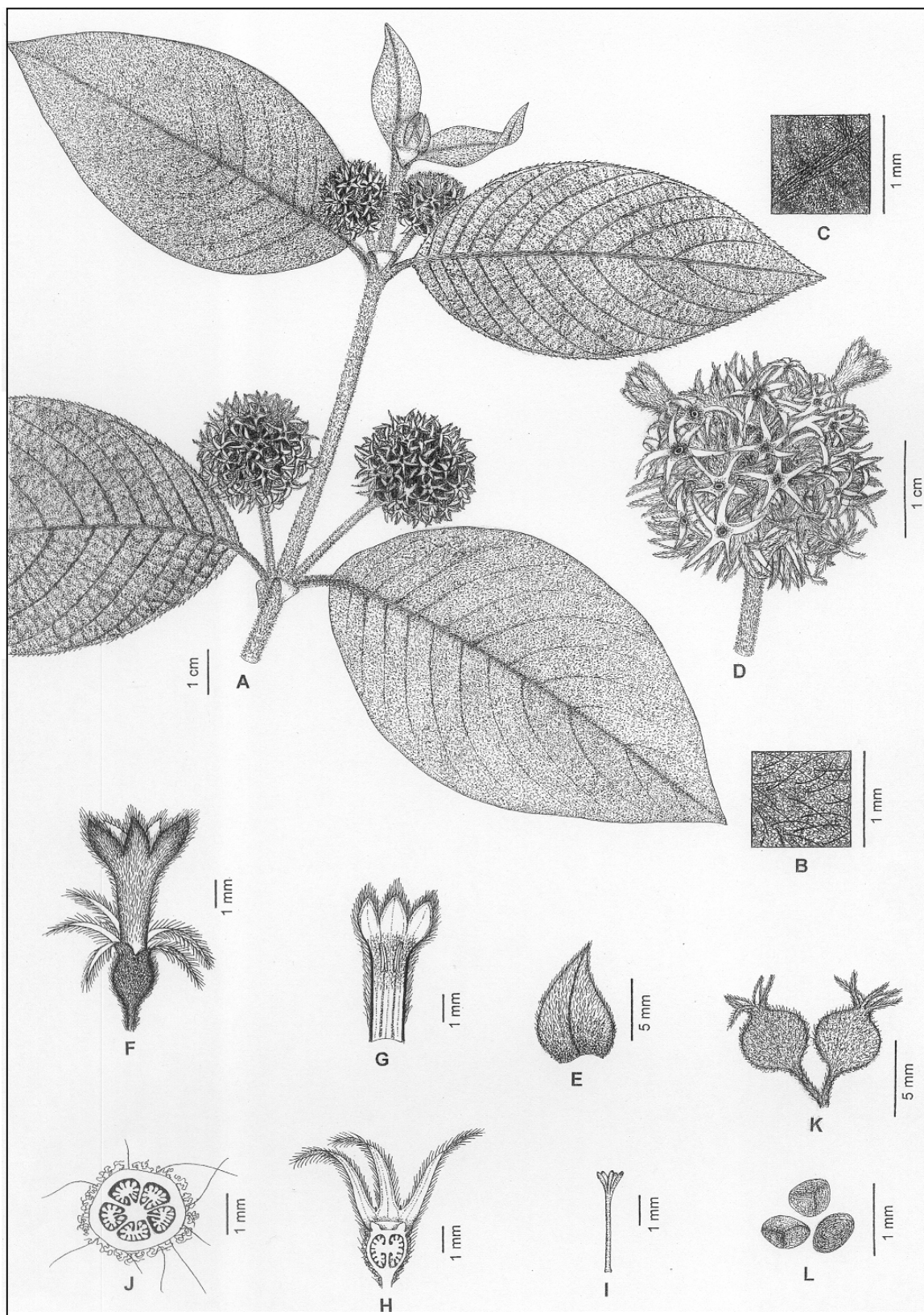


Figure 28. A–L. *Sabicea klugii*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Inflorescence. —E. Outer stipule surface. —F. Flower. —G. Inner corolla surface showing anther's position. —H. Longitudinal section through calyx and ovary. —I. Style and stigmas. —J. Transversal section through ovary. —K. Fruits. —L. Seeds.

tubes, isolatedly to sparsely lanuginose at tubes, trichomes (0.1–)0.6–1.6 mm long, (sub-)appressed to patent; *stamens* 5 per flower, attached to corolla tube at 3.8–4.2 mm from the base, anthers 1.6–1.8 × 0.2–0.3(–0.4) mm; *style* 2.6–3.1 mm long, stigmatic lobes 1.2–1.5 × 0.2–0.3 mm; *ovaries* 1.8–2.1 × 1.2–1.8 mm, 5-locular, each locule 1.2–1.4 × 0.5–0.7 mm. *Fruits* 3–6 × 3–6 mm when immature, color unknown, abaxially isolatedly to sparsely pilosulous to sericeous and lanuginose; *seeds* 0.4–0.6 × 0.4–0.5 mm.

*Discussion.* *Sabicea klugii* is known only from the type collected in Peru (Fig. 12). This species is recognizable by its characteristic floccose or lanuginose plus pilosulous to sericeous indumentum composed of long trichomes on the adaxial surface of leaves (Fig. 28B) and calyces, usually diffuse lanuginose to arachnose indumentum of abaxial surface of leaves, longer, straight and erecto-patent cilia at the margins of stipules, bracts, and calyx lobes, 9–16-flowered umbellate inflorescences, and narrowly lanceolate, apically acuminate to acute calyx lobes (Fig. 28F, H). Almost all characters mentioned by Standley (1936b) are compatible to our observations. The protologue gives the stipules as apically subobtusate, which is contrasting to our observed acuminate apices of stipules. This species seems close to *Sabicea erecta* and *S. tayloriae* due to its compact-pedunculate inflorescences. It can be set apart from both *Sabicea erecta* and *S. tayloriae* by its characteristic floccose or lanuginose indumentum at the adaxial surface of leaves in addition to the pilosulous to sericeous indumentum composed of longer trichomes, longer cilia at the margins of stipules, bracts, and calyx lobes, and narrowly lanceolate calyx lobes. Additionally, it is distinguishable from *Sabicea erecta* by its 9–16-flowered umbellate inflorescences, and curled to tortuous trichomes at the abaxial surface of calyx lobes and corolla tubes, whereas, from *S. tayloriae* by its ample sericeous or villosulous to pilosulous indumentum at branchlets, lower surface of leaves, and outer surface of inflorescences, umbellate inflorescences, and apically acuminate to acute and marginally denticulate calyx lobes. Although *Sabicea klugii* is poorly documented it deserves to be considered as a distinct species due to its clear-cut characteristics.

**21. *Sabicea liedea*** Liede, Meve & Khan, sp. nov. TYPE: Mexico. Oaxaca: 5 miles by road from Valle Nacional, along the Highway to Oaxaca, 500 m, 10 Oct. 1962 (fl & fr), *R. McVaugh* 21796 (holotype, NY!). Figure 29A–M.

*Plantae prostratae vel scandentes, ramulis, paginis superioris stipularum, foliis et inflorescentiis arachnoideis ad lanatis, inflorescentiis confertim paniculatis, calycibus campanulatibus, lobis calycorum 6–9 mm longis, ciliolatis; tubis corollarum 6.5–9 mm longis, exteris sericeis.*

Prostrate shrubs to vines; terminal flowering branchlets densely pilosulous and arachnose, trichomes (0.2–)0.6–2.9 μm long. *Stipules* ovate to widely ovate, antrorse to recurved, 6–10 ×

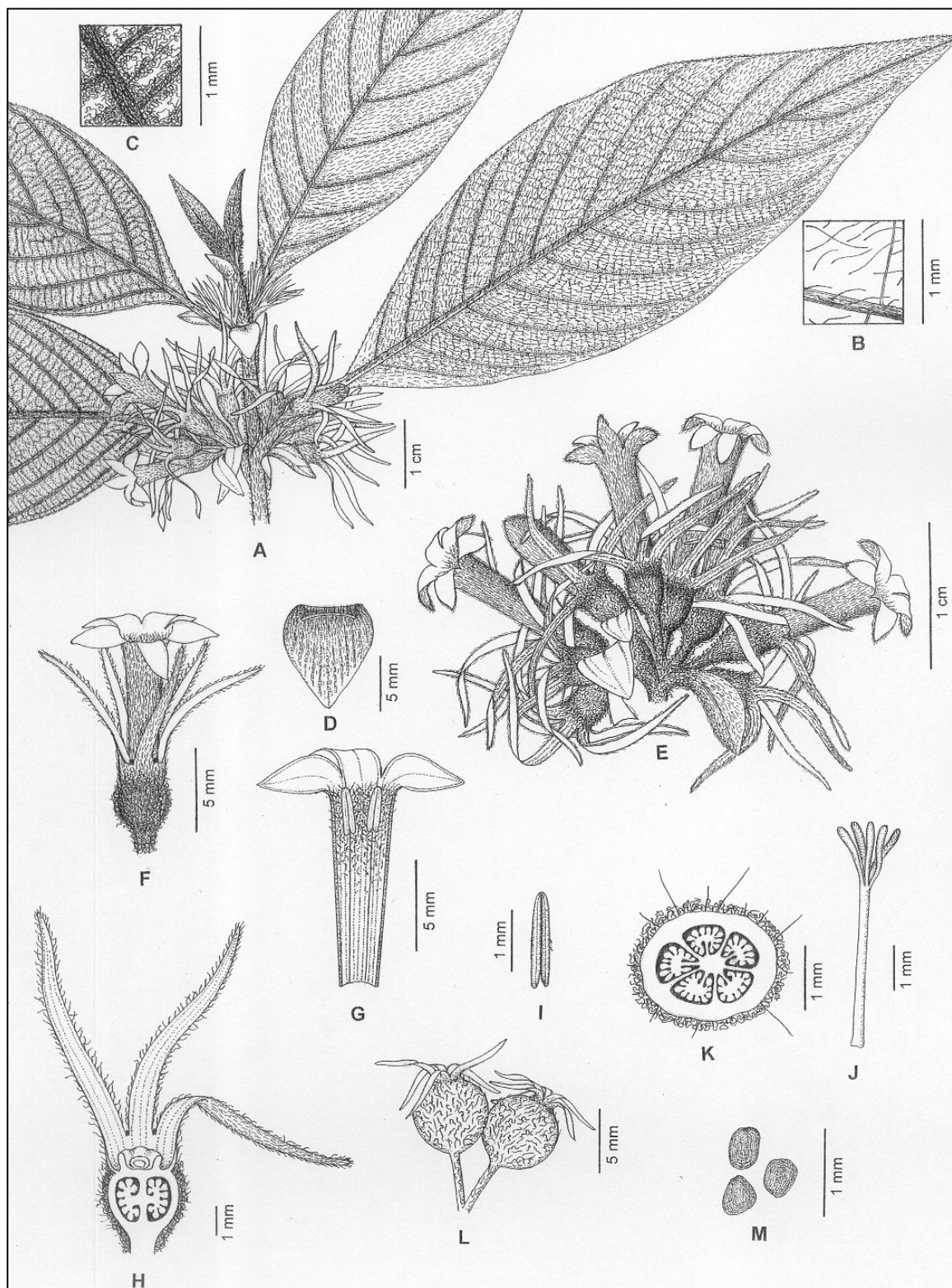


Figure 29. A–M. *Sabicea liedae*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Outer stipule surface. —E. Inflorescence. —F. Flower. —G. Inner corolla surface showing anther's position. —H. Longitudinal section through calyx and ovary. —I. Face view of Anther. —J. Style and stigmas. —K. Transversal section through ovary. —L. Fruits. —M. Seeds.

6–11 mm, apically acute, membranous, margins wavy, ciliolate with (0.3–)0.7–1.1 mm long cilia, adaxially glabrous excluding the basal part, abaxially densely pilosulous and arachnose to lanuginose at the base and along the veins, sparsely to densely in between, trichomes 0.4–0.8(–1.2) mm long, 10–14-veined, colleters 2–14, 0.4–1 mm long. *Leaf blades* lanceolate to narrowly elliptic or oblong, 5.5–10(–12.2) × (1.5–)2.2–4.6(–5) cm, apically acute to acuminate, basally (sub-)acute to obtuse, membranous to papyraceous, margins entire to slightly wavy, ciliolate with 0.2–0.8(–1.2) mm long cilia, adaxially sparsely to densely strigulose to pubescent at lamina and secondary veins, densely strigulose to pilosulous and occasionally arachnose at costa, trichomes (0.4–)0.6–1.2 mm long, abaxially densely sericeous at the costa and secondary veins, sericeous to pilosulous in between, and densely arachnose or lanuginose to lanate all over, trichomes (0.2–)6–2.8 mm, secondary veins (9–)10–14 pairs, costa and secondary veins protruding abaxially and usually plain or sometimes protruding adaxially, tertiary veins prominulous and quaternary veins usually distinct, sometimes prominulous abaxially; *petioles* (6–)8–12(–18) mm long. *Inflorescences* in both opposite leaf axils of each node, 8–14-flowered, compact-paniculate to umbellate, 1.2–1.8 × 1.5–2.2 cm, primary axis 0–1.5(–2.8) mm long, main inflorescence branches 0–4, 0.7–0.8(–1) mm long; *peduncles* (0–)1–2(–4) mm long; *bracts* (sub-)exinvolucrate, membranous, incompletely isolated into 2–3 parts, isolated parts (5–)6–8 × 2–2.5(–4) mm, narrowly to widely elliptic or oblong, apically acute, margins wavy at the upper part, entire at the lower part, ciliolate with cilia 0.4–0.9 mm long cilia, adaxially and abaxially indumenta almost same to those at stipules, , 3–8-ribbed, bracteoles 1.9–9.1 × 0.8–3.6 mm, lanceolate to oblanceolate or elliptic, colleters 2–4, 0.4–0.6 mm long. *Flowers* pedicellate, pedicels 0.5–3(–4.5) mm long; *calyx* campanulate, 5-lobed, tubes (1)1.5–2 × 1.7–2.5 mm, lobes 6–9 × 0.6–1(–1.5) mm, antrorse to spreaded or incurved, widely linear to narrowly lingulate or elliptic, apically acute, margins slightly wavy to entire, ciliolate with 0.6–1.3 mm long cilia, adaxially glabrous, abaxially densely to sparsely pilosulous, trichomes (0.2–)0.8–1.3 mm long, 3(–5)-ribbed, colleters 1–2(–3) in each sinus, 0.2–0.4 mm long; *corolla* salverform, tubes 6.5–9 × 0.9–2 mm, lobes (2–)3–4.5 × 1.3–2 mm, widely lanceolate to narrowly ovate, somewhat recurved, adaxially the indumentum of orifice extends up to 2–3(–5) mm inside the tubes, trichomes (0.2–)0.4–0.8 mm long, abaxially usually densely sericeous, trichomes (0.8–)1.3–1.7 mm long; *stamens* 5 per flower, attached to corolla tube at 2.9–3.2 mm from the base, anthers 1.4–1.6(–2.5) × 0.2–0.3 mm; *style* 2.7–3.5 mm long, stigmatic lobes 1.5–1.7(–2.5) × 0.2–0.3 mm; *ovaries* 1.5–1.7 × 1.5–1.8 mm, abaxially usually 5-lobed or wavy to plain, densely strigulose to pilosulous and isolatedly to densely arachnose, 5-locular, each locule 1.8–1.9 × 0.5–0.6 mm. *Fruits* pink, 3–6.5 × 3–6 mm when mature, abaxially isolatedly to sparsely strigulose to pilosulous and arachnose; *seeds* 0.3–0.4 × 0.3 mm.

*Phenology, distribution and habitat.* Flowering occurs in July and October and fruiting in

October. *Sabicea liedeeae* is endemic to Mexico. Its distribution seems limited to northeast Oaxaca. It is found in moist evergreen or wet tropical forests. It grows on moist red clay soil exposed to filtered sun; 720–1500 m (Fig. 19).

*Discussion.* *Sabicea liedeeae* seems close to other two Mexican species *S. chiapensis* and *S. mexicana*. However, it is marked by arachnose to lanuginose or lanate indumentum, densely all over the abaxial surface of leaves (Fig. 29C), and sparsely to densely at branchlets and abaxial surface of stipules, peduncles, bracts, pedicels and hypanthia. Additionally, it differs from *Sabicea chiapensis* by its shallowly bent and spreading calyx lobes (Fig. 29E), and sericeous external indumentum of corolla tubes (Fig. 29F, G). *Sabicea grisea* with narrower and longer calyx lobes looks similar as well, but *S. liedeeae* can be set apart by the compact-paniculate inflorescences, shallowly bent, slightly wavy to entire, adaxially glabrous and abaxially pilosulous calyx lobes, and externally densely sericeous shorter corolla tubes.

*Additional specimens examined.* MEXICO. **Oaxaca:** 19.5 km N of the pass between Valle Nacional and Ixtlán de Juárez and 29.8 km S of Valle Nacional, *Bartholomew et al.* 3342 (HUH); Ixtlan, Comaltepec, approx, 1 km from highway 175 on road to Soyalapan, *Martin* 559 (BM, US, NY).

**22. *Sabicea liesneri*** Steyererm., *Pittieria* 9: 15. 1981. TYPE: Venezuela. Táchira: primary wet forest, sandy soil, vicinity of Las Minas, north of La Laguna, 16 km southwest of Santa Ana, 7°36'N, 72°13'W, 1150–1250 m, 28 July 1978, (fl), *J. A. Steyermark & R. L. Liesner 118876* (holotype, VEN, not seen, photo VEN!; isotypes, F!, MO!). Figure 30A–H.

Climber; terminal flowering branchlets densely hirtellous, puberulous, hirtellous trichomes (0.1–)1–1.6 mm long. *Stipules* ovate to deltate, recurved, 6–11 × 5–8(–10) mm, apically subacute, membranous, margins entire, complanate, ciliate with 0.2–0.8 mm long cilia, adaxially glabrous excluding the base, densely to isolatedly at rest of the surface, eventually glabrate, trichomes 0.07–0.6 mm long, abaxially densely strigulose to hirtellous or pilosulous all over, 12–14-veined, slightly raised abaxially, colleters 9–12, 1–1.3 mm long. *Leaf blades* lanceolate to ovate or elliptic to oblong, 5.5–9.5 × 2–5 cm, apically acuminate to acute, basally obtuse to acute, papyraceous, adaxially densely to sparsely hispidulous to hirtellous at secondary veins and lamina, densely at costa, trichomes, (0.1–)0.2–1.4 mm long; abaxially sparsely to moderately densely hirtellous or pilosulous and isolatedly puberulous on lamina, densely hirtellous to pilosulous, sparsely puberulous on costa and secondary veins, cilia and trichomes (0.1–)0.2–1.6 mm long, secondary veins 12–13 pairs, protruding abaxially, plain or distinct adaxially, tertiary veins distinct abaxially; *petioles* (2–)10–20 mm long, very densely



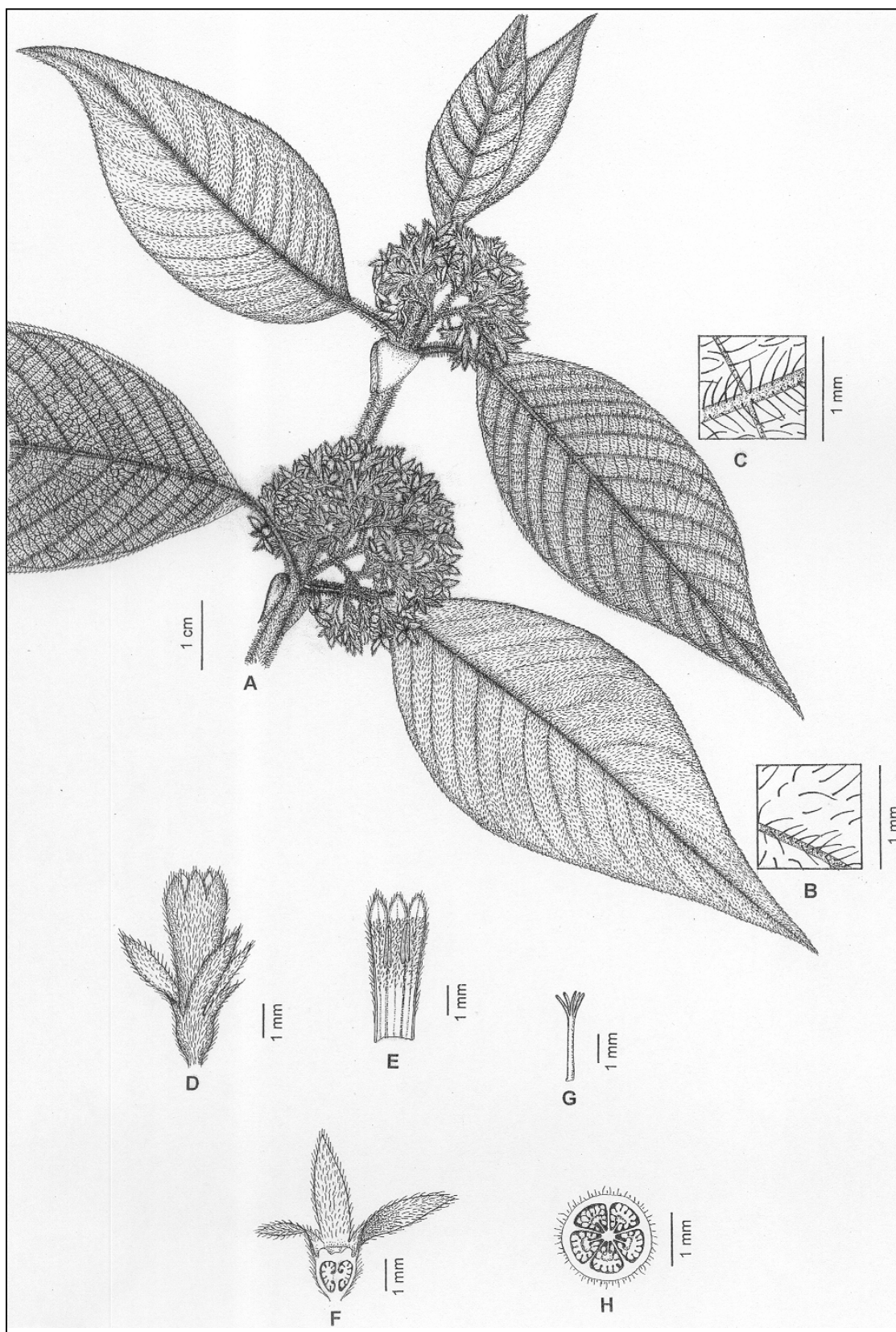


Figure 30. A–H. *Sabicea liesneri*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Flower. —E. Inner corolla surface showing anther's position. —F. Longitudinal section through calyx and ovary. —G. Style and stigmas. —H. Transversal section through ovary.



hirtellous or pilosulous. *Inflorescences* in one leaf axil of each node, (12–)26–36-flowered, variously branched and moderately lax- to compact-umbellate, 1.5–3.5 × 2–3.8 cm, main axes 4–5, (1.5–)2.5–5 × 0.5 mm, compound dichasia; *peduncles* (1–)3–8 mm long; *bracts* exinvolucrate, papyraceous, incompletely isolated into 2–3 parts, isolated parts 7–9 × 4–5 mm, ovate to elliptic, apically acute, basally obtuse, margins entire, cilia 0.4–0.8 mm long, indumentum same to those at stipules, 3(–5)-ribbed, bracteoles 3–7 × 0.5–0.6 mm, linear or oblanceolate; *colleters* 2, 0.3–0.3 mm long. *Flowers* pedicellate, pedicels 1–5.2 mm long; *calyx* campanulate, markedly unequal, 4–5-lobed, tubes 0.8–1.3 × 1.5–2.5 mm, lobes (1.5–)2.5–5.5(–6.5) × 0.5–1.8(–2.1) mm, spreaded to antrorse or recurved, narrowly elliptic to lanceolate, occasionally linear, apically acute, margins entire, ciliolate with cilia 0.03–0.09 mm long, adaxially pilosulous at the lobes up to the upper part of tube, abaxially sparsely hirtellous or pilosulous, trichomes 0.07–1 mm long, *colleters* 1–2 in each sinus; *corolla* salverform, tubes 3.1–4.5 × 1.8–2.1 mm, lobes 1.1–1.8 × 1.1–1.6 mm, ovate, antrorse, apically acute, adaxially the indumentum of orifice extends up to 1.1–1.8 mm inside the tubes, abaxially pilosulous, trichomes 0.2–0.6 mm long; *stamens* 5 per flower, attached to corolla tube at 2.1 mm from the base, anthers 1.8–2.1 × 0.3–0.4 mm; *style* 2–2.1 mm long, stigmatic lobes 0.7–0.9 × 0.1–0.1 mm; *ovaries* 1.1–1.5 mm long, 1–1.2(–1.5) mm, abaxially uneven, 5-locular, each locule 0.8–1.1 × 0.4–0.5 mm. *Fruits* and *seeds* are not seen.

*Discussion.* *Sabicea liesneri* is known only known through the holotype collected from Venezuela (Fig. 9). *Sabicea liesneri* is remarkable for its variously branched umbellate inflorescences, erecto-patent trichomes at the branchlets, leaves, stipules, outer surface of inflorescences, smaller, unequal, usually narrowly elliptic to lanceolate and spread to antrorse calyx lobes, trichomes at the upper part of the adaxial surface of stipules, bracts and calyx lobes, and a comparatively small corolla. *Sabicea liesneri* seems close to *S. novo-granatensis*, especially of Venezuela, from which it differs by variously branched inflorescences, smaller (usually 2.5–5.5 × 0.5–1.8 mm in contrast to 4–9 × 1.2–3) and unequal calyx lobes and shorter (3.1–4.5 mm in contrast to 6–10 mm) corolla tubes with shorter (0.2–0.6 mm in contrast to 0.5–2 mm) external trichomes, and shorter (1.1–1.8 mm in contrast to 2.4–3.8 mm) corolla lobes.

*Sabicea liesneri* differs from its close ally *S. pearcei* by longer (1.2–2 cm) petioles (Fig. 30A), variously branched umbellate inflorescences, indumentum of adaxial surface of stipules, bracts and calyx lobes, and narrowly elliptic and markedly unequal calyx lobes (Fig. 30D, F). The characters of *Sabicea liesneri* showing the differences with *S. novo-granatensis* or *S. pearcei* are not known from enough specimens. However, we maintain this species, as the distinguishing characters of its type specimens are not found in its close allies.

**23. *Sabicea mattogrossensis*** Wernham, Monogr. *Sabicea* 62. t. 8. f. 5–8. 1914. TYPE: Brasil. Mato Grosso: Santa Cruz, 1891/1892 (fl), S. Moore 785 (holotype, BM!; isotypes, B, presumably destroyed, K not seen, NY!). Figure 31A–O.

Scrambling or twining woody vines or lianas or low shrubs; stems to 5 m tall, terminal flowering branchlets, sparsely to densely pilosulous to sometimes strigulose, eventually glabrescent, trichomes (0.1–)0.2–1(–2.1) mm long. *Stipules* 4–12(–14) × (2.5–)4–8(–12) mm wide, membranous, reflexed, deltate to ovate or lingulate, apically (sub-)acute or obtuse, occasionally minutely bifid, margins entire, ciliolate with 0.7–1.1 mm long cilia, adaxially glabrous excluding the basal part, abaxially isolatedly to sparsely strigulose to puberulous or pilosulous at lower part, trichomes 0.7–1.9 mm long, colleters 6–16, colleters (6–)8–12(–16) mm long, 9–16-veined. *Leaf blades* usually narrowly elliptic to oblong, occasionally narrowly ovate, (3.5–)5–14(–17) × 1.8–5.5(–9) cm, papyraceous, apically (sub-)acute or acuminate, basally acute to obtuse or attenuate, margins entire, ciliolate with (0.07–)0.1–0.9 mm long cilia, adaxially glabrate to glabrescent or sparsely strigulose to hirtellous and puberulous on lamina, sparsely to moderately densely strigulose to hirtellous and puberulous on costa, trichomes 0.1–0.5(–0.8) mm long, abaxially glabrate or sparsely strigulose to puberulous on lamina, usually densely strigulose, occasionally pilosulous to puberulous on costa and secondary veins, trichomes (0.07–)0.1–0.9(–1.4) mm long, lateral veins 9–14 pairs per leaf, costa and secondary veins protruding abaxially and plane or distinct adaxially; *petioles* (4–)7–15(–22) mm long. *Inflorescences* one to two per node, 5–12(–16)-flowered, moderately lax- to compact-umbellate, 1.8–3.5 × 1.8–4 cm, main axes 1–5 mm long; *peduncles* (4–)10–40(–45) mm long; *bracts* (sub-)exinvolucrate, papyraceous, incompletely isolated into 2(–3) parts, (8–)10–12(–14) × 6–10(–13) mm when involucre, isolated parts 8–12 × 6–9 mm, 0(–3)-lobed, lobes 1–3 × 1–2 mm, usually deltate to ovate, apically obtuse to (sub-)acute, margins entire, usually eciliate, sometimes ciliolate, adaxially glabrous excluding the basal part, abaxially glabrate or sparsely strigulose or pilosulous to puberulous, bracteoles 1.5–6 × 0.8–7 mm, deltate to ovate or elliptic, colleters 2. *Flowers* pedicellate, *pedicels* (1–)2–8(–11) mm long; *calyx* campanulate, tubes 1.1–1.5 × 1.4–2.7 mm, lobes 3–5, (3–)6–11 × (1–)2–4(–7) mm, antrorse or spreading, usually elliptic to obovate, occasionally lingulate, apically acute to obtuse, margins unequal or entire, ciliolate with (0.7–)0.4–0.7(–0.9) mm long cilia, adaxially glabrous, abaxially usually glabrous to glabrescent, rarely isolatedly to sparsely strigulose to puberulous, 3–6-ribbed with costa, parallelodromous, colleters 1(–2) in each sinus, 0.1–0.2 mm long; *corolla* white, salverform, tubes (8–)10–12(–15) × 2–3 mm, lobes 2–5.6 × 1–2 mm, widely lanceolate to narrowly ovate, antrorse, apically acute, adaxially the indumentum of orifice extends up to 5.5–6.5 mm inside the tubes, trichomes (0.2–)0.5–1.1(–1.5) mm long, abaxially sparsely to densely strigulose, occasionally pilosulous to pubescent or glabrescent, trichomes (0.2–)1.2–1.6(–2) mm long, *stamens* 5 per flower, attached to corolla tubes at 10–

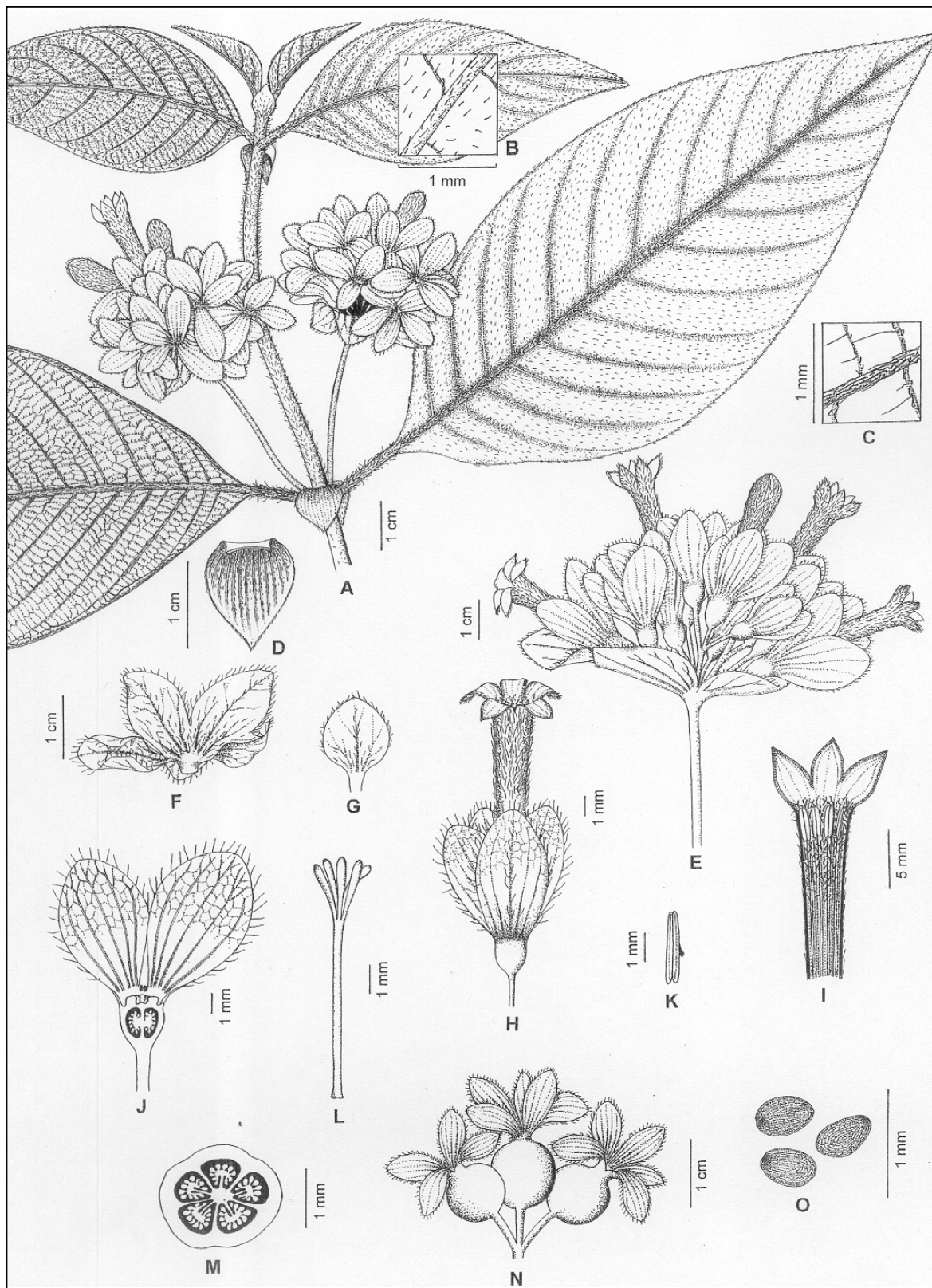


Figure 31. A–O. *Sabicea mattogrossensis*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Outer stipule surface. —E. Inflorescence. —F. Side view of bract. —G. Bracteole. —H. Flower. —I. Inner corolla surface showing anther's position. —J. Longitudinal section through calyx and ovary. —K. Face view of Anther. —L. Style and stigmas. —M. Transversal section through ovary. —N. Fruits. —O. Seeds.

11 mm from the base, anthers  $2.2\text{--}2.5 \times 0.4\text{--}0.5$  mm; style 6–7 mm long, *stigmatic lobes* 5, (2–)3.2–3.5  $\times$  0.2–0.3 mm; *ovaries* 1.5–2  $\times$  1.5–2 mm, abaxially shallowly 4–5-lobed or uneven, usually glabrous, occasionally glabrescent, rarely sparsely strigulose, 5-locular, each locule 1–1.5  $\times$  0.4–0.8 mm. *Fruits* blackish blue or dark purple, 8–10  $\times$  8–10 mm when mature, glabrous or glabrescent; *seeds* 0.4–0.6  $\times$  0.4–0.5 mm.

*Phenology, distribution and habitat.* Flowering almost throughout the year and fruiting in late January to March, May to June and October to November. Recorded from the lower to upper Amazonian, eastern edge of central Andean (Puna) and western Brazilian regions. The disjunct distribution of *Sabicea mattogrossensis* in Brazil, Peru and Colombia might raise questions about its specific circumscription. However, the specimens collected from these very distant areas were found as similar to *S. mattogrossensis* and it was impossible to consider these specimens under any infraspecific limit. Generally it occurs in wetland or stunted swampy to humid savanna, moist or evergreen dry tropical or premontane forest to somewhat logged out rain-forest, much overgrown by lianas or undergrowths, in pastures and fencerows, roadsides or along river banks and in floodplain vegetation. It grows on dry to sandy clay or black argillaceous soil; 170–300 m (Fig. 9).

*Discussion.* *Sabicea mattogrossensis* is characterized by the following combination of characters: 1) the lamina adaxially sparsely strigulose to hirtellous and puberulous with short (mostly 0.1–0.5 mm; Fig. 31A, C) trichomes, eventually glabrate, and abaxially sparsely strigulose to puberulous or glabrate; 2) stipules, bracts (except for the base) and calyx lobes adaxially glabrous all over (Fig. 31J); 3) inflorescences usually compact-umbellate or fascicled (Fig. 21E); 4) long peduncles and pedicels (usually 1–4 cm and 2–8 mm respectively) and 5) usually elliptic to obovate and large (6–10  $\times$  2–7 mm) calyx lobes.

Wernham (1914) noted the morphological similarity of *Sabicea mattogrossensis* with the African *S. calycina*, from which he distinguished it by its basally acute leaves and strigulose peduncles in contrast to basally cordate or rounded leaves and glabrous peduncles. This differentiation, however, is not always clear-cut, because some plants of both species have basally obtuse leaves, and occasionally the peduncles of *Sabicea mattogrossensis* are glabrate. The greenish color of calyx lobes of this species in contrast to pinkish to light rose color of *Sabicea calycina* seems useful in addition to the leaf base and peduncle hairiness in distinguishing these two species. The molecular analysis of *Sabicea* (Khan et al., 2007) adds confidence that *S. mattogrossensis* and *S. calycina* are two well distinct species, as all American species form a monophyletic clade and are thus more closely related to each other than to any African species. *Sabicea mattogrossensis* seems close to *S. novo-granatensis* in inflorescence type and size and shape of calyx lobes, but can be easily distinguished by its leaf blades that are adaxially sparsely covered with strigulose to hirtellous and puberulous indumenta comprised of mostly short (0.1–0.5 mm in contrast to 0.2–1.3 mm) trichomes and

eventually glabrate, usually (sub-)appressed trichomes at abaxial surface of leaves and corolla tubes, adaxially glabrous stipules, bracts and calyx lobes (excluding the bases), and usually glabrous to glabrescent pedicels and hypanthia.

*Sabicea mattogrossensis* is distinct from *S. hirta* by its stipules not wider than long and basally always obtuse, and apically acute (Fig. 31D), apparently shorter trichomes at the adaxial surface of leaves, appressed trichomes at abaxial surface of leaves, calyx lobes and corolla tubes, 2 colleters near the margins of the base inside the bracts, 1(–2) in colleters each sinus, longer corolla tubes, and anthers. Some *Sabicea mattogrossensis* specimens are very similar to *S. burchellii* by leaf shape and size, indumentum of adaxial leaf surface, and lingulate calyx lobes. However, they differ from *Sabicea burchellii* by their moderately lax- to compact-umbellate inflorescences with long peduncles and pedicels, glabrate hypanthium, and usually elliptic to obovate calyx lobes. No consistency was observed in the division of stipule apices or erecto-patent indumentum at abaxial leaf surfaces (as in *Sabicea villosa*) as a base for identifying separate varieties. In *Guareco 284* (NY) and *Nee 48395* (NY), hypanthium and pedicels are sparsely to densely covered with indumentum in contrast to glabrous to glabrescent hypanthium and pedicels of most *Sabicea mattogrossensis*, but as most of other characters including stipules abaxial surface, bracts and calices are as in *S. mattogrossensis*, these specimens have been included in *S. mattogrossensis*.

Some specimens were collected in very remote areas of Brazil and Peru, and Colombia. Considering the localities of these specimens, the distribution of this species seems fragmented. It doesn't mean that these specimens (e.g., *Karsten s.n.* from of Colombia) are misidentified; rather, it might be due to the mistake in citing the locality by the collector or the restricted attention of different collectors to non-adjointing regions or occasional long distance seed dispersal of the species.

*Selected specimens examined.* BOLIVIA. **Beni:** Along Río Yata, ca. 40 km SW of Guayaramerín, *Anderson 11908* (NY), *Anderson 11983* (NY, US); Yacuma, E of San Borja, Bosque de Chimanes, 14°59'S, 66°23'W, *Foster 12507* (F); Ballivián y Yacuma, *Guareco 284* (NY); Comunidad Tierra Santa, Tigrra Arenosa Estación Biológica, *Rivero 241* (NY); Vaca Diez, Ribaralta, *Solomon 16774* (M, NY, U). **Cochabamba:** Carrasco, near Puerto Villarroel, *Casas FC7929* (NY); Carrasco, 1.5 km east of Mariposa, *Ritter 1438* (W). **La Paz:** Iturrealde, Luisita, *Beck & Haase 9986* (NY). **Santa Cruz:** Ichilo, ca. 2 km W of Villa San Germán on highway from Buena Vista to Río Ichilo, 17°21'S, 64°06'30'', *Nee 48395* (NY). BRASIL. **Amazonas:** Rio Canumã, varzea land, *Cooper-III s.n.* (US, NY). **Acre:** Senador Guimard, basin of Rio Purús, Rio Iquiri, *Daly et al. 9238* (MO); Plácido de Castro, Km 20, AC-40 (Plácido de Castro-Rio Branco), Igarapé Visionário, *Rivero et al. 343* (MO). **Amapá:** Vila do Maruanum-Macapá-AP, *Rabelo et al. 968* (NY); Ariramba, quadrícula SA-22-VB.ponto 402, *Rosa & Alfeu 4396* (NY, MO). **Rondônia:** Costa Marques, Área militar do Forte Príncipe da Beira, *Ferreira 8744* (MO). Rio Branco, Fazenda Rio, Vermelho, Próximo á Villa Boa União,

Nov 28, 1984, *Emmerich et al.* 5547 (US). COLOMBIA. **Cundinamarca**: Bogotá, Gauduas, *Karsten s.n.* (W). PERU. **Loreto**: On east bank along Río Hualaga in vicinity of Laguna, *Croat* 17834 (F, G); Quebrada Tahuayo above Tamishiyaco, 3°58'60S, 73°10'W, *Croat* 19809 (MO); De Cornel Portillo, 5 km WSW Pucallpa, valley of Río Ucayali, 8°28'S, 74°40'W, *Fosberg* 28933 (MO, NY, US); Pucallpa, *Vigo* 961 (F, HUH, MO, NY, US). Madre De Dios: Tambopata, ca. 5 km from Puerto Maldonado near Río Tambopata, *Gentry & Reville* 16268 (F, NY, MO); 30 air km or 70–80 river km SSW Puerto Maldonado at effluence Río La Torre (Río D'Orbigny/Río Tambopata, SE Bank), Tambopata Nature Reserve, 12°49'S, 69°17'W, *Barbour* 5168 (F, G, MO); 39 km SW of Puerto Maldonado, shoreline of Laguna Cocacocho, 5.1 km down main Trail from Explorer's Inn, near confluence of Río La Torre & Río Tambopata, 12°50'S, 69°20'W, *Smith* 292 (G), Along Río La Torre Trail, Explorer's Inn, near confl. of Río Tambopata & R. La Torre, *Smith* 356 (F, NY, U); *Smith et al.* 1540 (HUH, S, US, WIS), Tambopata wildlife reserve, 30 km S of Puerto Maldonado, along Río Torre, 12°15'S, 69°17'W, *Young & Stratton* 112 (MO); Cuzco Amazónico, across Río Madre de Dios on road to Lago Sandoval, *Gentry et al.* 68967 (MO), Cuzco Amazónico, trail to Lago Sandoval across Río Madre de Dios, ca. 12 km E of Puerto Maldonado, *Gentry & Núñez* 69356 (MO); Cuzco Amazónico, Las Piedras, a lo largo de la Quebrada Gamitana, límite este de la reserva, 12°29'S, 69°03'W, *Timaná et al.* 1407 (MO); Cuzco Amazónico, Las Piedras, InventaRío Permanente, en la Quebrada Gamitana, *Timaná & Jaramilo* 3213 (MO); Tambopata, in *Cecropia* forest along Río La Torre, *Gentry & Ortiz* 78217 (MO).

**24. *Sabicea mexicana*** Wernham, Monogr. *Sabicea* 41. t. 5, f. 1, 2. 1914. TYPE: Mexico: Jun 1842 (fl), *Liebmann* 43 (lectotype, designated here, K!; duplicate, B, presumably destroyed, BR, G & P not seen). Figure Sessé & Mociño s.n. (Torner collection 1665 and DC. 456, White et al. 1998 & G).

Shrubs or vines; terminal flowering branchlets densely pilosulous to occasionally strigulose, trichomes (0.2–)0.8–1.5(–2.2) mm long. *Stipules* ovate to widely ovate, erect to recurved, 9–10 × 8–9 mm, apically acute, membranous, margins wavy, ciliolate with (0.4–)0.7–1 mm long cilia, adaxially glabrous excluding the basal part, abaxially sparsely to densely strigulose to pubescent, trichomes (0.4–)0.8–1.6) mm long, 9–14-veined, protruding at both surfaces, colleters 7–14, (0.5–)0.6–1.1 mm long. *Leaf blades* elliptic to narrowly, (6–)7–12(–15) × (2–)3–5(–7) cm, apically acute to acuminate, basally obtuse, membranous to papyraceous, margins entire or slightly wavy, ciliolate with (0.2–)0.7–1.3 mm long cilia, adaxially sparsely-densely strigulose to pubescent at lamina and secondary veins, densely to very densely at costa, trichomes 0.2–1.5 mm long; abaxially isolatedly-densely strigulose at lamina, and densely at costa and secondary veins, trichomes (0.2–)0.5–1.8 mm long, secondary veins (9–)10–12(–15) pairs, costa and secondary veins protruding abaxially and usually plain or sometimes protruding adaxially, tertiary veins prominulous and quaternary

veins usually distinct, sometimes prominulous abaxially; *petioles* (4–)6–16(–20) mm long. *Inflorescences* 2 per node, 5–12-flowered, compact-paniculate to umbellate, subsessile 1.2–1.8 × 1.5–2.2 cm, primary axis 0–3 mm long, main inflorescence branches 0–4, 0.8–0.9(–1.2) mm long; *peduncles* (0–)1–3(–6) mm long; *bracts* (sub-)exinvolucrate, membranous, incompletely isolated into 2–5 parts, isolated parts (5–)6–7.5(–8.3) × 2–2.7(–4.4) mm, rarely 2-lobed, narrowly to widely elliptic or oblong, apically acute, margins wavy at the upper part, entire at the lower part, ciliolate with 0.6–0.9 mm long cilia, indumentum same to those at stipules, sparsely to densely on veins, 3–8-ribbed, bracteoles 1.8–8 × 0.7–3.1 mm, lanceolate to oblanceolate or elliptic, colleters 2(–4), (0.5–) 0.8 mm long. *Flowers* pedicellate, pedicels 1–6 mm long; *calyx* campanulate, 5-lobed, tubes 0.6–1(–1.2) × 1.7–2.1 mm, lobes 6–7.7 × 0.7–1.5(–2) mm, antrorse to gently incurved, narrowly lanceolate to elliptic or lingulate, apically acute, margins slightly wavy to entire, ciliolate with 0.6–1.3 mm long cilia, adaxially glabrous, abaxially sparsely strigulose, trichomes (0.2–)0.8–1(–1.3) mm long, 3(–5)-ribbed with costa, abaxially prominulous, adaxially plain, colleters 1–2 in each sinus, 0.2–0.5 mm long; *corolla* salverform, tubes (6.5–)7–10(–11.2) × 1–2(–2.5) mm, lobes (2–)2.2–2.4 × (0.8–)1.3–2.4 mm, ovate, somewhat recurved, adaxially the indumentum of orifice extends up to 2.4–3.5(–5.3) mm inside the tubes, trichomes 0.2–0.1 mm long, abaxially densely strigulose, trichomes (0.8–)1.2–1.8 mm long; *stamens* 5 per flower, attached to corolla tube at 3–3.5 mm from the base, anthers 1.4–1.7(–2.9) × 0.2–0.3 mm; *style* 2.8–3.6 mm long, stigmatic lobes 1.6–2.3(–3) × 0.2 mm; *ovaries* 1.6–1.9 × 1.7–2.1 mm, abaxially usually 5-lobed or wavy to plain, sparsely to densely strigulose or pilosulous, 5-locular, each locule 1.8–2 × 0.5–0.8 mm. *Fruits* dull rose violet to pink, 2.9–7.1 × 3–6.5 mm when mature, isolatedly strigulose or pilosulous; *seeds* 0.3–0.5 × 0.3–0.4 mm.

*Phenology, distribution and habitat.* This species seems restricted to Oaxaca, Mexico. It is found in moist red clay soil, moist lower cloud or wet tropical evergreen forest, on steep slopes, mountainsides and along streams (Fig. 19).

*Discussion.* Andersson (1999) merged *Sabicea mexicana* with *S. panamensis*. We disagree with Andersson's decision and resurrect *Sabicea mexicana* as a distinct species as it differs from *S. panamensis* by its longer (6–7.7 mm in contrast to ([0.2–]1–5[–6]) mm) and antrorse to spread calyx lobes, and longer (1.2–1.8 mm in contrast to 0.2–1.1 mm) external trichomes of corolla. Some *Sabicea panamensis* have antrorse calyx lobes but these are either very short (<3 mm long), and ovate to triangular or somewhat longer (1–6 mm) but the inflorescences are apparently elongated- thyrsoid. *Sabicea mexicana* is characterized by the combination of its compact-paniculate to umbellate inflorescences, long, widely linear to narrowly lanceolate or lingulate to elliptic, antrorse to spread, adaxially glabrous calyx lobes, strigulose indumentum of lower leaf surfaces and external surface of calyces and corolla

tubes. *Sabicea mexicana* appears as close to *S. burchellii*, *S. hirta*, *S. chiapensis*, and *S. liedeeae* due to its superficially nearly similar inflorescences or calyx lobes. It differs from *Sabicea burchellii* by its strigulose indumentum at lower leaf surfaces, compact-paniculate to umbellate inflorescences with distinct peduncles, pedicels and distinct to indistinct (0–3 mm) primary axis, and apparently shorter and ovate corolla lobes. *Sabicea mexicana* is distinguishable from *S. hirta*, by its compact-paniculate to umbellate inflorescences, apically acute stipules and calyx lobes, (sub-)exinvolucrate bracts with apically acute lobes, shorter peduncles, narrower calyx lobes, strigulose external indumentum of corolla tubes and longer corolla lobes. It is distinct from *Sabicea chiapensis* by its strigulose indumentum at abaxial leaf surfaces and corolla tubes, and adaxially glabrous and shorter calyx lobes.

In *Sabicea mexicana* the arachnoid to lanuginose indumentum is not restricted to the costa and secondary veins, rather spread over lamina, in contrast to *S. chiapensis*, where these are limited to the abaxial costa and secondary veins. *Sabicea mexicana* is distinct from *S. liedeeae* by its indumentum usually lacking curled to tortuous trichomes at branchlets, and lower surface of leaves, and always at outer surface of inflorescences. *Sabicea mexicana* seems close to *S. umbellata* from which it can be distinguished by its shorter petioles (usually 6–16 mm in contrast to 20–40 mm long), peduncles (usually 1–6 mm long in contrast to 6–25), inflorescence axes (usually 0–1.5 mm in contrast to 5–7 mm long), longer (0.6–1.3 mm in contrast to 0.2–0.5 mm) and appressed cilia of calyces and longer corolla tubes (usually 7–11.2 mm in contrast to 5.5–6.5 mm).

Wernham (1914) did not comment on one of Sessé and Mociño's illustrations, subsequently referred as Torner collection 1665 and DC. 456 and published by White et al. (1998). De Candolle (1830) annotated it as *Sabicea stipularis* (McVaugh, 2000) and commonly considered it as a Mexican plant. Hemsley (1881) recognized it as *Sabicea hirta* and mentioned its distribution in South Mexico, Nicaragua, Jamaica, and Trinidad. McVaugh (2000) argued that this is a *Sabicea aspera*-like species of *Sabicea* perhaps from Puerto Rico rather than from Mexico. We compared this illustration with all observed specimens of *Sabicea* from Mexico and Puerto Rico. In fact, this illustration mostly represents Wernham's (1914) *Sabicea mexicana*, not *S. aspera*, and is clearly different from the Puerto Rican *Sabicea*. The illustration of Sessé and Mociño seems similar also to the new Mexican species *Sabicea chiapensis* in shape of stipules, and inflorescences including bracts, especially the shape of calyx lobes, whereas, to *S. liedeeae* in stipules, leaves and inflorescences including bracts but not calyx lobes. This illustration superficially appears as also similar to the Jamaican species *Sabicea hirta* in leaves and inflorescences, but not in shape of stipules, structure of bracts, and calyx-apices. Although Wernham (1914) described *Sabicea mexicana* as the "sole representative of the genus" in Mexico, he described another Mexican species, *S. flagenioides* from Yucatánand, although its status is uncertain (Lorence, 1999; see *S. flagenioides* under insufficiently known names/ taxa). Its small (ca. 5 × 1.5 cm) and lanceolate leaves with "subulate-setaceous" stipules seems contrasting to all Neotropical *Sabicea*.



Hemsley (1881) mentioned the distribution of *Sabicea glabrescens*, *S. hirsuta*, and *S. hirta* to include Mexico, which is unsupported.

Wernham (1914) cited two syntypes for *Sabicea mexicana*. Between the two specimens, *Galeotti* 2662 appeared as better in condition, but this specimen of BR & G is without corolla and of US with immature flower. *Liebmann* 43 (K) was observed as not better than *Galeotti* 2662 superficially, but as representing the species mostly. We have selected it as the lectotype for this species.

*Additional specimens examined.* MEXICO. Mexico: **Oaxaca:** 8 km S of Vista Hermosa, 17°30'N, 96°30'W, *Hahn* 639 (NY); Choapam (La Chinantla), 2 km al N de Comaltepec, *Mendoza et al.* 1329 (NY), a 1–5 km al NE de Comaltepec, *Lorenæ* 4391 (NY); Km 75,5 on Highway 175 between Tuxtepec and Oaxaca, *Holmes* 4509 (MO, NY); Jalahui, 27 km al SW de Boca de Monte, brecha Playa Vicente-Chaopan, *Torres & Tenorio* 4501 (BR); de Ixtlán, Comaltepec, 3 km al S de Metates, carr. Tuxtepec-Oaxaca, *Torres & Cortez* 7266 (F); Entre Vista Hermosa y Comaltepec, km. 82 carr. Tuxtepec-Oaxaca, Sierra Juárez, *Martínez* 257 (MO); Faldas del Cerro Picacho, 7.5 km al NW de Guevea de Humboldt, Tehuantepec, *Torres & Martínez* 5956 (F); Puerto Antonio, 5.3 km al N de Vista Hermosa, carr. Oaxaca-Tuxtepec, Comaltepec, 17°38'N, 96°22'W, *Tenorio & Torres* 11029 (MO); Mixe, rancho La Garrapata, 6 km al E de Totontepec, *Ramírez & Ramírez* 412 (MO). **Puebla:** Along rd. to Teziutlán, 10 mi. by rd. SW of Tlapacoyan, ca. 19°53'N, 97°20'W, 4000 ft, *Webster & Breckon* 15451 (MO); Finca Los Flores, al SE de Xochical, Cuetzalam, 20°01'N, 97°29'W, 800, *Tenerio et al.* 13935 (MO). **Veracruz:** Atzalan, La Calavera, *Ventura* 13995 (G), Ranchito El Caballo, *Ventura* 14370 (MO), Cerro Del Aguila, *Ventura* 19741 (MO); Veracruzvic, Cerro del Aguila, 19 km N of Altotonga, on road to Tlapacoyan, vic. Cerro del Águila, 19°53'N, 97°13'W, *Nee & Hansen* 18568 (F, HUH, NY). About 6 km (by air) S of Tlapacoyan on road to Altotonga, 19°55'N, 97°13'W, *Nee & Diggs* 24882 (F).

**25. *Sabicea mollissima*** Benth. ex Wernham, Monogr. *Sabicea* 47, t. 12. 1914. TYPE: Brasil. about Santarém, Feb. 1850 (fl), *R. Spruce* 684 (lectotype, designated here, BM!; duplicate, K!, G!, B, presumably destroyed, P, not seen, photo NY!). Figure 32A–I.

Erect to eventually scandent herbs or small shrubs, terminal *flowering branchlets* densely villosulous to pubescent and arachnose, trichomes (0.9–)2–2.8 mm long. *Stipules* ovate to triangular, antrorse to slightly reflexed, (4–)5–12 × (4–)5–7 mm, apically usually undivided, sometimes shortly bifid (1.5–2.7 mm long), acute to acuminate, membranous, ciliolate with (0.5–)0.8–1.4 mm long cilia, adaxially glabrous at upper part, abaxially sparsely to densely villosulous to pubescent and arachnose, 6–9-ribbed, actinodromous perfect reticulate, distinct or raised adaxially and raised abaxially. *Leaf blades* narrowly to widely elliptic to oblong or ovate, (2.5–)3–12(–13.5) × (1–)2.5–5(–7) cm, apically acute to acuminate, papyraceous,

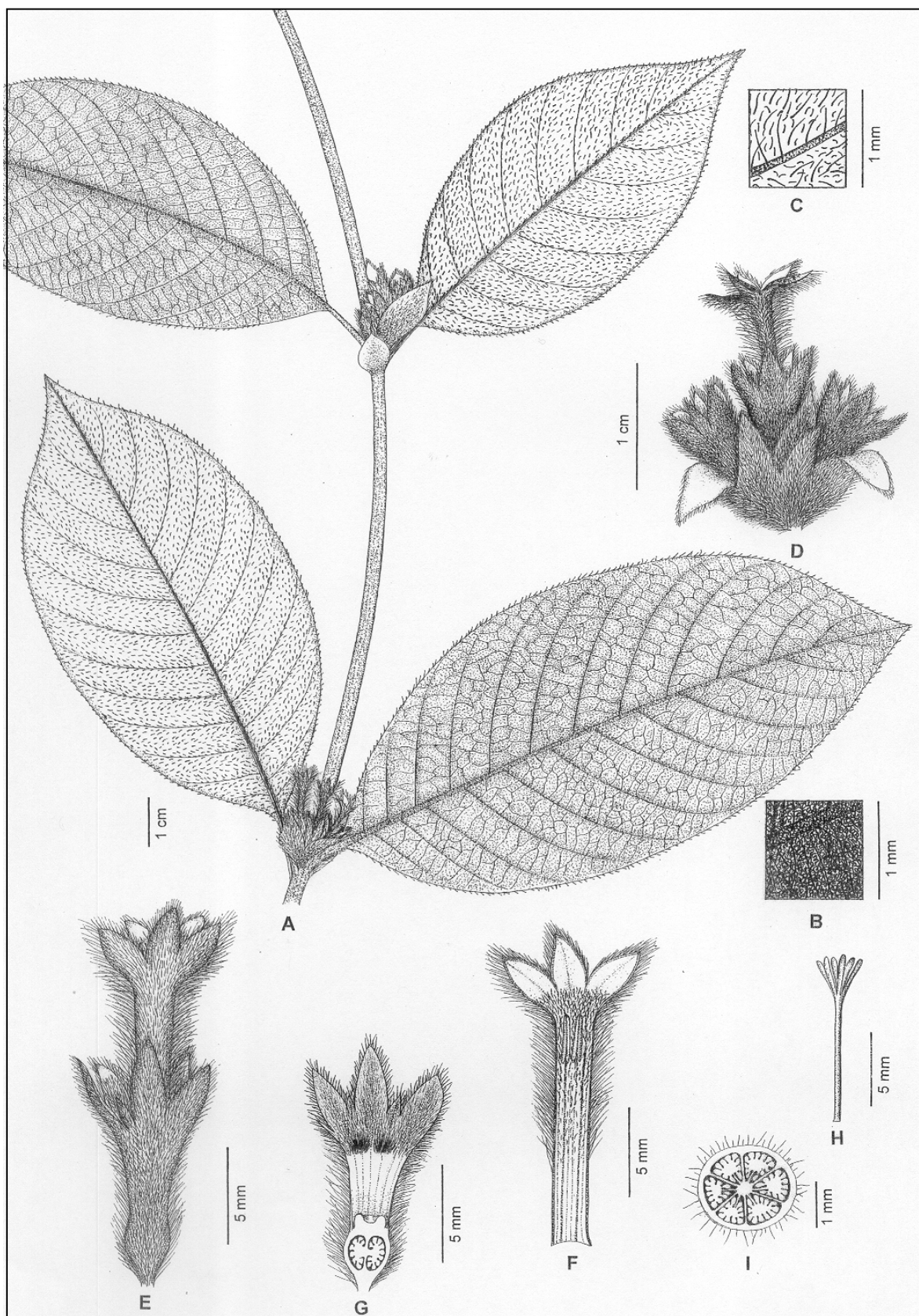


Figure 32. A–I. *Sabicea mollissima* var. *mollissima*. —A. Part of flowering branchlet. —B. Indumentum of lower leaf surface. —C. Indumentum of upper leaf surface. —D. Inflorescence. —E. Flower. —G. Longitudinal section through calyx and ovary showing colleter's location inside the calyx tube. —F. Inner corolla surface showing anther's position. —H. Style and stigmas

ciliolate with (0.2–)0.5–1.3 mm long cilia, adaxially lamina puberulous to pubescent, costa densely pubescent to moderately velvety, trichomes 0.1–1.5 mm long; abaxially lamina sparsely villosulous to pubescent, densely arachnose or lanate to lanuginose, costa and secondary veins densely villosulous and arachnose or lanate to lanuginose, trichomes (0.9–)2.1–2.8 mm long, secondary veins 9–14 pairs, (sub-)sulcate or plain adaxially, protruding abaxially, tertiary veins usually indistinct abaxially; *petioles* (2–)3–8(–13) mm long. *Inflorescences* one per node, (1–)3–5-flowered, compact-fascicled, 1.5–2.3(–2.5) × 1.5–2 cm; *peduncles* 0(–4) mm long; *bracts* (sub-)involucrate, papyraceous, (9–)12–15 × 7–8 mm, 3–4-lobed, lobes widely lanceolate to narrowly ovate or triangular to lingulate, 1–9 × 1–5 mm, apically acute, margins entire to denticulate, ciliolate with (0.4–)0.6–1.2(–1.5) mm long cilia, adaxially sparsely to densely sericeous almost all over, trichomes 0.20–1(–1.3) mm long, abaxially densely villosulous or pilosulous and arachnose, trichomes 0.7–1.7(–1.8) mm long, flexuose (&1), bracteoles 5–9(–11) × 2–5 mm, elliptic or oblanceolate, apically acute or acuminate. *Flowers* sessile, *calyx* infundibuliform, 5–7(–10)-lobed, tubes 3–7(–9) × (1.4–)1.8–4.5 mm, lobes (1–)2–6(–9) × (0.5–)1–2 mm, antrorse, narrowly elliptic to lingulate to triangular or lanceolate, apically acute to obtuse, adaxially covered with shaggy sericeous to villosulous indumentum, trichomes 0.2–1.4(–1.6) mm long, abaxially densely villosulous and arachnose, trichomes (0.6–)1.1–1.6–2.10 mm long; *corolla* salverform, tubes 7–14(–15) mm long, lobes 1.5–2.5(–5) × 1–1.5 mm, ovate, antrorse, apically acute, adaxially the indumentum of orifice extends up to 5–7 mm, abaxially densely villosulous, isolatedly to sparsely arachnose, trichomes 1.6–2.8 mm long; *stamens* 5 per flower, attached to corolla tube at 10–11 mm from the base, anthers 1.8–2.1(–2.5) mm; *style* 7–8(–11) mm long, stigmatic lobes 5–6, 1.3–1.8 × 0.06–0.1 mm; *ovaries* abaxially uneven, 5–6-locular, each locule 1.5–2 × 0.9–1.5 mm. *Fruits* reddish, 6–8 × 6–8 mm, abaxially sparsely arachnose to sericeous or villosulous; *seeds* 0.5–0.8 × 0.5–0.6 mm.

*Phenology, distribution and habitat.* Flowering from January to April and July to November and fruiting from July to August. This species is distributed in Suriname and northeast to northern Brazil. It is found in open savanna bordered by forest and low scrub, savanna near coastal region, open exposure, on secondary growth near airstrip; 125–450 m (Fig. 6).

*Discussion.* *Sabicea mollissima* is characterized by its arachnose or lanate to lanuginose in addition to villosulous or pubescent indumentum of branchlets and abaxial surface of stipules, leaves and inflorescences excluding corolla, adaxially pubescent leaf blades (Fig. 32B); infundibuliform calyces with antrorse and lanceolate to narrowly ovate or triangular to lingulate lobes, erect to erecto-patent cilia at the margins of bracts and calyces, dense indumentum at the upper part inside the bracts, location of colleters near the middle to basal part inside the calyx tubes, and shaggy indumentum inside the calyces that usually completely covers the

colleters (Fig. 32G). It is known only from type specimen. *Sabicea romboutsii* seems different from Wernham's *S. mollissima* in the shape of its calyx lobes that is usually triangular to widely lanceolate, occasionally lingulate with narrow upper part or apices. In *Sabicea mollissima*, the shape of calyx lobes is variable from lingulate with narrow upper part or lanceolate to triangular. The costa and secondary veins of abaxial surface of leaves of *Sabicea romboutsii* (Rombouts 522 & 320) seem exposed (in contrast to completely covered with indumentum) due to the isolated to sparse arachnoid indumentum. The variation in these notable characters is not found as distinct in the examined specimens. However, *Sabicea romboutsii* appears as differentiable from *S. mollissima* only on the basis of lengths-breadth ratios of calyx lobes. Therefore, we have merged *Sabicea romboutsii* with *S. mollissima* with maintaining it as a separate variety based on just this quantitative character.

We agree with Bremekamp (1936) in considering *Sabicea traillii*, *S. amazonensis*, and *S. romboutsii* (here synonymized under *S. mollissima*) as close allies. Bremekamp mentioned that *Sabicea romboutsii* resembles *S. brasiliensis* and *S. camporum*, which is not confirmed in this study. *Sabicea mollissima* differs from its closest ally *S. amazonensis* by its shorter corolla and inflorescences, adaxially pubescent leaf blades, abaxially partially arachnose stipules, and completely arachnose bracts and calyces, and shaggy indumentum of adaxial surface of calyx lobes (see *Sabicea amazonensis* for contrasting characters). Due to the almost similar infundibuliform calyces, *Sabicea mollissima* appears close to *S. surinamensis* and *S. traillii*, from which it is distinct by its arachnose indumentum at branchlets, lower leaf surfaces leaves, and adaxial sides of bracts and calyces as well as shaggy indumentum inside the calyces, which usually covers the colleters. *Sabicea mollissima* superficially appears close to *S. velutina* by its almost identical inflorescences, and dense arachnose or lanate to lanuginose indumentum of abaxial surface of stipules, leaf blades, bracts and calyces. However, it is distinct from *Sabicea velutina* by its infundibuliform calyces, shorter (0.1–1.5 mm in contrast to [1.5–]2–2.3 mm) trichomes at the adaxial surface of leaves, manifestly straight trichomes at abaxial surface of leaves and outer surface of inflorescences, location of colleters below the sinus near the middle to basal part inside the calyx tubes, shaggy indumentum inside the calyces from apex up to the base of colleters that usually completely covers the colleters. The collection *Guanchez & Melqueiro 3674* (MO) is found as an intermediate of *Sabicea amazonensis* and *S. mollissima*. Both of the two syntypes of *Sabicea mollissima* (*R. Spruce 320*, M!, photo F, MO, NY! and *R. Spruce 684*) are seen in good condition. We select *Spruce 684* (BM) as the lectotype as it appeared better than the other.

#### Key to the varieties:

1a. Length-breadth ratio of calyx lobes (2.5–)3.6–4.5, calyx tubes usually 3–5 mm long

.....25a. *S. mollissima* var. *mollissima*

- 1b. Length-breadth ratio of calyx lobes (1.1–)1.3–1.8(–2.3), calyx tubes usually 4–9 mm long.....25b. *S. mollissima* var. *romboutsii*

**25a. *Sabicea mollissima* Benth. ex Wernham var. *mollissima***

Known only from type specimens.

**25b. *Sabicea mollissima* Benth. ex Wernham var. *romboutsii* (Bremek.) Liede, Meve & Khan, comb. et stat. nov.**

*Sabicea romboutsii* Bremek., Recueil Trav. Bot. Neerl. 33: 709. 1936. TYPE: Suriname. Sipaliwini: Granielberg, Kamp 22, at outcrops at granite in the savannah near Brazilian border, 03 Mar. 1936 (fl), *H. E. Rombouts* 522 (holotype, U!, photo NY!; isotypes, BR!, K!).

*Additional specimens examined.* BRASIL. **Amapá:** Macapá, Curiaú, *Fróes* 27370 (U), Porto Platon, na estrada Porto Santana Porto Platon, Km 100, *Mattos & Mattos* 10001 (US); 48 km, road to Amapa, *Pires & Cavalcante* 5197 (NY). **Amazonas:** Maués Airport Road, between Maués and airport, *Campbell et al.* P22154 (US, NY, U). **Pará:** In vicinibu Santarém, *Spruce s.n.* (NY, W); Melgaço, Estação Científica Ferreira Penna, margem direita do Rio Caxiuanã, baía de Caxiuanã, *Silva et al.* 3143 (NY); Macau airstrip, 1/2 hrs, upstream from Lageira airstrip, on Rio Maicuru, *Strudwick et al.* 3479 (MO); Sere Varas airstrip on Rio Curua, *Strudwick et al.* 4361 (MO, NY, WIS). FRENCH GUIANA. Roche Koutou-Bassin du Haut-Marouini, Autour du sommet de l'inselberg, Broussaille autour du sommet, *Granville et al.* 9411 (U); Bassin du Ha, Camp N°3-Roche N°1 Akouba Booka goo Soula-Bassin du Ha 500 m au Sud-Ouest, *Granville et al.* 9767 (NY, U); Saül, Savane-roche Dachine, forêt claire sur inselberg, face nord de l'inselberg, *Cremers & Crozier* 14682 (MO, NY, U); Mont Saint-Marcel, zone sud-est du massif, *Granville et al.* 15306 (MO); Monts d'Arawa, Savane-roche centrale, *Granville et al.* 15214 (MO). SURINAME. **Sipaliwini:** Sipaliwini Sip., In Savannis ps. Kamp. 22, *Rombouts* 543 (K, MO, U). Savanna area Brazilian frontier, South of "4-Gebroeders" Mts, *Oldenburger et al.* 162, (K, U), *Oldenburger et al.* 835, (U); American Village on Lawa River, *Hammel* 21210 (MO).

**26. *Sabicea morillorum* Steyerl., Fl. Venezuela 9: 511. 1974. TYPE: Venezuela. Territo Río Federal Amazonas, Chaparal, 2–3 km N San Carlos de Río Negro, carretera San Carlos-Solano, 100 m, 24 Apr. 1974 (fl), *G. Morillo, B. de Morillo & C. Wood* 3903 (holotype, VEN, not seen; isotype, NY!). Figure 33A–I.**

Scandent; *terminal flowering branchlets* densely arachnose to lanuginose, eventually glabrescent. *Stipules* narrowly ovate to elliptic, antrorse to (sub-)reflexed, 6–8 × 2.6–3.8 mm,

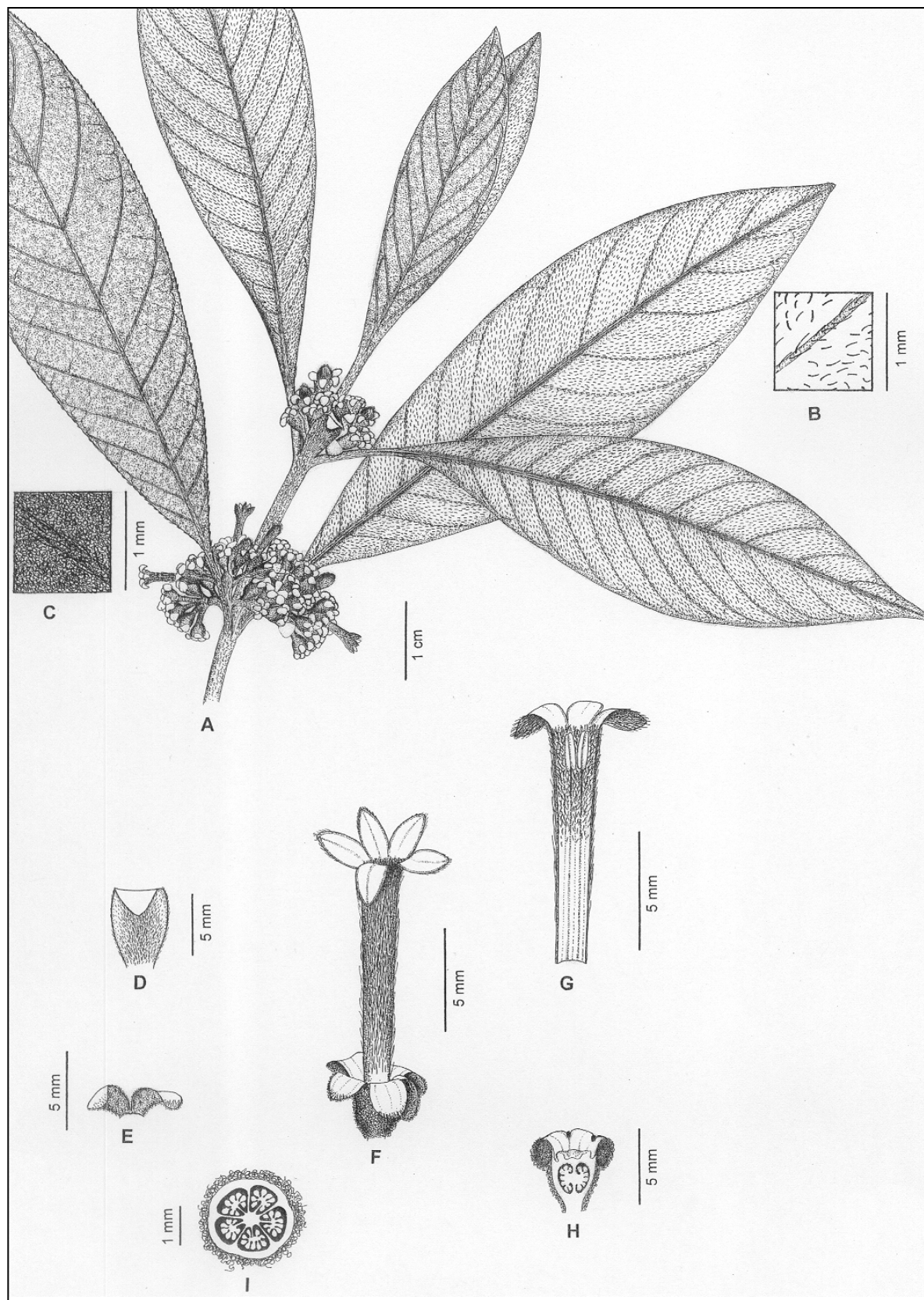


Figure 33. A–I. *Sabicea morillorum*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Outer stipule surface. —E. Side view of bract. —F. Flower. —G. Inner corolla surface showing anther's position. —H. Longitudinal section through calyx and ovary. —I. Transversal section through ovary.

apically (sub-)acute to obtuse, membranous, margins entire, complanate, ciliolate with 0.1–0.5 mm long cilia, adaxially glabrous excluding the basal part, abaxially densely arachnose to lanuginose, and sparsely to densely strigulose all over, trichomes 0.1–0.7 mm long, colleters 5–7, 0.2–0.4 mm long. *Leaf blades* elliptic to oblong, 3.5–8.5 × 1.5–2.5 cm, apically and basally acute, membranous, ciliolate with 0.2–0.7 mm long cilia, adaxially sparsely hirtellous to puberulous at lamina and secondary veins, densely at costa, trichomes 0.07–0.8 mm long, abaxially densely arachnose, at lamina, sparsely to densely strigulose to pubescent and densely arachnose at costa and secondary veins, trichomes 0.6–2 mm long, secondary veins 10–13 pairs, plain adaxially, protruding abaxially, tertiary veins occasionally distinct abaxially; *petioles* 5–10 mm long. *Inflorescences* two per node, (16–)18–30-flowered, moderately lax- to compact-paniculate, 1.5–2.2 × 2.5–3.6 cm, primary axis 2–5 mm long, main lateral axes 2–4, simple to compound dichasia or paniculate; *peduncles* 5–7 mm long; *bracts* (sub-)exinvolucrate, membranous, incompletely isolated into 2–3 parts, isolated parts 5–7 × 3–5 mm, 2-lobed, lobes 2.5–3.5 × 2–3 mm, ovate to deltate or suborbicular, apically obtuse to subacute, margins entire, adaxially glabrous or isolatedly strigulose or puberulous near apices in addition to the basal part, trichomes 0.07–0.2 mm long, abaxially densely arachnose almost all over, bracteoles 1–4.5 × 0.6–4 mm, ovate to deltate or lingulate to elliptic, apically (sub-)acute to obtuse, margins entire, colleters (0–)2. *Flowers* pedicellate, pedicels (1–)2–5 mm long, *calyx* campanulate, 5-lobed, tubes (0.5–)0.6–1 × 1.5–1.8(–2.1) mm, lobes (0.5–)0.8–2.4(–2.8) × 0.6–1.8(–2.1) mm, usually spreaded to reflexed, ovate to obovate or widely lingulate to suborbicular, apically obtuse to subacute, margins entire, ciliolate with 0.1–0.4 mm long cilia, adaxially glabrous to isolatedly puberulous at the apices, trichomes 0.07–0.2 mm long, abaxially densely arachnose, usually 3-ribbed, colleters 1–2 in each sinus, 0.1–0.2 mm long, *corolla* white, salverform, tubes 7.5–10.5 × 0.9–1.8 mm, lobes (1.5–)2–2.5 × 1–1.5 mm, ovate to widely lanceolate, antrorse, apically (sub-)acute, adaxially the indumentum of orifice extends up to 4–6.7 mm inside the tubes, abaxially densely sericeous to pilosulous, trichomes 0.10.1–0.5 mm long; *stamens* 5 per flower, attached to corolla tube at 5.6–9.2 mm from the base, anthers 1.7–2 × 0.2–0.4 mm; *style* 4.5–7.5 mm long, stigmatic lobes 1.6–2.1 × 0.1–0.2 mm; *ovaries* 1.2–2 × 1.2–2.4 mm, abaxially uneven to slightly 5-lobed, densely arachnose, 5-locular, each locule 0.9–1.1 × 0.5–0.7 mm. *Fruits & seeds* not seen.

*Phenology, distribution and habitat.* Flowering in April. Endemic to Venezuela. Steyermark (1974) mentioned its distribution in southwest Venezuela and territory of Federal Amazonas. It occurs on white sandy ground in Chaparral with low vegetation surrounded by forests; floodable land to 100 m (Fig. 9).

*Discussion.* *Sabicea morillorum* seems close to *S. calophylla* from which it distinct by its shorter petioles, abaxially densely arachnose to lanuginose stipules, bracts, hypanthium and



calyces, reflexed and ciliolate calyx lobes, and bracts and calyx lobes that are apically adaxially glabrous to isolatedly covered with trichomes (Fig. 33E, F, H). It differs from *Sabicea calophylla* also by its apically acute and adaxially hirtellous to puberulous leaf blades and narrower (2.6–3.8 mm) stipules. *Sabicea morillorum* seems near to *S. cuneata* due to its almost similar inflorescences and arachnoid to lanuginose indumentum. It is distinct from *Sabicea cuneata* by its arachnose branchlets, peduncles, pedicels and abaxial surface of bracts, hypanthium, and calyces and reflexed-, lingulate- to subglobose-calyx lobes with obtuse apices, shorter (generally 0.8–2.4 mm in contrast to 2.6–3.5 mm) calyx lobes, and adaxially (excluding the base) glabrous stipules and bracts.

*Additional specimens examined.* VENEZUELA. **Amazonas:** 12–15 km NE de San Carlos de Río Negro, cerratera San Carlos-Solano, *Morillo et al.* 4176 (paratype; MO, US).

**27. *Sabicea noelii*** Liede, Meve & Khan, sp. nov. TYPE: Bolivia. Santa Cruz: Velasco, Parque Nacional Noel Kempff M. Los Fierros, 2 km al NW del Campamento Flor de Oro, frontera con Rondônia, 13°32'S, 61°01'W, 200 m, 15 Nov. 1993 (fl), *Gutiérrez, Killeen & Quevedo* 446 (holotype, MO!). Figure 34A–N.

*Species lobis calycum longis, linearis ad lingulatis, et antrorsis, trichomatibus ramulorum, foliorum, pedunculorum et tuborum corollarum abaxialium brevibus et erecto-patentibus, colleteres calycum sub sinuibus locatis.*

Creeping herbs, subshrubs or shrubs; stems 0.5–1.1 m long; terminal flowering branchlets densely pubescent to hirtellous, sometimes strigulose, trichomes 0.1–0.9(–1.2) mm long. *Stipules* widely ovate, antrorse, 3.5–4.2 × 2.6 mm, apically acute, papyraceous, ciliolate with 0.07–0.3(–0.6) mm long cilia, adaxially glabrous excluding the basal part, abaxially densely strigulose, eventually glabrate at the apices, trichomes (0.07–)0.2–0.8 mm long, 5–7-veined, colleters 4–7(–9) × (0.4–)0.6–0.8 mm long. *Leaf blades* narrowly ovate to oblong or lanceolate, (1.5–)4.2–9 × (1–)2–4.5 cm, apically acute to obtuse, basally (sub-)acute to obtuse to slightly (sub-)cordate, papyraceous, cilia (0.07–)0.1–0.7 mm long; adaxially lamina sparsely to moderately densely hirtellous to puberulous, costa densely hirtellous to puberulous or strigulose, trichomes (0.07–)0.1–0.7 mm long, curved; abaxially fulvous, lamina densely hirtellous, to puberulous, costa and lateral veins densely hirtellous to strigulose or sericeous, and puberulous, (0.7–)1.2–1.6 mm long, secondary veins 8–12 pairs, plain adaxially; *petioles* (2–)6–15 mm long. *Inflorescences* one to two per node, (3–)5–12(–21)-flowered, capitate to compact-fascicled, 1.5–3 × 1–3 cm excluding (0–)2–6(–11) mm long peduncles, main inflorescence branches 0–3, main axes 0–5 mm long; *bracts* (sub-)exinvolucrate, papyraceous, incompletely isolated into 2–3 parts, isolated parts (1.8–)3–7 × (1.2–)2–6 mm, rarely 1–2-lobed, lobes 1.2–1.5 × 0.3–0.6 mm, ovate to deltate or lanceolate,



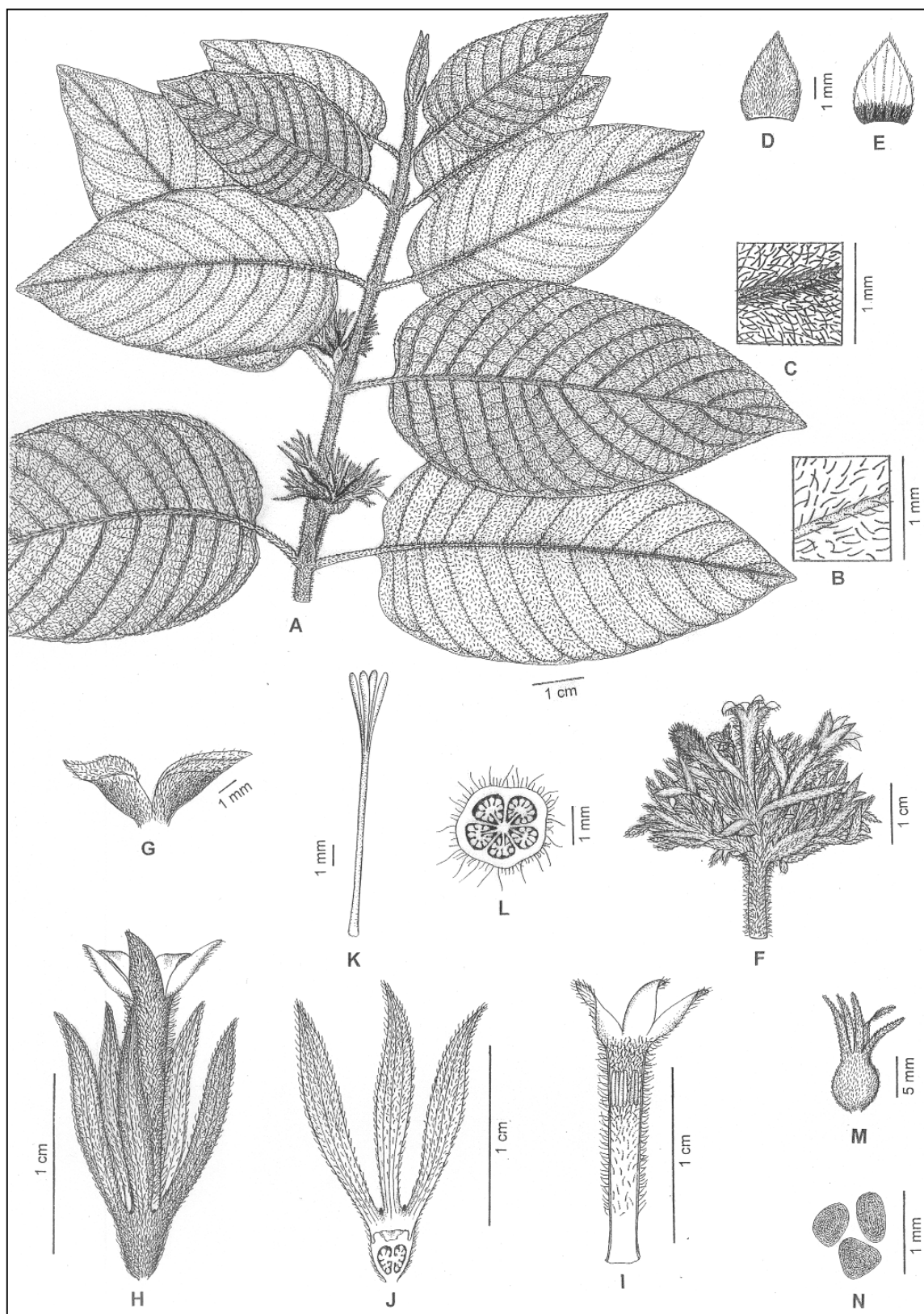


Figure 34. A–N. *Sabicea noelii*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Outer stipule surface. —E. Inner stipule surface showing colleters at the base. —F. Inflorescence. —G. Side view of bract. —H. Flower. —I. Inner corolla surface showing anther's position. —J. Longitudinal section through calyx and ovary. —K. Style and stigmas. —L. Transversal section through ovary. —M. Immature fruit. —N. seeds.

apically acute to obtuse, ciliolate with (0.07–)0.3–0.7 mm long cilia, adaxially upper part sparsely strigulose excluding the basal part, abaxially sparsely to densely strigulose, sometimes glabrate towards the apices, bracteoles lanceolate to lingulate, (2.5–)3–6.5 × 0.8–2.4 mm, apically acute or acuminate, colleters 2, 0.2–0.3 mm long. *Flowers* (sub-)sessile, pedicels 0 (–1.5) mm long; *calyx* campanulate, 5(–6)-lobed, tubes 1.5–1.8(–2.1) × 2.5–3.2 mm, lobes (1.8–)5–11 × (0.3–)1–2.1 mm, antrorse to spreaded, very narrowly elliptic to lingulate or linear to widely lanceolate, apically (sub-)acute, margins usually shallowly denticulate, ciliolate with 0.4–0.7 mm long cilia, adaxially lobes isolatedly to sparsely strigulose trichomes (0.07–)0.1–0.5 mm long, abaxially sparsely to densely) strigulose all over, trichomes (0.5–)0.2–0.7(–1.1) mm long, lobes 3(–5)-ribbed, colleters 1–2, slightly below the sinus, 0.3–0.5 mm long; *corolla* white, salverform, tubes 12–13 × 1–2 mm, lobes (2.7–)3.5–4.2 × 1.2–1.8 mm, widely lanceolate or narrowly ovate, antrorse or spreaded, apically (sub-)acute, adaxially the indumentum of orifice extends up to 4.1–5.3 mm inside the tubes, abaxially densely pilosulous to strigulose, trichomes (0.3–)1.2–1.5 mm long; *stamens* 5 per flower, attached to corolla tube at 8.2–9.7 mm from the base, anthers 2–2.2 × 0.3–0.4 mm; *style* 9.5–12 mm long, stigmatic lobes 4–5, (2.1–)2.8–3.2 × 0.3–0.4 mm; *ovaries* 1.2–1.5 × 1.2–1.5 mm, abaxially shallowly 5-lobed or uneven, densely strigulose, 4–5-locular, each locule 0.8–1.1 × 0.4–0.5 mm. *Fruits* 4–6 × 4–6 mm when immature, color unknown, abaxially isolatedly or sparsely strigulose; *seeds* 0.6–0.8 × 0.5–0.8 mm.

*Phenology, distribution and habitat.* Flowering in February–March and November. *Sabicea noelii* is reported from the northern La Paz and northeast Santa Cruz Departments of Bolivia. It is collected from argillaceous-sandy grounds of humid savannas or pampas or from the transition zone between forest and pampas (Fig. 14).

*Discussion.* This species is characterized by its long, linear to lingulate, and antrorse calyx lobes, short, uniform and erecto-patent trichomes on branchlets (Fig. 34A, B), both surfaces of leaves, the leaf-bases are shallowly cordate leaf bases, erecto-patent trichomes outside the corolla tubes, sparsely to densely pubescent inner surface of bracts and calyx lobes, and colleters located below the sinus. Among the Neotropical *Sabicea*, only *S. chocoana* has similar trichomes, but *S. noelii* it clearly by its manifestly compact inflorescences comprised of sessile flowers, antrorse to spreading and longer ([1.8–]5–11 mm in contrast to [0.3–]1.2–2.2 mm) calyx lobes (Fig. 34H), and colleter's location inside the calyces slightly below the sinus. It seems closely allied to *Sabicea burchellii* due to almost similar inflorescences and calyx lobes, though it differs by apparently erecto-patent trichomes on the leaves and outer surface of corolla tubes, shorter stipules, longer calyx tubes, colleter's location below the sinus, shorter (0.2–0.7 mm in contrast to 0.7–1.1 mm) and longer (1.2–1.5 mm in contrast to 0.7–1.1 mm) trichomes on outer surface of calyx lobes and corolla tubes respectively, and longer

corolla tubes.

It differs from *Sabicea aspera* by its larger and antrorse to spreaded calyx lobes (usually  $5\text{--}8 \times 1\text{--}2.1$  mm in contrast to  $0.8\text{--}4 \times 0.5\text{--}0.9$  mm) and indumentum at upper inner surface of bracts and calyx lobes. Like *Sabicea aspera*, this is transitional for the pedunculate and non-pedunculate species. *Sabicea noelii* differs from both *S. grisea* and *S. trianae* by its apparently non-arachnoid indumentum at branchlets, lower surface of leaves, and outer surface of stipules, bracts, and calyces, and usually distinct peduncles. *Sabicea noelii* superficially appears close to some *S. novo-granatensis* specimens from Venezuela with compact inflorescences and narrowly elliptic or lingulate calyx lobes but it is distinct by its capitate to compact-fascicled inflorescences, short trichomes of leaves, adaxially glabrous and smaller ( $3.5\text{--}4.2 \times 2.6$  mm in contrast to  $7\text{--}16 \times 5\text{--}14$  mm) stipules, and strigulose trichomes of hypanthium.

*Additional specimens examined.* BOLIVIA. **Santa Cruz:** 5 km camino al aserradero Tarbo, Pampa inundada,  $14^{\circ}35'S$ ,  $60^{\circ}53'W$ , *Gutiérrez et al.* 794 (MO), Pampa Toledo, Parcela permanente en estudio,  $14^{\circ}37'15''S$ ,  $60^{\circ}51'10''W$ , *Gutiérrez et al.* 737 (MO), Velasco, Parque Nacional Noel Kempff Mercado, a 10 km del campamento Los Fierros,  $14^{\circ}36'39''S$ ,  $60^{\circ}51'35''W$ , *Jiménez et al.* 1158 (MO). **La Paz:** Iturralde, Luisita, W del Río Beni, *Beck & Haase* 9928 (NY), *Beck & Haase* 10056 (NY).

**28. *Sabicea novo-granatensis*** K. Schum., Fl. Bras. 6(6): 303. 1889. TYPE: Colombia.

Cundinamarca: Guaduas, Magdalena valley, no date (fl), *Karsten s.n.* (holotype, B, not seen, presumably destroyed, photo F!; isotypes, G!, MO!, NY!, W!). Figure 35A–P, 34A–F (Steyermark, 1967).

*Sabicea cinerea* Karst. non Aubl. ex K. Schum., *loc. cit.*

*Sabicea aristeguietae* Steyermark., Mem. New York Bot. Gard. 17(1): 309, f. 34, 1967. TYPE:

Venezuela. Barinas: Cerca de Ciudad Bolivia (Pedraza), Feb. 1953, *L. Aristeguieta* 1649 (holotype, VEN, not seen, photo VEN!).

*Sabicea sastrei* Steyermark., Brittonia, 33(3): 398. 1981. TYPE: Colombia. Meta: Chemin

longeant le Río Guatequia, 12 km en amont de Villavicencio, Quebrada de la Mendoza, 4 Mar. 1971, *C. Sastre* 934 (holotype, P!; isotype [photo], VEN!).

Plants woody climbers to suffrutescent vines; stems ca. 1.5 m tall; terminal flowering branchlets densely pilosulous to villosulous or hirtellous, and sparsely to densely puberulous, trichomes, (0.07–)0.4–1.8(–2.3) mm long. *Stipules* widely ovate to triangular or oblong, (7–)10–12(–16)  $\times$  5–12(–14) mm, membranous, reflexed, apically acute, margins entire, ciliolate with (0.1–)0.2–0.8 mm long cilia, adaxially isolatedly to densely strigulose to puberulous all over or on lower part and glabrous to glabrescent on upper part in addition to sericeous basal

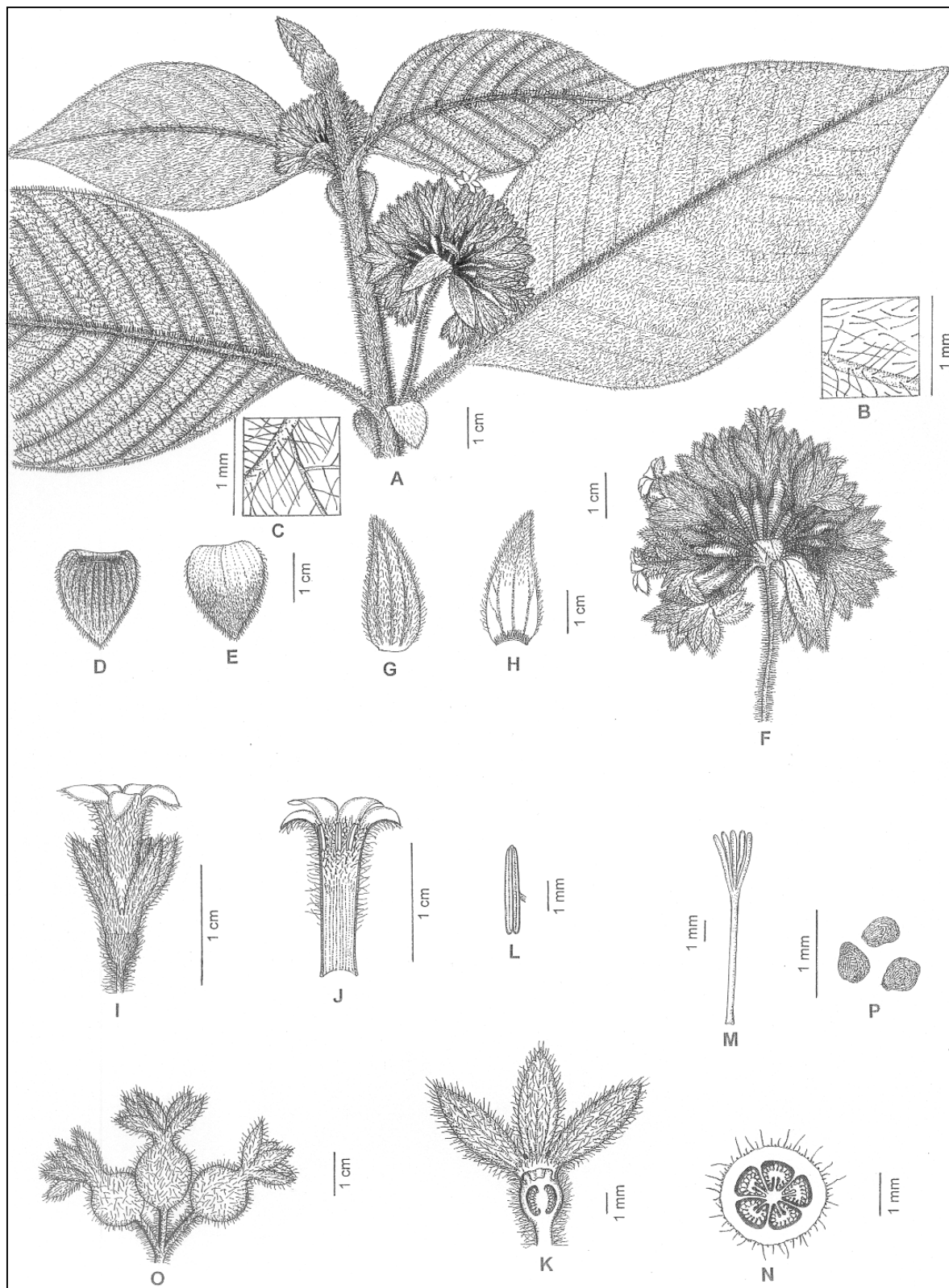


Figure 35. A–P. *Sabicea novo-granatensis*. A. —A part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Outer stipule surface. —E. Inner stipule surface. —F. Inflorescence. —G. Outer bract surface. —H. Inner bract surface. —I. Flower. —J. Inner corolla surface showing anther's position. —K. Longitudinal section through calyx and ovary. —L. Face view of Anther. —M. Style and stigmas. —N. Transversal section through ovary. —O. Fruits. —P. Seeds.

part, trichomes (0.1–)0.2–1.2(–1.5) mm long, abaxially usually densely pilosulous to pubescent, sometimes strigulose all over, trichomes (0.1–)0.2–1.2 mm long, 11–18-veined, colleters 8–12, 0.5–0.8 mm long. *Leaf blades* ovate to widely lanceolate or elliptic to oblong, (4–)7–15(–17) cm long, (1.5–)2.5–5.5(–7.5) cm wide, apically acute to acuminate, papyraceous, margins entire, ciliolate with 0.4–1.1(–1.6) mm long cilia, adaxially densely pilosulous to villosulous or puberulous, occasionally tomentulose all over, trichomes, (0.07–)0.2–1.8(–2.3) mm long, abaxially sparsely to densely pilosulous to villosulous, occasionally sparsely puberulous at lamina and lateral veins, relatively more densely at costa, trichomes 0.5–1.5(–1.7) mm long; lateral veins 9–15 pairs, costa and lateral veins protruding abaxially and plain or distinct adaxially; petioles (3–)5–25(–35) mm long. *Inflorescences* one per node, (4–)8–16(–26)-flowered, moderately lax- to compact-umbellate, 2–2.5(–3.5) × 2.5–4(–5) cm, main axes 0.5–1.2 mm long; *peduncles* 2–25(–35) mm long; *bracts* (sub-)exinvolucrate, membranous to papyraceous, incompletely isolated into 2–5 parts, 7–16(–30) × 8–10 mm when subinvolucrate, isolated parts 7–12(–26) × 4–6 mm, 0–5-lobed, lobes 1–27 × 3–10 mm wide, widely lanceolate to deltate or ovate, apically (sub-)acute, rarely acuminate, margins entire, ciliolate with 0.2–1.1 mm long cilia, adaxially usually sparsely to densely strigulose to puberulous, occasionally glabrescent on upper part in addition to the basal part, abaxially usually densely pilosulous to puberulous all over, bracteole 1.4–6 × 0.2–2.1 mm, widely lanceolate to ovate or oblong to elliptic, colleters 1–3(–5), 0.4–0.5 mm long. *Flowers* pedicellate, pedicels (1.8–)3–6.5(–8.5) mm long; *calyx* campanulate, 5-lobed, tubes 0.6–1.4(–2) × 0.8–1.7(–2.5) mm, lobes (4–)5, (2.6–)4–9(–11) × (0.5–)1.2–3(–4) mm, usually antrorse, elliptic, occasionally lingulate, rarely widely lanceolate or ovate, apically acute to acuminate or obtuse, margins entire, ciliolate with 0.2–1.1 mm long cilia, adaxially sparsely to densely strigulose to puberulous, rarely glabrescent, abaxially densely to sparsely pilosulous, rarely glabrescent, trichomes (0.4–)0.8–1.1 mm long, 3–5-ribbed with costa, ribs abaxially prominulous, adaxially plain, colleters 1(–2) in each sinus, 0.1–0.20.2 mm long; *corolla* white, salverform, tubes (6–)8–10(–11) × 1.7–2.4 mm, lobes 2.4–3.8 × 1.1–2.4 mm, ovate, antrorse to slightly reflexed, apically (sub-)acute, adaxially the indumentum of orifice extends up to 4.1–4.6 mm inside the tubes, abaxially densely pilosulous, trichomes (0.5–)0.7–1.4(–2) mm long; *stamens* 4(–5) per flower, attached to corolla tube at (5.6–)6.5–7.2(–8.2) mm from the base, anthers 1.4–2(–3.2) × 0.3–0.6 mm; *style* 3.5–6(–7.7) mm long, stigmatic lobes (4–)5, (1.5–)1.7–2.3(–2.9) × 0.2 mm, narrowly lingulate to oblanceolate; *ovaries* 2–2.5 × 2–2.2 mm, outer surface slightly irregularly 5-lobed or uneven, densely to sparsely pilosulous to puberulous, rarely glabrescent, 5-locular, each locule 1.5–2 × 0.6–0.7 mm wide. *Fruits* dark red to black, 7–11 × 8–10 mm when mature, abaxially isolatedly to sparsely pilosulous to puberulous; *seeds* 0.4–0.5 × 0.3–0.5 mm.

*Phenology, distribution and habitat.* Flowering from March to April and June to January and fruiting in March and September to November. Recorded mainly from the northern Andean

(Paramo) region. In Colombia, it occurs at 0–770 m, only. Generally it is confined in dry scrubs, along roads, in and around forests and along streams as secondary thickets or undergrowths; 0–1500 m (Fig. 9).

*Discussion.* *Sabicea novo-granatensis* is characterized by its moderately lax- to compact-umbellate inflorescences, erect to erecto-patent trichomes at branchlets, leaves, and outer surface of stipules and inflorescences including corolla, indumentum at the upper part or apices of adaxial surface of stipules, bracts and calyces and usually elliptic and large calyx lobes (Fig. 35A-I). Schumann (1889) mentioned the sepals of this species as ovate that are in fact elliptic, rarely widely lanceolate or ovate. *Sabicea aristeguietae* from Venezuela is not distinct from Colombian *S. novo-granatensis* with variable size of inflorescences and shape and size of calyx lobes. *Sabicea aristeguietae* seems different from *S. novo-granatensis* basically due to its lanceolate to narrowly elliptic leaves, usually few-flowered inflorescences and narrowly elliptic calyx lobes in contrast to the generally ovate to widely elliptic leaves, usually many-flowered inflorescences and widely elliptic calyx lobes of *S. novo-granatensis*. On the other hand, the specimens of these two species with longer (i.e. 5.5 mm) peduncles usually have ovate to widely elliptic leaves, dense indumentum consisting of longer and flexuous trichomes and many flowers, whereas, those with peduncles less than 5 mm long usually possess lanceolate to narrowly elliptic leaves, sparse to dense indumentum consisting of relatively shorter and almost straight trichomes and few flowers. However, none of these variations has been found to be discrete with regard to these two species or the groups of their specimens. Therefore, we have merged *Sabicea aristeguietae* with *S. novo-granatensis* and avoided the consideration of two or more infraspecific taxa within this group, as the overlap between the entities described above is too large to permit their recognition. The species-specific characters of *Sabicea sastrei* as noted by Steyermark (1981b) are found as well in range of typical *Sabicea novo-granatensis*. These characters are also not consistent in the Colombian or Venezuelan specimens of *Sabicea novo-granatensis*. Therefore, we have synonymized *Sabicea sastrei* under *S. novo-granatensis*.

Schumann (1889) distinguished *Sabicea novo-granatensis* by its ovate sepals and large leaves. Based on these two characters, it is impossible to recognize this species from *Sabicea mattogrossensis*. *Sabicea novo-granatensis* seems very similar to *S. mattogrossensis* with regard to the inflorescences and calyx lobes. However, *Sabicea novo-granatensis* is easily distinguished from *S. mattogrossensis* by its dense-pilosulous to villosulous and puberulous indumentum on adaxial leaf surfaces comprised of mostly longer trichomes, patent indumentum on abaxial surface of leaves and corolla tubes, indumentum of adaxial surface of stipules, bracts, pedicels, hypanthium, and calyx lobes.

*Sabicea novo-granatensis* seems closely allied to *S. hirta* due to similar inflorescences, calyces and indumentum. However, it is distinguishable from *Sabicea hirta* by its stipules that are not wider than long and basally always obtuse and adaxially strigulose to puberulous

(excl. base), (sub-)exinvolucrate bracts with 1–3(–5) colleters at the margins of the base, adaxially strigulose to puberulous, apically acute to acuminate, and obtuse calyces with 1(–2) colleters in each sinus. Some *Sabicea novo-granatensis* specimens, especially those from Venezuela, are reminiscent of *S. liesneri* from which they differ by their compact-umbellate and unbranched inflorescences, larger and usually equal calyx lobes and longer corolla tubes externally covered with longer external trichomes, and longer corolla lobes. *Sabicea novo-granatensis* is distinct from *S. pearcei* by its umbellate inflorescences, indumentum at the adaxial surface of stipules, bracts and calyx lobes, and narrowly to widely elliptic and larger calyx lobes. Some *Sabicea novo-granatensis* of Venezuela with compact inflorescences and narrowly elliptic or lingulate calyx lobes seem similar to *S. noelii* from which it is distinct by its moderately lax- to compact-umbellate inflorescences, longer trichomes of leaves, adaxially glabrous and larger stipules adaxially covered with indumentum, and pilosulous to puberulous indumentum of hypanthium.

Vegetatively it might not be easy to differentiate some *Sabicea novo-granatensis* of Venezuela from typical *S. villosa* var. *villosa*, but in the flowering stage they markedly differ considering the wider (usually 1.2–3 mm, in contrast to 1–1.5 mm) and usually elliptic (in contrast to narrowly lingulate to lanceolate or ovate) calyx lobes, longer corolla tubes (usually 8–10 mm in contrast to 3.5–5 mm), distinct peduncles (2–25[–35] mm in contrast to 0–0.6[–2] mm) and pedicels ([1.8–]3–6.5[–8.5] mm in contrast to 0–0.5[–1.5] mm), presence of indumentum on the adaxial side of bracts and calyx lobes, and patent indumentum on the abaxial side of the corolla tube. The collections *Berti et al.* 983–039 (BR, NY), *Steyermark et al.* 111531 (F, US), *Breteler* 4193 (M, NY, S, US,) and *Steyermark* 126880 (MO) with (sub-)sessile inflorescences seem similar to *Sabicea villosa* var. *villosa*, but they have the typical calyx lobes of *S. novo-granatensis* of Venezuela. The specimen *Barkley & Bouthillette* 38C014 (HUH) collected from Villavicencio has glabrate pedicels, hypanthium and adaxial surface of stipules. It has been included under *Sabicea novo-granatensis* due to its patent indumentum almost all over and sparse indumentum at adaxial surface of bracts and calyx tubes or lobes.

*Selected specimens examined.* COLOMBIA. **Casanare:** Tauramena, *Uribe* 4868 (MO). **Cundinamarca:** Medina, Vereo Choatal, Via Gachalá, *Stella Tellez et al.* 001 (MO). **Meta:** near Villavicencio, *Alston* 7586 (BM, US, S, U); Los Llanos, *Cuatrecasas* 4506 (F); Toward El Parrao, *Cuatrecasas* 4647 (F); 12 km SE of Villavicencio, *Haught* 2534 (F, HUH, NY, US, U); Along the Caño Rosa Blanca, *Kirkbride Jr.* 377 (MO, NY); Río Guatiquia, alrededores de Villavicencio, *Molina & Barkley* 18 M.030 (US); márgenes del río Orotoy, *Uribe* 2096 (U); between Cumaral and San Nicolas, 10 km from San Nicolas, *Zuloaga* 3899 (MO). **Valle Del Cauca:** Buenaventura, Road Queremal-Anchicaya, Km 35, *Andersson et al.* 2096 (S). **Vichada:** Río Orinoco, Puerto Carreño, *Cuatrecasas* 4056b (F, US). VENEZUELA. **Apure:** Reserve forest of San Camilo, along the Nulita River, north of the small village San Camilo (El

Null), *Steyermark et al.* 101333 (VEN). **Barinas:** 2 km from Barinitas along road to Apataderos, *Breteler* 4193 (F, G, M, US, NY, S, L, U); Near Barinitas, *Breteler* 4590 (G, US, NY, U); Pedraza, trail from El Algarrobo to Mesa de Canagua, on the eastern boundary of the Parque Nacional Sierra Nevada, 8°31′–32′N, 70°35′–39′W, *Dorr et al.* 4713 (NY). **Lara:** Along Río Pedrogoso, between Peña Blanca and Anzoátegui, *Steyermark & Rabe* 97446 (NY); Palavecino, next to the south of Terepaima, 20 km to the south of Cabudare, *Steyermark et al.* 103296 (NY); Iribarren, Laguna Negra 10–19 km south of Río Claro, 9°52′–53′N, 69°18′–20′W, *Steyermark et al.* 111531 (F, US). **Portuguesa:** Caserío Villa Rosa, 20 km E of Biscucuy, 16 Jun 1985, *Aymard et al.* 3627 (NY, MO); beside the highway at Guayabital, Case Río Las Flores, *Aymard et al.* 4222 (NY). Between Chabaquen and Córdoba, 6 km from Córdoba, *Berti et al.* 983–039 (BR, NY). Ospino, National Park El Gouache, Chorro of San Miguel, *Licata & Naño* 960 (NY, MO), Montaña La Estrella, 9°31′11.65″N, 69°34′41.33″W, *Licata et al.* 731 (MO), highway to La Estación and Palma Sola, *Stergios et al.* 3006 (MO). Throughout the Cerro Seco, adjacent areas of Cerro Córdoba, 17–20 km, Chabasquén, 9°26′–27′N, 69°54′–55′W, *Steyermark* 126880 (MO), 17.8 km. from La Estación, 30 km from Ospino, *Steyermark et al.* 126959 (MO).

**29. *Sabicea oblongifolia*** (Miq.) Steyer., Mem. New York Bot. Gard. 17(1): 316. 1967.

TYPE: Suriname. 1850 (fl), *Miquel s.n.* (lectotype, designated by Steyermark [1967], NY not seen, photo NY [6]!, K!). *Sabicea velutina* Benth. var. *oblongifolia* Miq., Linnaea 18: 615. 1844. *Sabicea glabrescens* var. *oblongifolia* (Miq.) Sandwith, Bull. Misc. Inform. Kew, 1939: 12. 1939. Figure 36A–L.

*Sabicea aspera* Aubl. var. *velutina* (Benth.) Schum., Fl. Bras. 6(6): 307. 1889. TYPE: silvis humidis, 1841/1842/1843 (fl), *Hostmann* 40 (lectotype, designated here, BM!; duplicate, HUH!, NY!, S!).

Scandent or scrambling vines or lianas to prostrate shrubs, stems 1.5–4 m long; *terminal flowering branchlets* densely pilosulous to villosulous, and arachnose, eventually glabrescent, trichomes 0.07–1.6(–2.1) mm long and rusty brown to maroon. *Stipules* usually narrowly to widely triangular to deltate or ovate, usually antrorse, occasionally slightly reflexed, 6–8(–12) × 5–8 mm, apically acute or acuminate, membranous, margins entire, complanate, ciliolate with 0.2–0.6 mm long cilia, adaxially densely sericeous, abaxially sparsely to densely strigulose almost all over, glabrous to glabrescent near the margins, trichomes 0.2–1.2 mm long, (9–)11–14-veined, colleters 5–7. *Leaf blades* usually narrowly elliptic to oblong, occasionally widely lanceolate, (2.3–)5–14.5 × (1.6–)3–9(–10) cm, apically acute to acuminate or mucronate, basally acute or obtuse, papyraceous to membranous, ciliolate with 0.2–0.9(–1.7) mm long cilia, adaxially isolatedly to sparsely hirtellous to pubescent at secondary veins



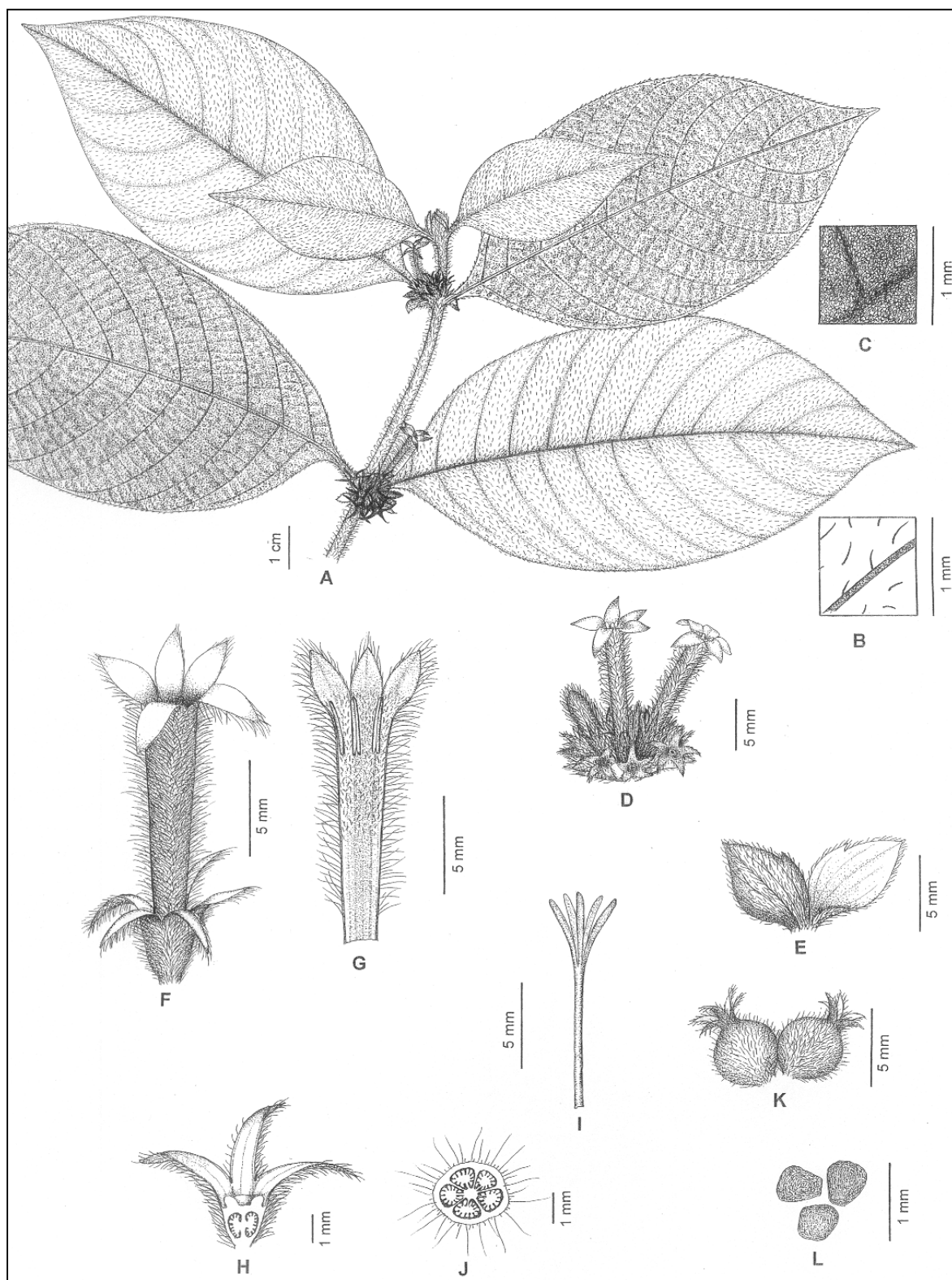


Figure 36. A–L. *Sabicea oblongifolia*. —A part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Inflorescence. —E. Outer and inner bract surface. —F. Flower. —G. Inner corolla surface showing anther's position. —H. Longitudinal section through calyx and ovary. —I. Style and stigmas. —J. Transversal section through ovary. —K. Fruit. —L. Seeds.

and lamina, densely at costa, trichomes 0.07–1.6(–2.1) mm long; abaxially densely, sometimes sparsely arachnose, occasionally isolatedly villosulous at lamina, usually densely arachnose and isolatedly to sparsely villosulous to pilosulous, trichomes (1–)1.2–2.4 mm long and rusty brown to maroon at costa and secondary veins, at least in young leaves, secondary veins 9–12(–14) pairs, distinct or plain adaxially and protruding abaxially, tertiary veins usually prominulous abaxially; *petioles* (3–)5–20 mm long, indumentum rusty or reddish-brown to maroon. *Inflorescences* usually in one leaf axil of each node, 5–9(–15)-flowered, verticillate, 1–1.5(–2) × 1–1.5(–2) cm; *bracts* exinvolucrate, membranous, incompletely isolated into 2 parts, isolated parts 5–7.8 × 4–5.5 mm, usually not lobed, sometimes 2-lobed, lobes when present 0.5–1.5 × 0.5–1 mm, ovate to deltate or triangular, apically acute to acuminate, margins entire, ciliolate with 0.1–0.7 mm long cilia, adaxially glabrous excluding the basal part, trichomes 0.5–1.6(–2.4) mm long, abaxially densely, eventually isolatedly strigulose almost all over, glabrescent towards the margins, trichomes 0.5–1.5 mm long, 5–7-ribbed, bracteoles 1.8–5.5 × 1.5–2.8 mm, colleters 2, 0.3–0.5 mm long. *Flowers* sessile, *calyx* widely campanulate, tubes 1.2–1.8 × 1.8–2.8 mm, lobes (1.1–)1.5–3.5 × 0.4–1.3 mm, antrorse or spreaded to recurved, narrowly triangular to lanceolate, apically acute, margins entire, adaxially glabrous, abaxially sparsely to densely pilosulous to pubescent, trichomes (0.7–)1–1.2(–1.5) mm long and rusty brown to maroon, 1–3-ribbed, colleters 1(–2) in each sinus, 0.2–0.4 mm long; *corolla* white, salverform, tubes 8–12(–16) × (1.2–)1.5–1.8 mm, lobes (2–)2.6–3.5(–4.2) × (1–)1.5–1.8 mm, ovate to widely lanceolate, antrorse or spreaded, apically acute, margins entire, adaxially the indumentum of orifice extends up to 6–7 mm inside the tubes, abaxially densely pilosulous, rusty brown to maroon, trichomes (0.7–)1–2.1(–2.8) mm long; *stamens* 5 per flower, attached to corolla tube at 8–10 mm from the base, anthers (1.8–)2–2.4 × 0.3–0.4 mm; *style* 4.5–8.8 mm long, stigmatic lobes 2–2.7 × 0.4–0.5 mm; *ovaries* 1.2–1.8 × 1–1.2 mm, abaxially uneven, densely strigulose to pilosulous, trichomes 0.8–2.2 mm long, 4–5-locular, each locule 1.1–1.5 × 0.6–1.2 mm. *Fruits* reddish purple to pink or violet, 3–4 × 3–4 mm when immature, 5–8 × 5–8 mm when mature, abaxially isolatedly strigulose to pilosulous; *seeds* 0.3–0.5 mm × 0.3–0.5 mm.

*Phenology, distribution and habitat.* Flowering almost throughout the year and fruiting from April to September. This species is mainly distributed in Suriname, French Guiana and Venezuela with a disjunct distribution in southwest Trinidad and Oriximiná of Pará state of Brazil. It is found along roadsides, in primary or secondary, wet humid forests, pastures or Savanna bush or thickets along river margins. It grows on lateric or red clayey soils to granite rocks; 0–400 m (Fig. 38).

*Discussion.* *Sabicea oblongifolia* is distinguishable by the combination of its usually rusty-brown to maroon indumentum at branchlets, petioles and costa and secondary veins of

abaxial surface of leaves, abaxial surface of stipules and corolla, arachnose indumentum of branchlets and abaxial surface of leaves (Fig. 36C), verticillate inflorescences, and erecto-patent external indumentum of corolla (Fig. 36F, G). *Sabicea oblongifolia* seems close to *S. aspera* due to its verticillate inflorescences, and similar calyx lobes. It is distinct from *Sabicea aspera* by its arachnose branchlets and abaxial surface of leaves, usually rusty-brown to maroon indumentum at branchlets, petioles and costa and secondary veins of abaxial surface of leaves, abaxial surface of stipules and corolla.

*Sabicea oblongifolia* with densely arachnose lower leaf surface appears confusable with *S. velutina* and *S. grisea*. It differs from these two species by its verticillate inflorescences, typical rusty-brown to maroon color of indumentum, external surface of stipules and inflorescences including corolla lacking curled or tortuous trichomes, and adaxially glabrous stipules. Additionally it differs from *Sabicea grisea* by its narrowly triangular calyx lobes, whereas, from *S. velutina* by its hirtellous to pubescent indumentum at the adaxial surface of leaves consisted of shorter (usually 0.07–1.6 mm in contrast to 2–2.3 mm) trichomes, villosulous to pilosulous at abaxial surface of leaf blades, shorter cilia at the margins of stipules, bracts, and calyces (0.2–0.7 mm in contrast to 0.8–1.7 mm at stipules and bracts, and 1.2–1.8 mm at calyx lobes). Steyermark's (1967) decision was right in separation of *Sabicea velutina* var. *oblongifolia* as a species. *Sabicea oblongifolia* seems close to *S. camporum* with few-flowered inflorescences. It is distinct from *Sabicea camporum* by its diffused indumentum of lower surface of leaves, erecto-patent external indumentum of corolla with longer tubes, narrowly triangular to lanceolate, apically acute to acuminate, rusty-brown to maroon indumentum usually at branchlets, petioles and costa and secondary veins of abaxial surface of leaves, abaxial surface of stipules and corolla.

Schumann (1889) did not mention the holotype but four syntypes for *Sabicea aspera* Aubl. var. *velutina*: Guiana Gallica, Mélinon 186; Guiana Anglica, *Schomburgk 25 & 1333* (not seen); Guiana Batava prope plantationem Berg en Daal in provincia Pará, *Wullschlägel 253* (BR!, W!); silvis humidis, *Hostmann 40* (BM!, HUH!, NY!, S!). We have selected *Hostmann 40* (BM) as the lectotype as it is well-preserved with flowers.

*Selected specimens examined.* BRAZIL: **Pará:** Oriximiná, Rio Caxipacoro, Km 72 on the road north of Cachoeira Porteira, 31 Jun 1980, (fl), *Davidson & Martinelli, CD10639* (NY, US). **Pará:** *l'Etan, 253* (U); *Wullschlägl 253* (BR, W); Jodensavanne-Mapene Creek Area, *Schulz, 8240* (U); Langs weg naar Zanderij ca. 3 km ten N, van de aftakking naar Republiek, Wegberm, zand met grint, in de volle zon, Slingerplant, vrij alg, hangend in kruiden en struiken, *Kramer & Hekking 2522* (U), *Lindeman 15263* (U). GUYANA. Roraima mountain, *Schomburgk 901* (BM, F, G, W); Kamakusa, upper Mazaruni River, *Cruz 4252* (MO, F, HUH, NY); Berbice-Corentyne, ca. 5 miles above Cow Falls, 4–8 km N of landing along road, *McDowell & Gopaul 2270* (MO, NY, U); Barima-Waini Region, Barima River Head, Eclipse Falls, 5 miles W of Arakaka, *Pipoly & Lall 8372* (NY, U), Barima River head, 1,5 m W Eclipse

Falls, W of Arakaka, *Pipoly & Lall 8281* (MO, NY, US, U); S of rail yard, Matthews Ridge to ridge of "Blue Bontain", *McDowell et al. 4483* (NY, US); West Damerara, Labbakabra Creek, Tiger Creek, Essequibo R, *Sandwith 1173* (G, NY, U), Essequibo, lower 7 km of Tiger Creek, *Henkel & Chin 445* (NY); Northwest District, Waini River, *Cruz 3613* (F, HUH, NY), Wanama River, *Cruz, 3964* (F, HUH, NY), White water, 3 km NW of Wauna, *Reinders & Thom, 158* (NY, U); Pomeroon, Kamwatta, *Cruz 1189* (HUH, NY), Pomeroon-Supernaam, Kabakaburi Mission village on Pomeroon River, about 25 km upriver from Charity, *Hoffman & Roberts 2447* (MO, NY, US, U). FRENCH GUIANA. Montagne du Rorota, Env de Cayenne, *Hallé 835* (U, US). SURINAME. van den Landbouw, *Lindig 91*(U); Flur Jaramacca, *Went 198* (U); Rabel Station, *Bureau 3421* (U); Savanna by Km 25, *Rombouts 5* (U); Vicinity Km 70, Sectie 0, *Maguire & Stahel 23610* (F, HUH, U); Joden savanne-Mapanecreek area, near Kamp 8, *Hekking 1217* (HUH, US, U); Inter flum. Coppename Dextrum et montes Emma., *Boer, 1383* (MO,U); Tiger Hill, N.W.D., *Grewal & Persuad 482* (U); Amakakondre, *Sauvain 270* (MO, U); Bajkutu, *Sauvain 293* (MO, U). **Brokopandro**: Brokopando secondary forest, *Donselaar 2893* (U). **Marowijne**: Albina aan de Marowijne, *Jonker-Vernhoef & Jonker 373* (U). **Nickerie**: Area of Kabalebo Dam project, near road Km 113, *Lindeman et al. 681* (F, MO, NY, S, U), *Lindeman et al. 82* (U), near Km 44, *Lindeman et al. 362* (U). Kopoewerie op wit, *Boerboom, 8653* (U), Klimmend in struiken langs pad in uitgedung hoog bos, *Kramer & Hekking 2672* (U), near Camp, *Vreden 11298* (U).. **Sipaliwini**: Jacob-Kondre, *Pulle 127* (U), Saramacca River headwaters, Jacob kondre, *Maguire 23884* (F, G, HUH, NY, S, US, U), Vicinity of Blanche marie waterfall on the Nickerie River, *Evans et al. 2720* (MO, NY), Vicinity of Ulemari River, ca. 150 km upstream from its confluence with Litani River, *Evans & Pockham 2892* (MO). **Wanica**: Lelydorp between Mochaweg and Waneweg, ca. 20 km S of Paramaribo, *Lindeman 5751* (WIS). **Trinidad**. Cap-de-Ville Road 5 miles from Erim, *Broadway 2226* (G, MO). VENEZUELA. **Amazonas**: IVIC study site 4 km NE of San Carlos de Río Negro (ca. 20 km S of confluence of Río Negro & Brazo Casiquire), *Liesner, 6129* (MO). **Delta Amacuro**. A. Diaz. Río Grande, 60 km., *Aymard 5439* (MO), Sierra Imataca, between Amacuri & mouth of Deadwater Creek Moa (Agua Muerto), Vicinity of Salto of San Victor, Río Amacuro, *Steyermark 87356* (F, HUH, NY, U). **Bolívar**: Alrededores de Tumeremo, camino Tumeremo-Bochinche, entre Puesto (GN) Corumo y Caño Matuco del río Negro, *Stergios et al. 3623* (NY), Reserva Forestal Imataca, Pica de la CVG que conduce al medio Río Botanamo, cerca de la confluencia Río Corumo, *Stergios et al. 6028* (MO, NY), *Stergios et al. 5318* (MO, NY).

**30. *Sabicea panamensis*** Wernham, Monogr. *Sabicea* 30, t. 12. 1914. TYPE: Panama: Chagres, Isthmus of Panama, Mar. (fl) 1850, *A. Fendler 181* (holotype, K!, photo NY!; isotypes, HUH!, MO!, US!). Figure 37A–N.

Vines or lianas to (sub-)shrubs with usually twining, creeping, scandent to sprawling and rarely erect, (0.6–)2–15 m long; terminal flowering branchlets densely strigulose or hirtellous

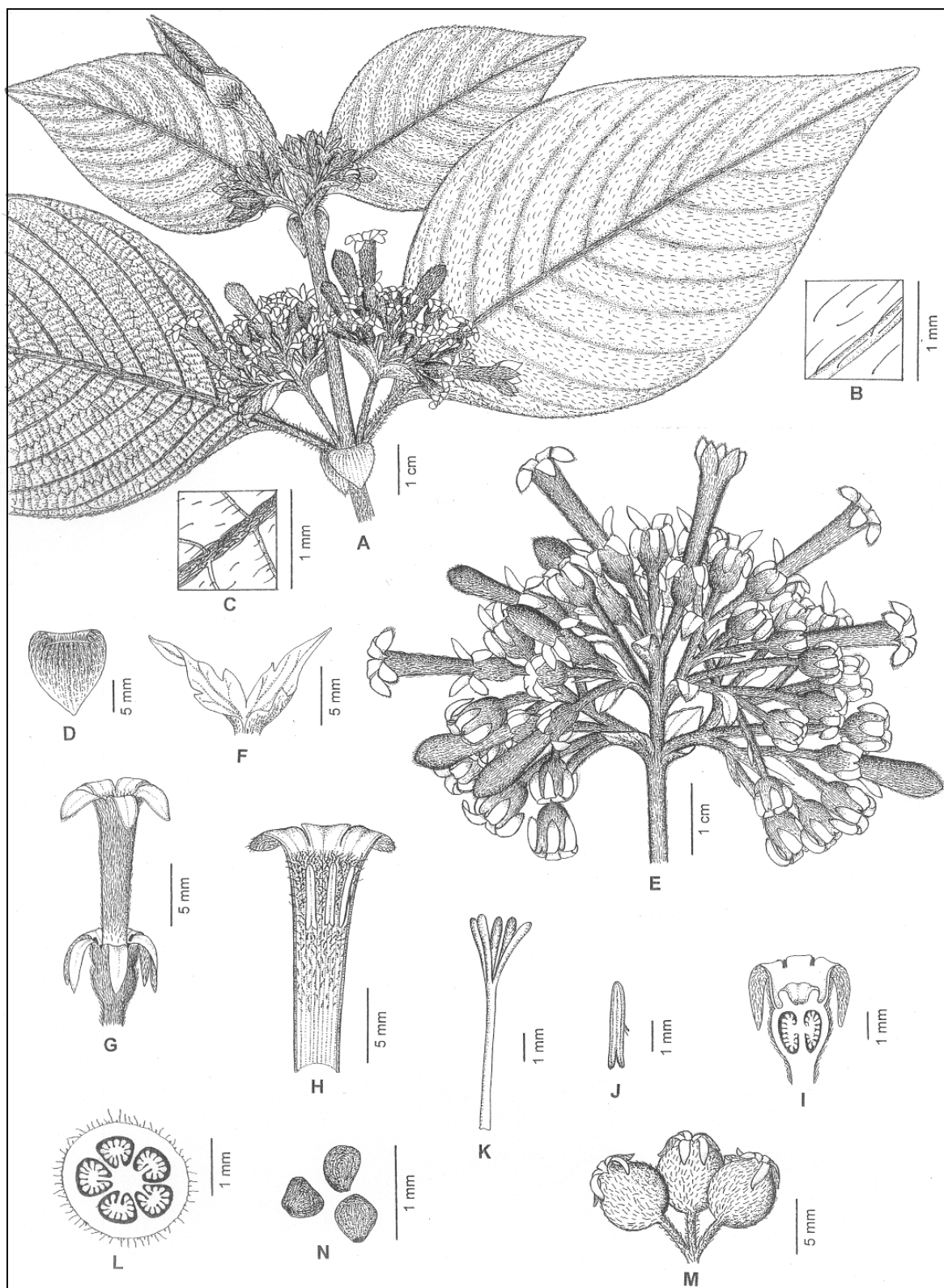


Figure 37. A–N. *Sabicea panamensis*. —A. Part of flowering branchlet. —B. Indumentum of lower leaf surface. —C. Indumentum of upper leaf surface. —D. Outer stipule surface. —E. Inflorescence. —F. Inner bract surface. —G. Flower. —H. Inner corolla surface showing anther's position. —I. Longitudinal section through calyx and ovary. —J. Face view of Anther. —K. Style and stigmas. —L. Transversal section through ovary. —M. Fruits. —N. Seeds.

to pilosulous, and puberulous, eventually glabrescent, trichomes (0.2–)0.4–1.6 mm long. *Stipules* triangular to deltate or ovate or oblong, antrorse to reflexed, (3.5–)6–14(–17) × (2.5–)4–10(–12) mm, rarely bifid, apically usually acute to acuminate, occasionally obtuse, membranous, margins entire, rarely shallowly wavy, ciliolate to eciliate, ciliolate with 0.1–0.2 mm long cilia, adaxially glabrous excluding the basal part, abaxially sparsely-densely strigulose or hirtellous to puberulous, trichomes (0.2–)0.3–1.7 mm long, 12–14-veined, colleters 12–18, 1.4–1.5 mm long. *Leaf blades* elliptic to ovate, (4–)6–12(–17.4) × (1.3–)3–5.5(–8.5) cm, apically usually acuminate to acute or obtuse or mucronate, basally acute to attenuate, membranous or papyraceous, margins complanate or abaxially slightly curved, ciliolate with (0.2–)0.6–1.3(–1.5) mm long cilia, adaxially usually sparsely strigulose, sometimes hirtellous and isolatedly to sparsely puberulous at lamina, usually densely strigulose, occasionally hirtellous, sometimes sparsely to densely puberulous at costa, trichomes (0.1–)0.5–1.3 mm long, abaxially sparsely to densely strigulose, isolatedly to sparsely puberulous, usually densely strigulose, sometimes isolatedly to sparsely puberulous, rarely hirtellous at costa and secondary veins, trichomes (0.1–)0.8–1.5 secondary veins 10–14 pairs, costa and secondary veins protruding abaxially, protruding or plain adaxially, tertiary veins and quaternary veins usually distinct and rarely prominulous abaxially; *petioles* (1–)3–30(–45) mm long. *Inflorescences* usually (1–)2 per node, (5–)9–64(–88)-flowered, usually moderately lax- to compact-, globose- to ovoid-paniculate or compact-thyrsoid with 3–7-flowered lateral axes, sometimes elongated- and cylindrical- or pyramidal-thyrsoid with 9–12-flowered lateral axes, and rarely umbellate, (1.5–)3–9.5 × (1.5–)2–8 cm excluding peduncles, primary axis (0–)2–10(–32) × (0–)0.8–1.5 mm, main lateral axes (0–)2–6 per inflorescence, 1–6(–10) mm long, simple to compound dichasia; *peduncles* (1–)4–35(–45) mm long; *bracts* (sub-)exinvolucrate, leafy papyraceous, incompletely isolated into 2–3 parts, isolated parts 5–12(–16) × (2.5–)3.5–9 mm, 4–8-lobed, widely lanceolate to deltate or narrowly ovate to oblong, apically usually acute to obtuse, margins entire, ciliolate with 0.2–0.3 mm long cilia, adaxially glabrous excluding the basal part, trichomes (0.8–)1–1.5(–1.6) mm long, abaxially densely strigulose at the lower and middle part, trichomes (0.4–)0.6–0.8(–1) mm long, 5–13-ribbed, lobes 1–3-ribbed, bracteoles (1–)1.5–9(–12) × (0.2–)1–4(–5) mm, oblong to ovate to deltate or lanceolate to triangular, rarely bilobed to trilobed including 1–2 short lateral lobes, colleters 2–9, 0.3–0.6 mm long. *Flowers* pedicellate, pedicels (1–)2–12(–15) mm long; *calyx* campanulate, 5-lobed, tubes (0.8–)1.1–1.6(–2.1) × (1.4–)1.5–1.8(–2) mm, lobes (0.2–)1–6 × (0.5–)0.8–1.4(–1.9) mm, recurved to reflexed, sometimes antrorse to moderately spreaded, narrowly lanceolate to narrowly lingulate, occasionally narrowly ovate to triangular, apically (sub-)acute, eciliate to ciliolate, ciliolate with 0.2–0.4 mm long cilia, adaxially glabrous, abaxially isolatedly to densely strigulose to pubescent, trichomes (0.1–)0.9 mm long, 3–5-ribbed, abaxially slightly prominulous, adaxially plain, colleters 1–2(–4) in each sinus, 0.2–0.3 mm long; *corolla* white or pinkish to purplish, salverform, tubes (4–)7–14 × (1.4–)1.5–2.7 mm,

lobes (1–)1.5–2.5(–3.3) × (1–)1.1–1.5(–1.9) mm, ovate to widely lanceolate, spreaded to somewhat recurved, adaxially the indumentum of orifice extends up to 3–6.5 mm inside the tubes, trichomes of orifice 0.3–0.9 mm long, abaxially densely strigulose (0.20.2–)0.2–1.1 mm long; *stamens* 5 per flower, attached to corolla tube at (5–)6–9(–11.5) mm from the base, anthers (2–)2.6–2.8 × 0.4–0.5 mm; *style* (2–)3–5.5(–8) mm long, stigmatic lobes (1.5–)1.6–3(–3.6) × 0.2 mm; *ovaries* (1.4–)1.7–2(–2.6) × (1.2–)1.5–1.8(–2.6) mm, abaxially usually uneven to plain, sometimes 5-lobed, usually densely strigulose to puberulous, 5-locular, each locule 1.4–1.6 × 0.4–0.8 mm. *Fruits* red to pink or maroon, 3–12 × 3.5–10 mm when mature, abaxially isolatedly strigulose to puberulous; *seeds* 0.5–0.7 × (0.3–)0.4–0.6 mm.

*Phenology, distribution and habitat.* In *Sabicea panamensis* var. *panamensis*, flowering and fruiting occur throughout the year. *Sabicea panamensis* var. *santanderensis* flowers from July-August and in November. Apart from *Sabicea villosa*, it the only species of *Sabicea* being distributed in both, Mesoamerica and South America. In Mesoamerica, *Sabicea panamensis* var. *panamensis* extends from Belize and Guatemala to Panama, presumably excluding El Salvador. In South America it is found in parts of Peru, Ecuador, Colombia, Venezuela, with a disjunction in Pará and Amazonas states of Brazil. It grows in nearly all types of humid tropical forests, savanna, pastures, swamps, shores, and open, also disturbed areas. It grows on clayish to sandy or lateritic soils. *Sabicea panamensis* var. *santanderensis* is restricted to Santander department of Colombia and Loreto province of Peru; (0–)5–1920 m (Fig. 38).

*Discussion.* *Sabicea asperula* is merged here under *S. panamensis* because the lack of any remarkable difference between these two species. *Sabicea panamensis*, especially *S. panamensis* var. *santanderensis*, is very close to *S. pyramidalis*. However, it can be set apart from *Sabicea pyramidalis* by its 9–12-flowered (in contrast to 3–7-flowered) lateral axes, longer (4–6 mm in contrast to 1.7–2.4[–3.8] mm) and antrorse to spreaded calyx lobes, and longer (7–10 mm in contrast to 4.5–5 mm) corolla tubes. *Sabicea panamensis* var. *santanderensis*, appears close to *S. thyrsoiflora* from which they differ by their apically acute stipules, bracts and calyx lobes, and narrowly lanceolate to narrowly lingulate and longer (4–6 mm in contrast to 2.5–3.8 mm) calyx lobes.

*Sabicea panamensis* with lax-paniculate (Fig. 37E) or thyrsoid inflorescences seems close to *S. chocoana* from which these can easily be distinguished by their strigulose indumentum and glabrous adaxial surface of bracts and calyx lobes (Fig. 37F, G, I). *Sabicea panamensis* appears as close to *S. cochabambensis* and *S. pearcei* from which it is distinct by its appressed indument at branchlets, leaves, and outer surface of inflorescences including corollas. Additionally it seems differ from these two species by its longer corolla tubes. *Sabicea panamensis* with few-flowered inflorescences are easily confusable with *S. aspera* and *S. mexicana*. Yet, these can be set apart from *Sabicea aspera* by their erecto-patent external indument of corolla tubes, and from *S. mexicana* by their apparently shorter, and

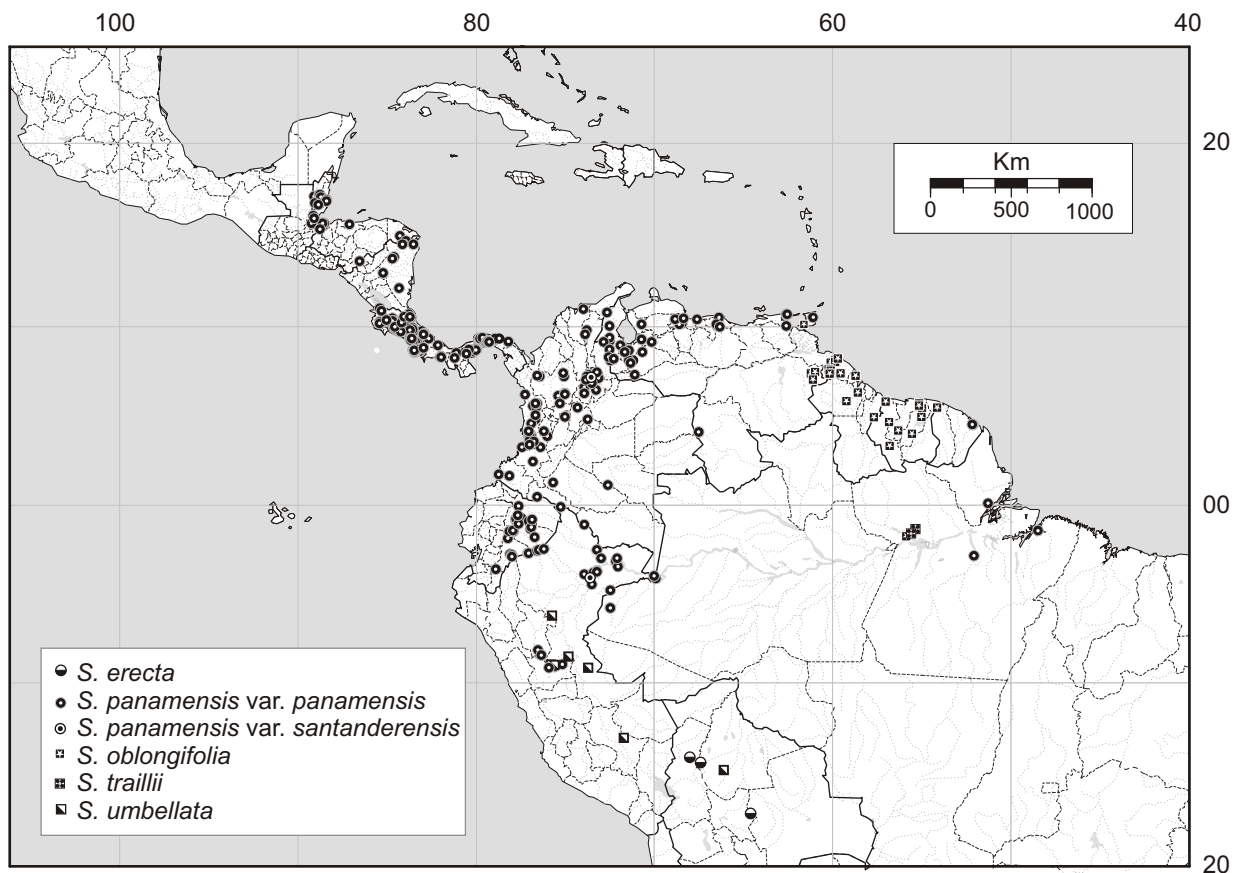


Figure 38. Map of parts of Mesoamerica and South America, showing the distribution of *Sabicea erecta*, *S. panamensis*, *S. oblongifolia*, *S. traillii*, and *S. umbellata*.

recurved to reflexed, occasionally antrorse calyx lobes, and shorter external trichomes of corolla.

*Sabicea panamensis* appears close to *S. cuneata* and *S. calophylla*, from which it is distinct by its non-arachnoid or non-lanuginose indumentum of branchlets, outer surface of inflorescences, and at the abaxial surface of leaves. It seems close to *Sabicea bariensis* from which it can be distinguished by its indumentum lacking curled to tortuous trichomes, smaller calyx types, and usually narrowly lanceolate to lingulate, and recurved to reflexed calyx lobes. *Sabicea panamensis* can be set apart from *S. umbellata* by the combination of its paniculate or thyrsoid inflorescences with usually shorter (1-5 mm in contrast to 5-7.5 mm long) calyx lobes or elongated-thyrsoid inflorescences, narrowly lanceolate to lingulate, narrowly ovate to triangular and straightened calyx lobes (Fig. 37G) with lower length-breadth ratios (0.4-3.7 in contrast to 5.5-7.5), and longer (usually 7-14 in contrast to 5-6.5 mm) corolla tubes. Wernham (1914) mentioned two syntypes: Brazil: Amazonas, Juruá Miry, *E. Ule* 5669 (F!, G!) and Peru: Sarayacu, *Castelnaus.n.* (not seen) are mentioned for *Sabicea paraensis* but no holotype. We have seen *Ule* 5669 (F) in good condition and selected it as the lectotype.

#### Key to the varieties:

- 1a. Inflorescence ovoid- to subglobose-paniculate, lateral axes 3-7-flowered; bracts (sub-)exinvolucrate, calyx lobes recurved to reflexed or antrorse when < 3 mm long.....30a. *S. panamensis* var. *panamensis*



- 1b. Inflorescence elongated-, ovoid- to cylindrical-thyrsoid, lateral axes 7–9-flowered; bracts subinvolucrate, calyx lobes antrorse to spreading and usually 4–6 mm long.....30b. *S. panamensis* var. *santanderensis*

**30a. *Sabicea panamensis* Wernham var. *panamensis***

*Manettia asperula* Ball., Journ. Linn. Soc. 22:142. 1886; *Sabicea asperula* (Ball) Wernham, Monogr. *Sabicea* 30. t. 12. 1914. TYPE: Colombia: coast near Buenaventura, shady places, 08 Apr 1882, *J. Ball* s.n. (holotype, K!).

*Sabicea colombiana* Wernham, Monogr. *Sabicea* 39. t. 12. 1914. TYPE: Venezuela. Carabobo., 914.40 m, 1842/ 1843 (fl), *I. Linden 1498* (holotype, BM!, photo NY!; isotypes, G!, K, BR, P, not seen, US!).

*Sabicea costaricensis* Wernham, Monogr. *Sabicea* 31. t. 12. 1914. TYPE: Costa Rica: 18 Jul. 1890, *H. Pittier 2904* (syntype, BM!, photo NY!), Costa Rica: on the savanna, no date; *H. Pittier 4025* (syntypes, BM, K, BR, G); Costa Rica: Buenos Aires, 300 m, *H. Pittier 6712*, Jan 1893, (syntype, BM! BR! G!, F[fragments]!, US!).

*Sabicea paraënsis* (K. Schum.) Wernham, Monogr. *Sabicea* 31. t. 12. 1914. TYPE: Brazil: Amazonas, Juruá Miry, Jul-Aug, 1901, (fl&fr), *E. Ule 5669* (lectotype, selected here, F!; duplicate, G!). *Sabicea umbellata* Pers. var. *paraënsis* K. Schum., Fl. Bras. 6(6): 304. 1889.

*Sabicea reflexa* Standl., Field Mus. Nat. Hist., Bot. Ser. 11(5): 270. 1936. TYPE: Colombia: Umbría, Comisaría del Putumayo, 325 m, Oct.-Nov. 1930, *G. Klug 1782* (holotype, F!; isotypes, BM!, G[fragments]!, MO, NY!, S!, US!). "Momoca Morada" & "Ruicha-O" (Huitoto Indian name).

*Selected specimens examined.* BELIZE: **El Cayo:** At the base of hill, 37 mile Section, Humming Bird Highway, *Gentle 8929* (F, S). **Stann Creek:** Stann Creek-Mullivis River road, *Gentle 1909*(F, HUH, NY, WIS); Cockscomb basin Wildlife Sanctuary, *Whitefoord 8246*(BM). BOLIVIA: **Cochabamba:** Chapare, Locotal, Chapare, *Steinbach 9417*(HUH, NY, S); 5 km below the town Locotal, highway to Chapare, *Ritter & Wood 1510*(W). BRAZIL: **Amazonas:** Rio Javari, *Lleras et al. P17046*, (NY). Pará: Belém, *Dahlgren & Sella 780* (F, HUH, US), Belém, Embrapa, margem da estrada do 15, *Rosa 1761* (NY). COLOMBIA. **Amazonas:** Leticia, Km 0–4 of the trail to Calderón from Km 21 on the Via Tarapacá, *Andersson et al. 2179*(NY, S). **Antioquia:** Mutatá, 4 km SW of Mutatá along the road to Pavandocito, *Zarucchi, J., Betancur, J., Echeverry, B. & Roldán, F.J. 5092*, (NY). San Rafael, Carretera Guatape-San Rafael, *Alzate et al. 240*(F). **Chocó:** Municipio de Quibdó, Carretera Quibdó-Tutunendo, 15 km de Quibdó, *Forero & Jaramilo 257* (NY); Guayabal, just N of Quibdo, *Juncosa et al. 705* (F). **Valle:** Río Calima (region del Choco), La Trojita, *Cuatrecasas 16633* (F); along highway from Buenaventura to Cali, *Killip & Cuatrecasas 39014* (F, S, US). COSTA RICA: **San José:** Parque Nac. Braulio Carrillo, *Delprete, P.5103* (NY); Vicinity of El General,

San José, *Skutch* 2973 (HUH, NY, S, US); 24 km NE of Turrialba on highway to Limón, Cartago, *Liesner et al.* 15376, (WIS); ; Z. P. La Cangreja, Santa Rosa de Puriscal, 1 km SE, *Morales* 566 (F). **Heredia**: Canton de Sarapiquí Rara Avis, ca. 15 km al suroeste de Horquetas, *Vargas & Frazee* 33 (F), En el lindero Norte de Puerto Viejo, Pcia. Alfonso, *Jimenez* 3439 (F); Near south east corner of the successional plot Finca La Selva, Puerto Viejo, Sarapiquí, *Hartshorn* 1502 (F); ca. 14 km beyond Puerto Viejo on the road to Horqueta, *Almeda et al.* 3180 (NY); Finca La Selva, the OTS Field Station on Río Puerto Viejo just E of its junction with Río Sarapiquí, *McDowell* 370 (NY); Parque Nacional Braulio Carrillo Estacion Magsasay, *Carballo* 80 (F); Horquetas de Sarapiquí, Reserva Rara Avis, Sector Catarata, *Martén* 1031 (F). **Limón**: Talamanca, Camino a Suretka y de regreso a Bribri, entrando por Uatsi (Volio), *Cascante et al.* 561 (F). **Puntarenas**: Hilly slopes, west of Villa Nueva and the Río Naranjo, *Burger et al.* 12309 (F); Parque Nacional Corcovado Cerro Rincon, Dos Brazos de Río Tigre, *Herrera* 4090 (F); Canton de Golfito. P.N. Corcovado, Peninsula de Osa, Estacion Los patos, *Agular* 2151 (BM). **Guanacaste**: Canton de La Cruz, on the N-NE slopes of Volcan Orosi, along the road from Santa Cecilia to the park station Pitilla, *Taylor et al.* 9802 (F), Volcan Orosi, Vicinity of Estacion Biologica Pitilla, *Short & Stafford* 31 (BM); Above Tuiz, road to Moravia de Chiripo, Cartago, *Hazlett* 5093 (F). ECUADOR. **Pastaza**: Hacienda San Antonio de Baron von Humboldt, 2 km al NE de Mera, *Neil et al.* 5857 (NY), Veracruz, *Sparre* 17610 (S); A 10 km del limite provincial con Napo. *Palacios* 3445 (G, NY). **Napo**: Along trail between Jondachi and Osoyacu on the trail between Baeza and Tena, *Ownbey* 2703 (F, NY, US); Napo Carretera Coca-Loreto, Entre la Comuna 10 de Agosto y el río Pinguillo, *Cerón & Iguago* 5304 (NY). **Morona Santiago**: Mera, *Asplund* 18489 (G, S). **Zamora Chinchipe**: Cantón Nangaritza, Destacamento Militar Shaime. Parroquia Guayzimi, *Jaramillo* 13390 (NY). FRENCH GUIANA. **Cayenne**: Montagne de Kaw, E end ca. 10 km from end of road, *Andersson et al.* 1941 (MO, NY, S). GUATEMALA. **Izabal**: Santo Tomás de Castilla, several km past Las Escobas, *Marshall et al.* 288 (NY); Izabal, along Río Bonita, *Steyermark* 41673, (F); along road between Puerto Barrios and Tomas, about 1.5 miles southeast of Puerto Barrios. *Steyermark* 39866 (F, HUH); Near Entre Ríos, *Standley* 72605 (F); Puerto Barrios, cerro San Gil, *Castillo et al.* 2463 (F). HONDURAS: **Atlantida**: Above Santiago River, between la Masica an la Ceiba, 5 km S of paved road. *Hazlett* 3280 (F); **Gracias A Dios**: Gracias A Dios (La Mosquitia). Alrededores de Mocerón, 60 km al SO de Puerto Lempira, *Torres* 134 (NY). NICARAGUA: **Atlántico Sur**: El Recreo, *Long* 197 (F). **Atlántico Norte**: Comarca de El Cabo, Sobre el matorral (de Río Leicus cerca del campo de aviacion de Tronquera, 35 kms SE de Waspan.), *Molina* 15169 (F), Comarca de El Cabo: La Tronquera, Río Leicus, *Molina* 14936 (F, NY). PANAMA. **Colón**: Summit of Cerro Santa Rita, *P. H. & Allen* 5100 (BM, F, G, NY); Canal Zone, Navy reservation, North of Gamboa, *Robyns* 65–49 (F, US). **Coclé**: Road from El Valle to La Mesa, *Spellman et al.* 585 (NY); 4 miles past Llano Grande on road to Cascajal, 200 yds past Continental divide, *Sytsma* 3921 (NY). **San Blas**: Navagandí, McDonagh et al. 398 (BM). **Panamá**: Cerro Jefe, Dwyer & Hayden 8091

(HUH). **Veraguas**: NW of Santa Fe. 8.8 km from Escuela Agricola Alto de Piedra, *Moriet et al.* 4017 (F). PERU: **San Martín**: Mariscal, Tocache Nuevo, *Vigo* 3757 (F, G); South of Uchiza, quebrada de Tranca, *Vigo* 5778 (F, US). **Loreto**: Maynas, Quebrada Orejon, Purma, *Ayala et al.* 2807 (F, MO), Trocha detras del CaseRío de Huanta, Monte secundario, *Díaz et al.* 531 (F), Alto Nanay, near Santa Maria de Nanay, *Simpson & Vigo* 704 (F, G), Iquitos, Ninarumi, *Vásquez & Jaramillo* 10396 (NY), Las Amazonas, Río Amazonas. Quebrada Yanamono, Below Indiana, *Rimachi Manuel* 1184 (NY); Pebas, Brillo Nuevo, Yaguasyacu River, affl. of Ampiyacu River, *Treacy & Alcorn* 360 (F, WIS). Puerto Almedra. Río Nanay above Iquitos, *Revilla* 1699 (F, NY). **Huánoco**: Daniel Alomias Robles, *Vigo* 9289 (F, G, NY); Quebrada Orejon, Purma, *Ayala et al.* 2807 (F, MO). VENEZUELA. **Táchira**: 4 km (air) west of La Fria, 15 km (road) west of La Fria from Puente Grita, *Steyermark et al.* 120410 (NY); Uribante, Empresa las Cuevas near La Fundación, *Werf* 4903 (F). **Miranda**: Parque Nacional Guatopo, vic. Agua Blanca, 24 km. NNW of Altagracia de Orituco, *Nee* 17679 (F, WIS); Las Perdices al Río Brazo Grande, *Meier & Llamozas* 3655 (HUH). **Zulia**: Perijá, 58 km S of Machiques near mission Los Angeles del Tukuko, *Bruijn* 1199 (M, NY, S), ca. 7 km E of the Maracaibo-La Fria Hwy (Hwy. 6) and ca. 4 km N of the Río Aricuaisá, *Davidse et al.* 18325 (NY). **Mérida**: Between Mucuchachi and Canagua *Steyermark* 56357 (F, HUH). **Yaracuy**: Nirgua, Serrania Santa Maria-Cerra La Chapa, 6 km al norte de Nirgua, *Meier & Llamozas* 966 (HUH).

**30b. *Sabicea panamensis* Wernham var. *santanderensis* Liede, Meve & Khan, var. nov.,**  
 TYPE: Colombia. Norte de Santander, Cordillera Oriental, Region del Sarare, Hoya del Río Margua, Bosques en la Quebrada del Río Negro, *J. Cuatrecasas* 12948 (holotype, F!; duplicate, US!).

*Sabicea panamensis* inflorescentiis ovoidiis ad cylindricis, bracteis subinvolucratis, axibus lateralibus 7–9 floribus, pedicellis 4–14 mm longis, lobis calycorum subacutis, antrorsis ad expansis, indistincte ciliatis; tubis corollarum 7–10 mm longis.

*Specimens Examined*: PERU. **Loreto**: Maynas, Iquitos, Carretera de Iquitos-Nauta, Km 6 de Quisto Cocha, *Rimachi* 11071 (NY). COLOMBIA. **Santander**: 25 km east of Barranca Bermeje, *Gentry* 15393 (NY).

**31. *Sabicea parva* Wernham, Monogr. *Sabicea* 57. t. 6, f. 4–6. 1914. TYPE: Brazil: near Cuburí, Río Negro, *J. W. H. Trail* 391 (holotype, K!).**

(Sub-)shrubs, scandent or sprawling; terminal flowering branchlets usually densely pilosulous or pubescent to sericeous or strigulose, occasionally isolatedly to sparsely lanuginose, eventually glabrescent, trichomes (0.6–)0.8–1.9 mm long. *Stipules* usually widely ovate to deltate, antrorse, 3.5–6.5 × 4–6 mm, papyraceous, apically obtuse to subacute,

ciliolate with 0.2–0.8 mm long cilia, adaxially glabrous excluding the basal part, abaxially the base or the lower part densely to sparsely strigulose or pubescent and the rest glabrate, 9–12-veined, colleters 5–9, (0.4–)0.6–1.3 mm long. *Leaf blades* elliptic to oblong, 3–11(–14) × (1–)2–5(–6) cm, apically acute to acuminate, papyraceous, cilia 0.4–1.4 mm long; adaxially secondary veins and lamina sparsely, and costa densely hirtellous to (sub-)strigulose and puberulous, occasionally arachnose at costa, trichomes 0.07–1.1 mm long; abaxially lamina usually sparsely hirtellous to pilosulous, costa and secondary veins densely pilosulous to strigulose, sometimes isolatedly to sparsely arachnose all over, trichomes (0.1–)0.4–1.9 mm, secondary veins 9–12 pairs, plain adaxially and protruding abaxially, tertiary veins distinct or slightly prominulous and quaternary veins distinct abaxially; *petioles* 4–18 mm long, hirtellous or pilosulous to puberulous. *Inflorescences* one per each node, (5–)7–12(–18)-flowered, verticillate, 1.5–2.2 × 1.5–2.5(–3) cm; *bracts* (sub-)exinvolucrate, incompletely isolated into 2 parts, isolated parts 3.5–4.5(–5.5) × 8.8–11 mm, (3–)5–6-lobed, lobes (0.3–)0.8–5.5 × (0.3–)0.8–3.5(–7.5) mm, ovate to deltate, apically acute to acuminate, margins entire to sparsely denticulate, ciliolate with 0.1–1.4 mm long cilia, adaxially glabrous excluding the basal part, trichomes 0.6–1.5 mm long, abaxially the lower parts densely strigulose to pubescent, 3–9(–12)-ribbed, bracteoles ovate to lingulate to elliptic, 1.2–4.5(–6.5) × 0.6–2.8 mm, apically acute, colleters 2(–4), 0.2–0.6 mm long. *Flowers* sessile; *calyx* usually campanulate, 4–5-lobed, tubes (1.5–)2–3(–3.5) × 2.6–3(–3.5) mm, lobes (0.4–)2–3.5(–5) × (0.4–)1.2–2.1(–2.5) mm, antrorse to gently reflexed to spreaded, ovate to triangular, apically (sub-)acute, margins entire to sparsely denticulate, ciliolate with 0.2–1.5 mm long cilia, adaxially glabrous or apically isolatedly to sparsely strigulose, trichomes 0.1–0.8 mm long, abaxially strigose to hirtellous, usually at the middle and lower part of lobes, trichomes (0.1–)0.6–1.3 mm long, lobes usually 3-ribbed, *colleters* 1(–2) at (0.3–)1–2 mm below the sinus, 0.2–0.4 mm long; *corolla* white, salverform, tubes (6–)8–12.5(–14.5) × 1.5–2.1(–2.4) mm, lobes (2–)3–4.5(–4.7) × (1–)1.2–1.8(–2.1) mm, widely lanceolate to narrowly ovate, antrorse, apically (sub-)acute, adaxially the indumentum of orifice extends up to (3.5–)4–4.7 mm inside the tubes, abaxially densely pilosulous excluding the 2–2.5 mm glabrous base, trichomes 0.2–2.5(–3) mm long, 18–20-ribbed; *stamens* 5 per flower, attached to corolla tube at 9.4–10.5 mm from the base, anthers 1.5–1.8(–2.1) × 0.1–0.3(–0.4) mm; *style* 7.6–8.5 mm long, stigmatic lobes (1.2–)2–2.8 × 0.3–0.4 mm; *ovaries* 1–2.1(–3) × 1–2(–2.5) mm, abaxially uneven to shallowly uneven to 5-lobed, densely strigulose to pilosulous, trichomes (0.6–)0.8–1.4(–2.1) mm long, 4–5-locular, each locule 0.8–1.1 × 0.5–6.9 mm. *Fruits* red to pink, 3–4 × 3–4 mm when immature, 4–5 × 4–5 mm when mature, isolatedly to sparsely strigulose to pilosulous; *seeds* 0.5–0.7 × 0.5–0.6 mm.

*Phenology, distribution and habitat.* Flowering throughout the year. Fruiting from January to February, April to November. It is found somewhat discontinuously in Brazil, and

Venezuela. It is collected from open humid and pluvial forests, forest clearings, scrubland, Savanna, roadsides to streamsides or riversides, beaches and pastures. It grows on sandy to clayey soil; 0–550 m (Fig. 7).

*Discussion.* Steyermark (1967) did not mention the relationships between *Sabicea brachycalyx* and *S. parva*. Superficially *Sabicea brachycalyx* seems to differ by larger leaves and calyx lobes, longer trichomes and cilia, and erecto-patent trichomes of stems. None of these characters, in which these two species seem differ, is invariant in the observed specimens. However, upper parts of *Sabicea brachycalyx* are characterized by an indumentum at the apex or adaxial upper part of calyx lobes. Therefore, *Sabicea brachycalyx* is included in *S. parva* as a separate variety.

*Sabicea parva* is characterized by the combination of its verticillate inflorescences, ample calyx tubes (usually 2–3 mm long), ovate to triangular and antrorse to spreading calyx lobes, colleter's location below the sinus, and erecto-patent external trichomes of corolla tubes. This species seems very close to *Sabicea aspera* and *S. villosa*, especially because of the verticillate inflorescences, but differs by its ovate to triangular and antrorse to spreading calyx lobes, longer calyx tubes, and colleter's location in calyces below the sinus. Additionally it differs from *Sabicea villosa* by its longer corolla tubes (usually 8–12.5 mm in contrast to 3.5–5 mm) externally covered with erecto-patent trichomes. The collection *Prance et al. P25127* (HUH, NY, US) is found as an intermediate of *Sabicea parva* and *S. trianae*. *Poeppig 2515* (NY, W), collected from Alto Amazonas in silvis caeduis ad Ega, was included in Schumann's (1889) *S. aspera* var. *scandens*, but it as a *S. parva* var. *parva*.

#### Key to the varieties:

- 1a. Calyx lobes adaxially glabrous; tomentellous or arachnose indument absent at the main veins of the lower surface of leaves.....31a. *S. parva* var. *parva*  
 1b. Calyx lobes adaxially sparsely strigulose at upper part or apices; tomentellous or arachnose indument present or absent at the main veins of the lower surface of leaves.....31b. *S. parva* var. *brachycalyx*

#### 31a. *Sabicea parva* Wernham var. *parva*

BRASIL. **Roraima:** on road between SEMA Estação and Boa Vista, 14 im from Island, 61°20'W, 3°18'N, *Hopkins et al. 813* (MO, NY). VENEZUELA. **Amazonas:** Flumina Casiquiciri, *Spruce 3275* (BM, BR, F, G[3], HUH); Capihuara, Alto Casiquiare, *Williams 15663* (F); Río Orinoco, Río Cunucunuma, near river Bank at Playa Alta, *Maguire et al. 29482* (NY, U); Santa Barbara savanna at junction of ríos Orinoco and Ventuari, *Cowan & Wurdack 32015* (NY); Río Negro, Entre la desembocadura del Río Casiquiare y San Carlos, *Morillo et*

*al.* 4043 (F, MO), Cerratera San Carlos de Río Negro-Solano, 1–4 km NE de San Carlos, *Morillo et al.* 3918 (MO), ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 1 km south of San Carlos, *Uhl* 75 (MO), selva pluvial po las orillas del Medio Casiquiare, desde la piedra La Esterita arriba del Raudal, 66°30'W, 2°15'N, *Stergios & Aymard* 7638 (NY), Brazo Casiquiare between Culimacare and its junction with the Río Negro, *Davidse* 27935 (NY, NY), Entre la boca del Caño Atamoni y 1 km abajo de la piedra Esterita, 66°28'W, 2°10'N, *Stergios et al.* 8299 (NY); al Río Casiquiare, entre Solano y Curimacare, 66°57'W, 1°58'N, *Stergios & Aymard* 9017 (MO, NY); Selva alta a lo largo del Río Coro-Coro, vecindades del aeropuerto de Yutaje, *Steyermark et al.* 113960 (MO); Atabapo, sabanas sobre altiplanicie E. del Cerro Mahedi, en la ribera N, del Río Ocamo Medio, 64°43'W, 2°58'N, *Huber* 4959 (NY), trail from Río Cunucunuma to Huachamacarí, 65°42'W, 03°49'N, *Liesner* 25939 (MO), Río Cunucunuma, at mouth of Caño Negro to 3 km down river, 65°43'W, 03°42'N, *Liesner* 24577 (MO[2]); Atures, 43 km al N-E de santa Barbara del Orinoco, Sab. Arbolada, mates y bosque de Galería en Peniplanicie, 66°42'W, 04°16'N, *Marin* 1063 (MO); Cerro Duida, Alto Orinoco, 65°37'W, 3°10'N, *Farinas et al.* 348-A (NY). **Bolívar:** Large savanna, vicinity of Urimán, *Steyermark* 75325 (F, NY-para-); Río auacapa afluente del apaeara, Arekuna: Zambari-Ya, *Bernardi* 1444 (NY); vicinity of Icabarú south side of Río Icabarú along road to Los Caribes, 61°44'W, 4°19'N, *Croat* 54065 (MO, VEN); Río Nichare, tributary of Río Caura, between mouth of Nichare and Caño Sarrapio (12 km), 65°02'W, 06°04'N, *Horner* 98 (MO); Río Nichare, tributary of Río Caura, Between mouth of Nichare and Caño Sarrapio (12 km), 65°02'W, 06°04'N, *Horner* 21 (MO); sandy beach on Río Caura, near base of Salto Para. Small Indian hut nearby, 10 m of sandy beach was exposed, 65°04'W, 6°03'N, *Horner et al.* 279 (MO); Municipio Aripao, Río Caura, Tramo Ceiato-B1 PAUJI, 64°17'27''W, 5°35'18''N, *Rosales* 1365 (MO).

**31b. *Sabicea parva* Wernham var. *brachycalyx* (Steyerm.) Liede, Meve & Khan, com. et stat. nov.**

*S. brachycalyx* Steyerm., Mem. New York Bot. Gard. 17(1): 313. 1967. TYPE: Venezuela: Terr. Fed. Amazonas, San Fernando de Atabapo, 125 m, Jun. 06 1959 (fl), *J. J. Wurdack & L. S. Adderly* 42833 (holotype & isotype, NY!).

*Specimens examined:* BRASIL. **Roraima:** Ilha de Maraca, Mun, Alto Alerge, SEMA Estacao, Open savanna close to Estacao, *Hopkins et al.* 581 (F[3], NY)]. GUYANA. **Upper Takutu-Upper Essequibo:** South Rupununi savanna, Kobawaizwarum 12 km NW of Aishalton, 59°22'W, 2°35'N, *Henkel & James* 3688 (MO, NY, US); Parabara Savanna, Trail from Karaudarnau to Kuyuwini R, 59°22'W, 2°11'N, *Clarke* 5109 (MO, US); Kuyuwini River trail, from river to Parabara savanna & Karaudarnau Village, 59°14'W, 02°05'N, *Clarke* 4415 (MO, U). VENEZUELA. **Amazonas:** Capibara, Río Casiquiare, *Medina* 300 (NY); a lo largo

del Orinoco, *Fariñas et al.* 344 (NY); San Carlos de Río Negro, al aeropuerto, 67°04'W, 1°55'N, *Steyermark & Bunting* 102701 (NY); Caserío de Piaraos, cerca de Boca del Río Guayapo, 1 km arriba de La Boca, *Morillo & Ishikawa* 3486 (NY); 30–34 km S of Puerto Ayacucho on side road from Puerto Ayacucho-Samariapo highway leading to Tobogan, 67°39'W, 5°25'N, *Gentry & Berry* 14533 (MO, NY); 22,23 km N of Samariapo on road to Puerto Ayacucho, *Gentry & Berry* 14562 (F, MO, NY); Sta. Borbara del Orinoco, *Berry* 706 (MO); Río Negro, San Carlos de Río Negro, 4 km from San Carlos de Río Negro on road to Solano, 67°1'W, 01°56'N, , *Berry* 1565 (MO), 3 km east of San Carlos de Río Negro, 67°4'W 01°56'N, *Liesner* 3491 (MO), San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, one km west of San Carlos, 67°03'W, 01°56'N, *Buschbacher* 30 (MO), San Carlos de Río Negro, carretera Sn. Carlos-Solano, *Stergios et al.* 4366 (MO), Alrededores de San Carlos del Río Negro, 66°55'W, 01°50'N, *Stergios & Aymard* 7738 (MO), San Carlos de Río Negro, C, 2 km along track running eastwards out of town from airstrip, C, 50 off track, *Stannard* 9 (G[2], U), ca. 20 km South of confluence of Río Negro and Brazo Casiquiare, 67°03'W, 1°56'N, *Boom et al.* 5339 (MO, NY), Selvas pluviales a 8 km al SE de San Carlos de Río Negro, por la carretera que va a Solano, *Aymard et al.* 3513 (MO, NY); Selva alta a lo largo del Río Coro-Coro, vecindades del aeropuerto de Yutaje, 66°10'N, 05°35'N, *Steyermark* 113690 (MO); Santa Barbara del Orinoco, Estación del M, A, R, N, R, Alrededores de Aeropuerto, Selva en galaría del Río Orinoco, *Ruiz et al.* 3924 (F, NY); Puerto Ayacucho, bosque del Río Cataniapo entre Saramasota y San Pedro de Cataniapo, 67°25'W, 06°25'N, *Castillo* 3138 (MO), Santa Rosa de Ucata, transecta entre conuco indigena, pasando por bosque medio, hasta arbustal de arena blanca, *Romero* 1875 (HUH); Aripao, Isla Ratón, Río Orinoco, 67°45'N, 05°09'N, *Velazco* 623 (MO); Río Sinapo-Cuao, Autana, *Castillo* 3830 (MO). **Bolívar:** Campo de Urimán, *Bernardi* 856 (NY); Caño Pablo, tributaRío del Río Caura 5–5,5 km sur Salto Para (Campamento Las Pavas), *Morillo & Liesner* 8931 (MO, NY); 65°04'W, 6°3'N, *Horner et al.* 364 (MO); a la cuenca media del Río Paragua, *Stergios* 10353 (MO, NY); Río Caura, a la altura de Chérkeriña (La Angostura), cerca de la isla Guanaguanadi, *Stergios & Delgado* 12996 (NY); Icabaru, *Dressler* 3009 (NY, US, VEN); De Heres Sabana de Topopo, W, margin of lower Río Caroni opposite Arekuna, 62°55'W, 6°30'N, *Prance & Huber* 28377 (NY); Municipio raul Leone Zona minera Aza Karón, Sector Piedra Pintada, 63°28'00''W, 6°19'11''N, *Diaz* 826 (F[2], NY).

**32. *Sabicea pearcei*** Wernham, Monogr. *Sabicea* 38. t. 3, f. 1. 1914. TYPE: Colombia. about Moro, 914.4–1219.2 m, Jan. 1886 (fl), *R. Pearce s.n.* (holotype, BM!). Figure 39A–J.

Scandent, *terminal flowering branchlet* sparsely to densely pilosulous to puberulous, trichomes 0.1–1.8 mm long. *Stipules* widely ovate, reflexed, 7–10 × 6–7 mm, apically acute to acuminate, membranous, ciliolate with 0.2–1.2 mm long cilia, adaxially glabrous excluding

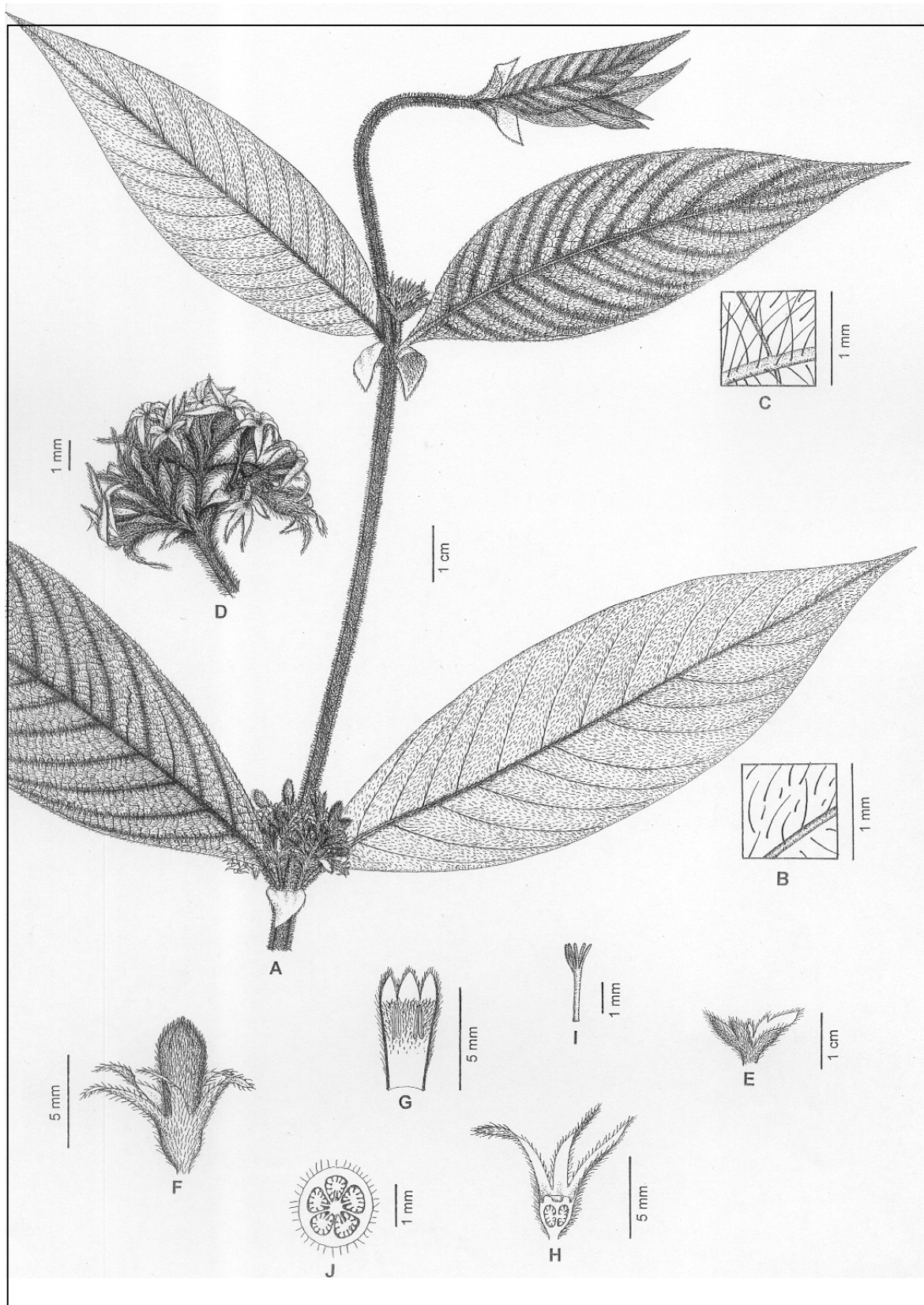


Figure 39. A–J. *Sabicea pearcei*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Inflorescence. —E. Side view of bracts. —F. Immature flower. —G. Inner corolla surface. —H. Longitudinal section through calyx and ovary. —I. Style and stigma. —J. Transversal section through ovary.



the basal part, abaxially sparsely to densely pilosulous, almost all over, 12–14-veined, plain, colleters not seen. *Leaf blades* narrowly elliptic to oblong or lanceolate, 7–12 × 2.5–4.3 cm, apically acuminate, basally acute, membranous, ciliolate with 0.2–1.5 mm long cilia, adaxially sparsely to densely pilosulous to pubescent all over, trichomes 0.2–1.8 mm long; abaxially densely pilosulous to puberulous all over, trichomes 0.2–2 mm long, secondary veins 11–13 pairs, plain adaxially and protruding abaxially, tertiary veins slightly prominulous and quaternary veins distinct abaxially; *petioles* 4–7 mm long. *Inflorescences* 2 per node, 6–9-flowered, subglobose, moderately lax-paniculate, 2–2.5 × 1.5–2 cm, primary axis 2–4 mm long, main lateral axes 2, 8–11 mm, simple to compound dichasia; *peduncles* 4–7 mm long; *bracts* exinvolucrate, membranous, incompletely isolated into 2–3 parts, isolated parts 9–11 × 3–6 mm, 3–6-lobed, lobes 2–3 × 1–5 mm, ovate to triangular, apically acute to acuminate, margins entire, ciliolate with 0.2–1.2 mm long cilia, adaxially and abaxially indumenta same to those at stipules, bracteoles 1, 3–7 × 0.8–3 mm, lingulate to elliptic or lanceolate, *colleters* 2, 0.2–0.4 mm long. *Flowers* usually pedicellate, occasionally sessile, pedicels 1–4 mm long; *calyx* campanulate, 5-lobed, tubes 0.9–1.2 × 1.8–2.1 mm, lobes 1.3–5 × 0.3–1.5 mm, ovate to lanceolate, antrorse to spreaded or gently reflexed to slightly twisted, apically acute, margins entire or serrulate, ciliolate with 0.2–1.2 mm long cilia, adaxially glabrous, abaxially sparsely pilosulous, at lobes and tubes, usually 3-ribbed, colleters 1 in each sinus, 0.2–0.4 mm long; *corolla* salverform, tubes when immature, 3.5–4 × 2–2.2 mm, lobes 1.2–1.5 × 0.8–1.2 mm, ovate, antrorse, the indumentum of orifice extends up to 1.8–2.1 mm, abaxially pilosulous all over the lobes and tubes, trichomes 0.9–2 mm long; *stamens* 5 per flower, attached to corolla tube at 3.5–3.8 mm from the base, anthers 1.7–2.1 × 0.4–0.4 mm; *style* 1.5–2.5 mm long, stigmatic lobes 1.2–1.3 × 0.2–0.2 mm; *ovaries* 1.5–1.8 × 1.5–1.8 mm, abaxially shallowly 5-lobed or uneven, 5-locular, each locule 0.9–1.2 × 0.4–0.6 mm. *Fruits & seeds* not seen.

*Discussion.* *Sabicea pearcei* is known only from its holotype from Colombia (Fig. 10). Standley (1931) argued that *Sabicea pearcei* has been incorrectly attributed to Colombia, instead it occurs in Peru. The protologue gives the patent shaggy indument of stem and leaves, short peduncles, and bracts, and appressed external indument of mature corolla tubes as significant. Any mature corolla has not been found in the type specimen, but an immature one, which is externally covered with patent indument. We maintain its species status due to its few characters that are distinct from its close allies. This species can be characterized by the combination of its erecto-patent indument at branchlets, stipules, leaves, and outer surface of inflorescences, short petioles and peduncles (Fig. 39A), adaxially (excl. base) glabrous stipules, bracts and calyces, compact-paniculate inflorescences with short primary axis, mostly 1.3–5 mm long narrowly lanceolate to linear calyx lobes (Fig. 39H). *Sabicea pearcei* appears closely related to *S. liesneri*, from which it differs by its apparently shorter petioles, paniculate inflorescences, glabrous adaxial surface of stipules, bracts and calyx

lobes, and narrowly lanceolate and usually uniform calyx lobes. It seems close to *Sabicea novo-granatensis* of Venezuela, from which it differs by its paniculate inflorescences, glabrous abaxial surface of stipules, bracts and calyces and narrowly lanceolate calyx lobes. *Sabicea pearcei* might be confused with *S. cochabambensis* due to their common main qualitative characters. However, it clearly differs from *Sabicea cochabambensis* by its larger lamina, shorter peduncles and petioles, smaller inflorescences with shorter primary axes and exinvolucrate bracts and ovate to lanceolate calyx lobes.

**33. *Sabicea pyramidalis*** L. Andersson, Fl. Ecuador 62: 110–112, f. 31. 1999. TYPE: Ecuador: Napo, Reserva Biológica Jatun Sacha. On Río Napo 8 km E of Misahuallí, 1° 4'S, 77°36'W, 450 m, 24 Apr-5 May 1987, C. E. Cerón 1265 (holotype, MO; isotypes, G!, WIS!).

Lianescent shrubs or lianas, stems 2 m long; terminal flowering branchlets sparsely to densely strigulose or pilosulous or hirtellous, sparsely puberulous to pubescent, 0.1–1.1 mm long. *Stipules* narrowly to widely ovate or cordate, reflexed, 6–7.1 × 6–6.8 mm, apically acute, membranous, ciliolate with 0.2–0.7 mm long cilia, adaxially glabrous excluding the basal part, abaxially densely strigulose or pilosulous at the lower part or at the base, isolatedly to sparsely at the upper part, 11–13(–14)-veined, colleters 8–12, 0.6–1.2 mm long. *Leaf blades* narrowly elliptic to oblong, (3–)6–12(–14) × (1.4–)2–6(–7) cm, apically acute to acuminate, basally cuneate or attenuate, thinly papyraceous, isolatedly ciliolate, adaxially isolatedly to sparsely hirtellous and puberulous at lamina, sparsely to densely strigulose to hirtellous and puberulous at costa, trichomes 0.2–0.9 mm long; abaxially isolatedly-densely strigulose and isolatedly puberulous at lamina, densely strigulose and sparsely to densely puberulous, at costa and secondary veins, trichomes 0.4–1.4 mm long, secondary veins 6–10(–12) pairs, costa and secondary veins protruding abaxially and plain adaxially, tertiary and quaternary veins usually distinct abaxially; *petioles* (4–)5–18(–22) mm long. *Inflorescences* one per each node, 10–40-flowered, elongated- and laxly pyramidal- to ovoid-thyrsoid, (3–)4–6(–7.5) × (4.5–)5–7(–7.5) cm, primary axis (15–)20–65 × 0.5–0.8 mm, main lateral axes 4–6(–8), 6–25 mm long, (2–)3–7-flowered; *peduncles* 25–35 mm long; *bracts* exinvolucrate, incompletely isolated into (2–)3–4 parts, isolated parts 2.1–4.4(–5) × 1.4–1.8(–2.1) mm, usually not lobed, rarely 2-lobed, lobes 0.6–0.7 × 0.7–1.1 mm, widely linear to lanceolate or narrowly elliptic to deltate, apically acute, margins entire, ciliolate with 0.1–0.6 mm long cilia, adaxially and abaxially indumenta same to those at stipules, bracteoles (2.1–)2.4–7.1 × (0.4–)0.6–1.6(–2.2) mm, elliptic to lingulate. *Flowers* pedicellate, pedicels (1–)3–8(–12) mm long; *calyx* campanulate, 5-lobed, tubes 0.6–0.7(–0.8) × 1.3–1.8 mm, lobes 1.7–2.4(–3.8) × 0.6–0.9(–1.3) mm, recurved to moderately reflexed, widely linear to narrowly lingulate, apically (sub-)acute, margins entire, ciliolate with 0.4–0.6 mm long cilia, adaxially glabrous, abaxially sparsely

hirtellous to strigulose only along the costa rib, sometimes glabrescent, usually 3-ribbed with costa, adaxially plain, abaxially plain to slightly prominulous, colleters 1 in each sinus, 0.1–0.3 mm long; *corolla* salverform or tubular, tubes 4.5–5 × 0.8–0.9 mm, lobes 0.8–1.2 × 0.6–0.7 mm, ovate, antrorse, adaxially the indumentum extends up to 1.7–3 mm along the tubes, trichomes 2–6 mm long, abaxially densely strigulose, occasionally hirtellous; *stamens* 5 per flower, attached to corolla tube at 4.5–4.6 mm from the base, anthers 1.4 × 0.2 mm; *style* 3–3.2 mm long, stigmatic lobes (0.9–)1.4–1.6 × 0.1–0.1 mm; *ovaries* 1–1.5 × 1–1.4 mm, abaxially almost plain or shallowly 5-lobed, densely strigulose to hirtellous, rarely puberulous, 5-locular, each locule 1.6–1.7 × 0.4–0.5 mm. *Fruits* purple, 5.8–6.5 × 5–5.6 mm when mature, isolatedly strigulose to hirtellous; *seeds* 0.5–0.6 × 0.4 mm.

*Phenology, distribution and habitat.* Flowering and fruiting in March to April. *Sabicea pyramidalis* is limited to Ecuador. It is collected from tropical humid forest; 250–450 m (Fig. 20).

*Discussion.* Andersson (1999) distinguished *Sabicea pyramidalis* (including *S. thyrsoiflora*) from *S. panamensis* based on inflorescence type and pedicel length, but this seems impossible because these characters clearly overlap in these species. Instead, the narrower primary axes, 3–7-flowered lateral axes, shorter and recurved to moderately reflexed calyx lobes and shorter corolla tubes are more useful in distinguishing these species. *Sabicea thyrsoiflora* is separated here from *S. pyramidalis* by its apically acute stipules, bracts and calyx lobes, exinvolucrate bracts and recurved to moderately reflexed, widely linear to narrowly lingulate calyx lobes. It seems close to *Sabicea chocoana* and *S. cochabambensis*. It is readily distinguishable from *Sabicea chocoana* by its usually strigulose indumentum, adaxially glabrous stipules, bracts and calices, apically acute stipules and bracts and mostly appressed trichomes at abaxial surface of corolla tubes. It differs from *Sabicea cochabambensis* by its (sub-)appressed and short trichomes of branchlets, leaves, and outer surface of inflorescences including corolla tubes, and (sub-)appressed and short cilia at the margins of stipules, leaves, bracts and calyces.

*Additional specimens examined.* ECUADOR. **Sucumbios:** Marian Cuatro, 0°1'S, 76°20'W, *Cornejo* 7455 (MO); Yasuní Scientific Research Station, Río Tiputini, NE of confluence with Río Tivacuno, 6 km E of Maxus Road, km 44, 0°42'S, 76°28'W, *Burnham* 1455 (F).

**34. *Sabicea subinvolucrata*** Wernham, Monogr. *Sabicea* 38, t. 3, f. 2, 3. 1914. TYPE: Eastern Peru: San Martín, near Tarapoto, no date (fl), *R. Spruce* 4370 (holotype, K!; isotype, IT).

Suffruticose, *terminal flowering branchlets* densely pilosulous or hirtellous, and isolatedly to sparsely lanuginose, trichomes 0.4–1.1 mm long. *Stipules* ovate to deltate, reflexed to recurved, 7–10 × 6–11 mm, apically (sub-)acute, membranous, margins entire, complanate to recurved, ciliate with 0.1–0.7 mm long cilia, adaxially glabrous excluding the basal part, abaxially hirtellous to pilosulous all over, trichomes 0.2–1 mm long, 12–14-veined, colleters 12–16, 0.5–0.9 mm long. *Leaf blades* usually narrowly elliptic, (5–)9–11 × (2.2–)4–4.5(–5) cm, apically acute to acuminate, papyraceous, ciliate with 0.1–0.7 mm long cilia, sparsely hirtellous to pilosulous at secondary veins and lamina, densely at costa, trichomes 0.1–0.8 mm long; abaxially sparsely to moderately densely strigulose to pilosulous and arachnose to lanuginose at lamina, and densely strigulose to pilosulous and isolatedly arachnose to lanuginose at costa and secondary veins, trichomes 0.2–1.3 mm long, secondary veins 9–13 pairs, costa and secondary veins plain or distinct adaxially and protruding abaxially, tertiary veins distinct abaxially; *petioles* 7–14 mm long. *Inflorescences* 1–2 per node, (16–)22–46(–56)-flowered, pyramidal thyrsoid with compact lateral axes or compact-, ovoid- or subglobose-paniculate, 1–5–8 × 2–4 cm, primary axis (1–)5–65 mm long, main lateral axes 3–4(–6), 2–10 mm long, compound dichasia; *peduncles* (10–)20–30 mm long; *bracts* subinvolucrate, leafy papyraceous, sometimes incompletely isolated into 2–3 parts, 16–17 × 9–11 mm when subinvolucrate, isolated parts 12–16 × 3–9 mm, 2–3-lobed, lobes 3.5–16 × 1–6 mm, widely ovate or lingulate or widely lanceolate, apically acuminate to acute, margins entire, ciliate with 0.1–0.7 mm long cilia, adaxially isolatedly to sparsely strigulose, occasionally glabrescent excluding the basal part, trichomes adaxially (0.1–1.1 mm long), abaxially sparsely to densely strigulose to pilosulous, isolatedly lanuginose almost all over, trichomes 0.5–1 mm long, 7–8-ribbed, lobes 3-ribbed, bracteoles 1.5–11 × 0.2–10 mm, narrowly lanceolate to ovate or deltate, colleters 2, 0.2–0.9 mm long. *Flowers* pedicellate, pedicels 1–4(–5) mm long, densely pilosulous, rarely isolatedly lanuginose, trichomes (0.2–)0.4–1.1 mm long; *calyx* campanulate, (4–)5-lobed, tubes (0.5–)1–1.2 × 1.5–2(–3) mm, lobes (3–)4–6 × 0.5–1.3 mm, usually antrorse to spreaded, sometimes slightly reflexed, linear to lanceolate, apically acuminate, basally truncate, margins entire to serrulate, ciliate with 0.1–0.6 mm long cilia, adaxially glabrous, abaxially isolatedly to moderately densely pilosulous all over the lobes and tubes, 3–4(–5)-ribbed, adaxially plain, abaxially gently prominulous, colleters 1–2 in each sinus, 0.3–0.4 mm long; *corolla* salverform, tubes 4–4.8 × 1.8–2.4 mm, lobes (1.8–)2–2.6 × 0.8–1.8 mm, ovate, antrorse, apically (sub-)acute, margins entire, adaxially glabrous, adaxially the indumentum of orifice extends up to 1.5–2.4 mm inside the tubes, abaxially sparsely to moderately densely strigulose; *stamens* 5 per flower, attached to corolla tube at 1.8–2.4 mm from the base, anthers 1.3–1.8 × 0.2 mm; *style* 1.8–2.4(–2.7) mm long, stigmatic lobes 0.8–1.5 × 0.1–0.1 mm; *ovaries* 1–1.5 × 1–1.5 mm, abaxially plain or uneven, only densely pilosulous or in addition isolatedly lanuginose, 5-locular, each locule 1–1.2 × 0.4–0.6 mm. *Fruits* and *seeds* not seen.

*Phenology, distribution and habitat.* Flowering in May. *Sabicea subinvolucrata* is endemic to Peru (San Martín department); 1350–1500 m (Fig. 10).

*Discussion.* *Sabicea subinvolucrata* is characterized by indumentum on branchlets, abaxial surface of leaves, bracts, and hypanthia based of curled to tortuous trichomes, (16–)22–46(–56)-flowered, pyramidal thyrsoid with compact lateral axes or compact-, ovoid- or subglobose-paniculate inflorescences, subinvolucrate bracts with larger lobes, linear to lanceolate, apically acuminate calyx lobes, and short corolla tubes with strigulose external indument. *Sabicea subinvolucrata* seems very similar to *S. erecta* due to their nearly identical indumentum types, stipules and inflorescence structure. However, it can be distinguished by the combination of its larger stipules, subglobose- and ovoid- to elongated- and pyramidal-thyrsoid inflorescences (in contrast to always (sub-)globose inflorescences), usually subinvolucrate and adaxially isolatedly to sparsely strigulose bracts with longer lobes.

*Additional specimen examined.* PERU: **San Martín:** San Roque, *Williams 7106* (F).

**35. *Sabicea surinamensis*** Bremek., *Recueil Trav. Bot. Neerl.* 33: 707.1936; et in *Meded. Bot. Mus. Herb., Rijks Univ. Utrechr*, No. 35, 707 (1936). TYPE: Suriname: along the river Corantyne, at a place said to be one day rowing above the Frederik-Hendrik Falls, 31 Aug. 1935 (fl), *H. E. Rombouts 165*, (holotype, U!, photo NY!).

Terminal flowering branchlets sparsely to moderately densely pilosulous, and isolatedly puberulous, eventually glabrescent, (0.2–)2.5–3 mm long. *Stipules* ovate to deltate, reflexed, 6–12 × 7–14.5 mm, undivided or apically minutely bifid, acute or obtuse, membranous, margins denticulate, complanate, ciliolate to ciliate with (1–)1.5–2 mm long cilia, adaxially glabrous excluding the basal part, abaxially isolatedly to sparsely sericeous to pilosulous at the lower part and at the middle, eventually glabrous, trichomes 0.5–2 mm long, (9–)12–14-veined. *Leaf blades* narrowly elliptic, (3–)8–13.5 × (1.4–)3–5.8 cm, apically acuminate, papyraceous, ciliate with (0.8–)1–2 mm long cilia, sparsely pilosulous to pubescent at secondary veins and lamina, densely at costa, trichomes (0.2–)0.5–2.3 mm long; abaxially sparsely pilosulous at lamina, moderately densely at costa and secondary veins, trichomes (1–)1.6–2.5 mm long, secondary veins (7–)9–11 pairs, usually plain adaxially and protruding abaxially, tertiary veins plain or prominulous and quaternary veins distinct abaxially; *petioles* 2–10 mm long. *Inflorescences* 1 per node, 3–4-flowered, compact-fascicled, 2–3 × 1–1.5 cm; *peduncles* 0–1.5 mm long; *bracts* involucrate, papyraceous, 5–10 × 9–12 mm, 3–5-lobed, lobes 3–9.5 × 3–12 mm, ovate to deltate, apically subacute to obtuse, margins denticulate, ciliolate to ciliate with (0.6–)1–1.8 mm long cilia, adaxially isolatedly to sparsely pilosulous to sericeous excluding the basal part, abaxially usually isolatedly to sparsely pilosulous, trichomes 0.8–2.2 mm long, colleters not seen, *calyx* infundibuliform, 5-lobed, tubes 4–9.4 ×

2.4–5.5(–6.5) mm, lobes 1.5–6 × 1.5–4 mm, antrorse, widely lanceolate, apices (sub-)acute, margins denticulate, ciliolate to ciliate with 1–1.5(–2) mm long cilia, isolatedly to sparsely pilosulous at upper part up to the middle of tubes, glabrous at lower part, trichomes (0.2–)0.6–1.5 mm long, abaxially isolatedly to sparsely pilosulous, trichomes (0.6–)1–2 mm long, tubes 9–12-ribbed in upper part, lobes 3–4-ribbed with costa, distinct abaxially, colleters 1–2, 4–5 mm below each sinus, 0.3–0.5 mm long; *corolla* hypocrateriform, tubes 17–22 mm × 1–2 mm, lobes 3–3.5 × 1.5–2 mm, widely lanceolate to narrowly ovate, antrorse, adaxially the indumentum of orifice extends up to 12–15 mm inside the tubes, abaxially densely pilosulous, trichomes (2.6–)3–3.5 mm long; *stamens* 5 per flower, attached to corolla tube at 16–21 mm from the base, anthers 2.5–3 × 0.3–0.4 mm; *style* 12–13 mm long, stigmatic lobes 5, 2.8–3.2 × 0.1–0.1 mm; *ovaries* 0.9–1.2 × 0.9–1.2 mm, abaxially densely pilosulous, 5-locular, each locule 0.6–7 × 0.3–0.4 mm. *Fruits* and seeds not seen.

*Discussion.* *Sabicea surinamensis* is known only from the type specimen. It is distinguishable by the combination of fascicled inflorescences, ample infundibuliform calyces, pilosulous indumentum of branchlets, stipules, leaves, and inflorescences lacking arachnose, lanuginose or lanate indumentum, widely lanceolate and apically (sub-)acute calyces with colleters inside the tubes below the sinus, and long corolla tubes. This species seems closely allied to *Sabicea amazonensis* due to its almost similar inflorescence characters, but it can be readily distinguished by its non-arachnoid branchlets, abaxial leaf surface and inflorescences. *Sabicea surinamensis* is confusable with *S. traillii* from which it differs by its longer corolla tubes (17–22 mm in contrast to 9–14 mm long), erecto-patent trichomes at adaxial leaf surfaces and longer trichomes at abaxial leaf surfaces (1.6–2.5 mm in contrast to 0.7–1.5 mm long) and corolla lobes (usually 3–3.5 mm in contrast to 1.2–2.8 mm long).

**36. *Sabicea tayloriae*** Rusby ex Liede, Meve & Khan, sp. nov., TYPE: Bolivia. Apolo, 1463.04 m, 17 Apr. 1902 (fl & fr), *R. S. Williams 173* (holotype, BM!; isotype, F!). Figure 40A–L.

*Inter species Sabicea distinguitur habitu scandente, indumento ramulorum, paginarum superiore stipulorum foliorumque, et inflorescentiarum arachnoso ad lanuginoso, petiolis 6–21(–25) mm longis, inflorescentiis capitatis pedunculatisque.*

Vines or lianas, stems 1–1.5(–8) m long; terminal flowering branchlets sparsely to densely arachnose to lanuginose or lanate, rarely pubescent, eventually glabrescent, trichomes, (0.6–)1–1.5(–2.1) mm long. *Stipules* ovate or deltate to or triangular, antrorse, 4–8(–9) × 3–6(–8) mm, apically (sub-)acute to acuminate, margins entire, complanate, ciliolate with 0.1–0.7 mm long cilia, adaxially isolatedly minutely sericeous at apices in addition to the basal part,

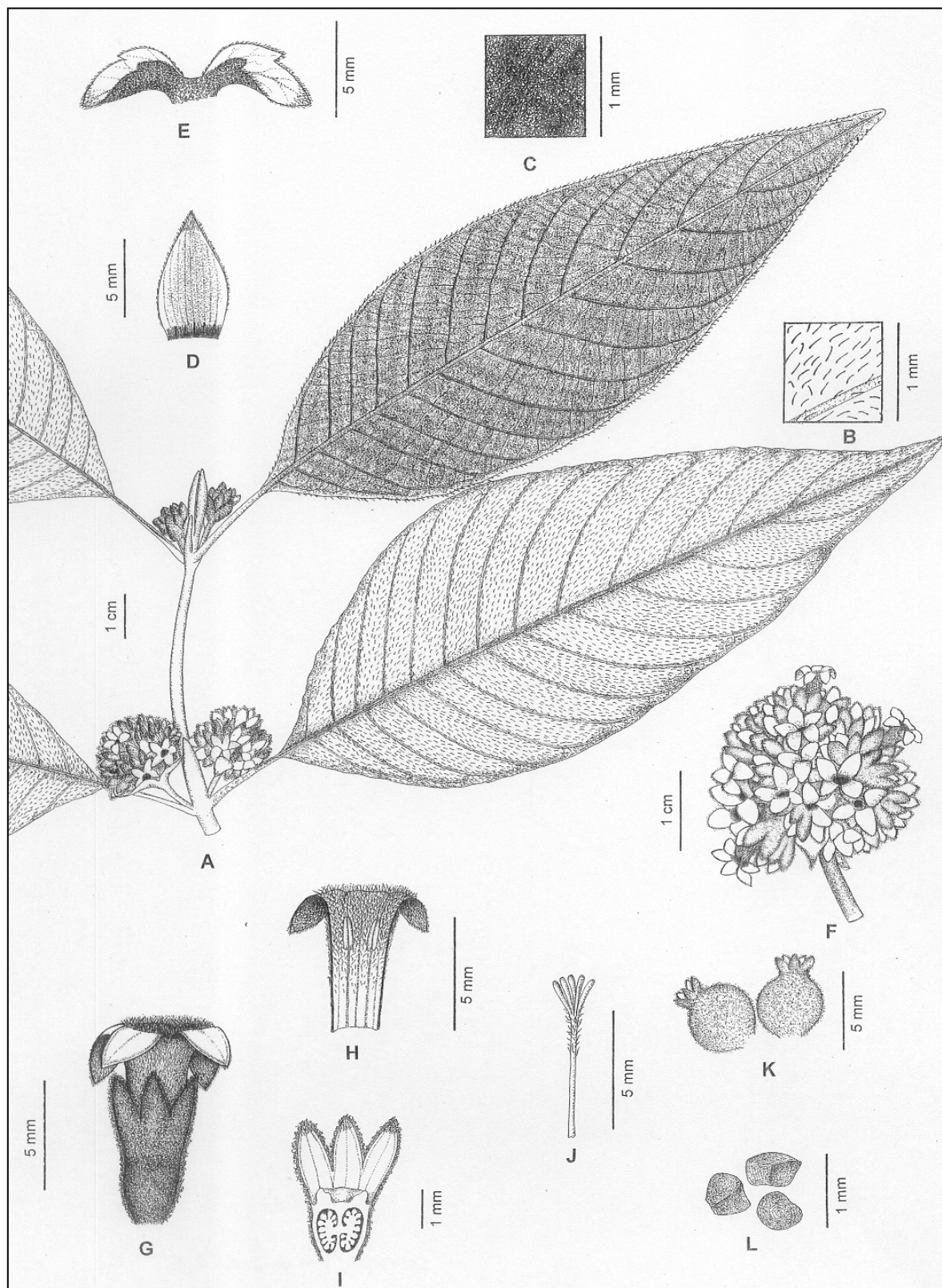


Figure 40. A–L. *Sabicea tayloriae*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Inner stipule surface. —E. Side view of bract. —F. Inflorescence. —G. Flower. —H. Inner corolla surface showing anther's position. —I. Longitudinal section through calyx and ovary. —J. Style and stigmas. —K. Fruits. —L. Seeds.

abaxially usually densely lanate to lanuginose all over, occasionally pubescent, trichomes (0.8–)1–2.1 mm long, 9–12-veined, veins slightly raised adaxially, colleters 2–3, 0.9–1.2 mm long. *Leaf blades* usually narrowly ovate to widely lanceolate or elliptic or oblong, (2.5–) 6–16(–18.5) × (1.5–3–6(–7.5) cm, apically usually acute to acuminate, rarely obtuse, basally acute, papyraceous, cilia almost same to those of stipules, adaxially sparsely to densely pubescent at secondary veins and lamina, densely pubescent to pilosulous at costa, trichomes 0.1–0.9 mm long; abaxially sparsely to moderately densely arachnose to lanuginose or lanate and occasionally isolatedly to sparsely strigulose all over, secondary veins 11–17 pairs, plain adaxially, protruding abaxially, tertiary veins prominulous and quaternary veins usually distinct abaxially; *petioles* 6–21(–25) mm long. *Inflorescences* one to two per node, 5–16(–21)-flowered, usually capitate with distinct, occasionally indistinct peduncle, 1.5–2.2 × 1.5–2.5 cm; *peduncles* 1–15 mm long; *bracts* (sub-)exinvolucrate, membranous, incompletely isolated into 2–5 parts, isolated parts 3–7(–12) × 4–6(–11) mm, 0–3-lobed, lobes 1–4.5 × 0.8–4 mm, ovate to deltate or widely elliptic, apically (sub-)acute to acuminate, margins entire, ciliolate with 0.2–0.8 mm long cilia, adaxially and abaxially indumenta almost same to those at stipules, 7–10-ribbed, lobes 3–5-ribbed, bracteoles 2–6 × 0.8–4 mm, ovate to lanceolate or elliptic, slightly cymbiform, apically acute to acuminate, base truncate or obtuse, margins entire, colleters 2, 0.3–0.5 mm long. *Flowers* usually sessile, rarely subsessile, pedicels 0(–1) mm long; *calyx* campanulate, (4–)5-lobed, tubes (0.8–)1–2(–2.5) × 2.5–3(–3.6) mm, lobes 0.8–3(–4) × (0.2–)0.8–2.1(–2.5) mm, antrorse to spreaded, triangular to ovate or lingulate to deltate, one lobe per calyx is usually smaller, apically widely acute to obtuse, margins entire, ciliolate with 0.2–0.8 mm long cilia, adaxially isolatedly to sparsely sericeous at apices and glabrous at rest of the surface, trichomes 0.07–0.5 mm long, abaxially lanuginose all over the lobes or tubes, trichomes (0.8–)1–2.1 mm long, 3–5-ribbed without any costa, usually abaxially plain, adaxially slightly prominulous to plain, colleters 1(–2) in each sinus, 0.1–0.4 mm long; *corolla* white to creamy, salverform, tubes 3.5–6.2 × 1.8–2.5 mm, (4–)5-lobed, lobes (2.5–)3–3.8 × 1.8–2.1 mm, narrowly ovate to lingulate or antrorse to moderately reflexed, apically (sub-)acute, margins entire, adaxially the indumentum of orifice extends up to 2.3–3 mm inside the tubes, abaxially densely sericeous to villosulous and lanuginose at lobes and upper part of tubes, trichomes (0.6–)0.8–2.1 mm long, *stamens* (4–)5 per flower, attached to corolla tube at 3.8–4.1 mm from the base, anthers 1.2–2 × 0.4–0.5(–0.6) mm; *style* 2.8–5.3 mm long, stigmatic lobes 4–5, (1.2–)1.4–1.8 × 0.2–0.4 mm; *ovaries* 1.5–1.8(–2.1) × 1.5–1.8 mm, abaxially shallowly 4 to 5-lobed or uneven, densely lanuginose, occasionally isolatedly to sparsely sericeous, trichomes 0.6–1.8 mm long, 4–5-locular, each locule 1–1.8 × 0.5–0.7 mm. *Fruits* purple or red-blue, 3–4 × 3–4 mm when immature, 6–8 × 6–8 mm when mature, isolatedly to sparsely lanuginose, occasionally sericeous; *seeds* 0.4–0.6 mm long, 0.3–0.8 mm.



*Phenology, distribution and habitat.* Flowering from January to July and November to December, fruiting in April. *Sabicea tayloriae* extends from central to northern west Bolivia to Peru and Acre state of Brazil with discontinuity. This species is found in humid sub-montane or tropical evergreen, primary or secondary forests, remnants of forests or cleared forest fields, orchards, pastures and fencerows, low land, slopes and bases of hills, highway embankments. It grows on sandy to clayey and gravelly soil; 140–1400 m (Fig. 12).

*Discussion.* *Sabicea tayloriae* is distinct by the combination of its lianoid or lianescent habit, exclusively or predominantly arachnose to lanuginose or lanate indumentum at the branchlets, abaxial surface of stipules, leaves, and inflorescences excluding corolla, long petioles, adaxially merely pubescent to pilosulous leaf blades (Fig. 40B) with plain secondary and tertiary veins, capitate inflorescences with usually distinct peduncles (Fig. 40A, F), adaxially isolatedly sericeous apices of stipules, bracts, and calyx lobes, flexuous cilia at the margins of leaf, stipules and bracts, densely sericeous to villosulous and lanuginose external indumentum of corolla, and glabrous styles.

*Sabicea tayloriae* superficially appears closely allied to *S. brasiliensis* and *S. cana* due to its indumentum of branchlets, lower surface of leaves, and inflorescences, shape and size of calyx lobes, and compact inflorescences. However, it is distinct from both *Sabicea brasiliensis* and *S. cana* by its exclusively and densely pubescent to pilosulous adaxial leaf blades (Fig. 40B). Additionally it is distinguishable from *Sabicea brasiliensis* by its lianoid or lianescent habit, longer petioles ([6–]8–25 mm in contrast to 1–4[–7] mm), capitate inflorescences with usually distinct peduncles (Fig. 40A, F), plain secondary and tertiary veins at the adaxial surface of leaf blades, whereas, from *S. cana* by its adaxially isolatedly sericeous apices of stipules, bracts, and calyx lobes, flexuous cilia at the margins of leaves, stipules and bracts, densely sericeous to villosulous and lanuginose external indumentum of corolla, and glabrous styles.

*Sabicea tayloriae* seems confusable with *S. klugii*, from which it is very distinct by its exclusively pubescent to pilosulous indumentum of adaxial leaf surfaces composed of shorter trichomes, capitate inflorescences, exclusively or predominantly arachnose or lanate to lanuginose indumentum at the branchlets, lower surface of leaves, and outer surface of inflorescences excluding corolla, shorter cilia at the margins of stipules, bracts and calyx lobes, and shortly triangular to ovate or lingulate, apically widely acute to obtuse and marginally entire calyx lobes (Fig. 40F, I). It is supposed that H. H. Rusby used the name *Sabicea pedunculata* in 1886 in determination of few specimens of this species but this name was never published.

*Additional specimens examined.* BOLIVIA. **Beni:** Ballivián, San Borja 49 km, hacia alto Beni, 14°49'S, 66°48'W, -Beck 13242 (MO); Al Sud de la Mision Fatima, Beck et al. 16340 (F, MO). **La Paz:** Chuquini, Río Tipuani, Tate 1124 (NY); Mapiri, Rusby 1905 (F!, BM!, F, G!,

HUHL, NY!, WIS!); San Carlos, *Buchtien* 1453 (BM); Apolo, -*Williams* 173 (BM, F); Cordillera Real, Chuquini, *Tate* 1124 (NY); Larecaja, 3,2 km al SO de Tipauni por el camino a Unutuluini, *Solomon* 17699 (MO, M, NY, U); Franz Tamayo, Apolo 47 km hacia Charazani, 17°10'S, 67°14'W, *Beck* 18599 (MO); Larecaja, Consata 7 kms, hacia Mapiri, 15°17'S, 68°31'W, *Beck* 4914 (MO); Chuquini, Cordillera Real, 15°19'S, 68°31'W, *Tate* 1137 (NY); Yungas, Below San Pedro, Yolosa-Caranavi road, valley of Río Coroico, *Gentry et al.* 44214 (MO, NY, U); 3.2 km from Tipuani, 15°33'S, 68°0'W, *Grifo & Solomon* 808 (MO); Saavedra, area natural de Manejo Integrado Apolobamba, Paujeyuyo, 15°02'40''S, 68°27'47''W, *Araujo-Murakami et al.* 760 & 798 (MO); Hacienda Simaco sobre el camino a Tipauni, *Buchtien* 5576 (F, HUH, NY, US); Chanpampa, *Buchtien s.n.* (M). **Santa Cruz:** Sara, Buena Vista, *Steinbach* 5234 (F, HUH, MO, NY); Ichilo, 2 km WSW of Buena Vista on road to El Cairo, 17°27'S, 63°41'W, *Nee & Coimbra* 36093 (MO, NY); 1 km ENE of bridge over Río Ichilo (and boundary with Dept. Cochabamba), 17°15'S, 64°19'W, *Nee* 46014 (MO, NY); 1,5 km SW of Villa Nuevo Horizonte, highway from Buena Vista to Villa Tunari, 17°20'S, 64°10'W, -, *Nee* 46472 (NY), 3,5 km SW of turn of at Villa San Isiro from new highway from Buena Vista to Río Ichilo, 17°20'S, 64°00'W, *Nee* 48542 (NY), ca. 2 km W of Villa San Germán on highway from Buena Vista to Río Ichilo, 17°21'S, 64°06'30''W, *Nee* 48400 (NY). **BRASIL. Acre:** Porto Walter, Río Juruá-Mirim, Comunidade Santo Antonio, 08°14'S, 73°03'W, *Delprete et al.* 7719 (MO, U). **PERU. San Martín:** Lamas, *Vigo* 5348 (F, G, HUH, NY). **Beni:** Ballivian Province, Carretera Caranavi-San Borja, Serranía del Pilón Lajas, 15°09'S, 67°31'W, *Smith et al.* 13950 (MO). **Junín:** Satipo, Gran Pajonal, between Paucarete and Tihuanaski, 10°45'S, 74°23'W, *Smith* 6562 (MO). **Loreto:** Alto Amazonas, Lagunas, Pasto Grande, 5°13'S, 75°38'W, *McDaniel & Rimachi* 16479 (MO). **Pasco:** Oxapampa, Gran Pajonal, northwest to Chequitavo, 10°45'S, 74°23'W, *Smith* 6677 (MO).

**37. *Sabicea thyrsoflora*** L. Andersson, Fl. Ecuador 62: 112, f. 30A, 32. 1999. TYPE: Ecuador, Esmeraldas, San Lorenzo, new road to "Proyecto NO", km 4–5, secondary tropical rain forest, 21 Aug. 1967, *B. Sparre* 18272 (holotype, S; isotype, MO!). Figure 41A–M.

Lianas or vines; terminal flowering branchlets sparsely to densely strigulose to hirtellous, and sparsely puberulous to pubescent, trichomes (0.1–)0.2–1.1(–1.3) mm long. *Stipules* ovate to deltate, recurved or reflexed, 6.5–7(–7.9) × (5.3–)5.5–7(–7.6) mm, apically acute to obtuse or rounded, membranous, margins entire, complanate, ciliolate with (0.07–)0.12–0.4 mm long cilia, adaxially glabrous excluding the basal part, abaxially very densely to sparsely strigulose or occasionally hirtellous, almost all over, at the base or at the lower part and along the veins, sparsely to isolatedly at the upper part, abaxially strigulose or hirtellous, trichomes (0.2–)0.5–0.9(–1.2) mm long, (9–)10–13(–14)-veined, plain adaxially, slightly raised abaxially, colleters 15–17, (0.5–)1–1.5 mm long. *Leaf blades* elliptic to widely lanceolate or oblong to ovate, (5.3–)7.5–10.4(–11.7) × (2.5–)2.6–5.2(–5.4) cm, apically bluntly acuminate, basally obtuse to

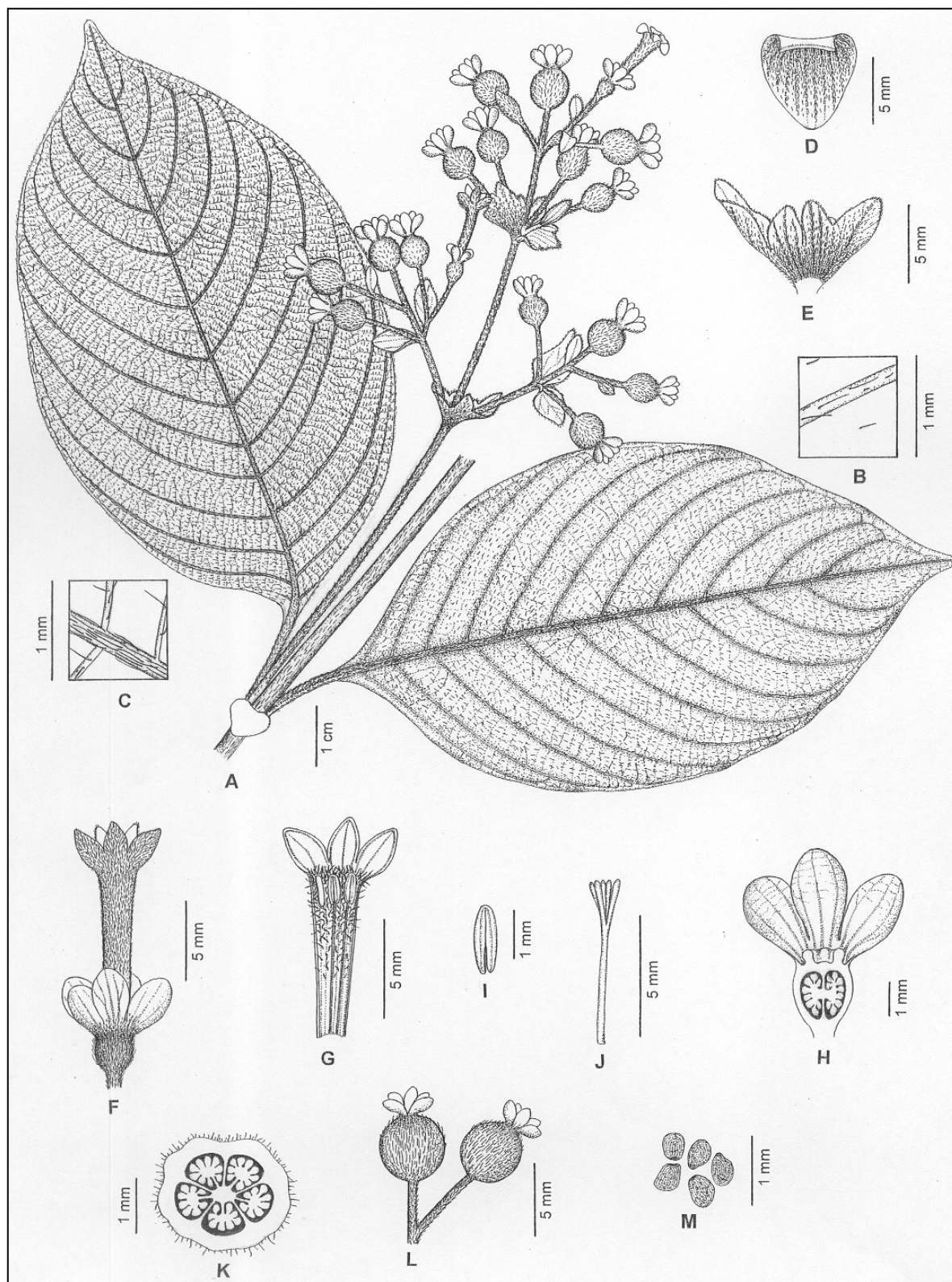


Figure 41. A–M. *Sabicea thyrsoiflora*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Outer stipule surface. —E. Side view of bract. —F. Flower. —G. Inner corolla surface showing anther's position. —H. Longitudinal section through calyx and ovary. —I. Face view of Anther. —J. Style and stigmas. —K. Transversal.

attenuate, membranous to papyraceous, margins entire or slightly wavy, cilia mostly similar to trichomes of abaxial costa and secondary veins; adaxially dark green, sparsely hirtellous at lamina, densely to sparsely strigulose to hirtellous and puberulous at costa and secondary veins, trichomes (0.1–)0.3–1(–1.3) mm long, puberulous trichomes (0.1–)0.12–0.3 mm long; abaxially light green or dark, densely strigulose, occasionally puberulous at costa and secondary veins, isolatedly to densely at lamina, trichomes 0.4–1.1(–1.3) mm long, secondary veins (9–)10–12 pairs, costa and secondary veins protruding abaxially, plain or protruding adaxially, tertiary and quaternary veins usually distinct abaxially; *petioles* 6–30 mm long, 1–2 mm, sparsely to densely strigulose to hirtellous or puberulous. *Inflorescences* 1 per node, (5–)21–32(–42)-flowered, elongated- and laxly pyramidal- to ovoid-thyrsoid, (2.5–)3.4–6.5(–7.5) × (2.5–)3–5.5(–6) cm, primary axis (5–)10–40(–50) mm long, lateral axes (2–)4–6, paniculate or dichasia; *peduncles* (15–)18–48(–65) mm long; *bracts* (sub-)involucrate, usually leafy, thick papyraceous, soft, occasionally incompletely isolated into 2–3 parts, 3–5.5 × 6–10 mm when subinvolucrate, isolated parts 2.9–5 × 4.7–6.5 mm, variously 3–5-lobed, lobes (0.4–)0.5–0.8(–2.4) × (0.4–)0.5–1.4(–1.9) mm, triangular to deltate, apically obtuse to subacute, basally truncate to obtuse, margins entire, ciliolate with (0.2–) 0.4–0.6 mm long cilia, adaxially and abaxially indumenta nearly same to those at stipules, involucre 10–12-ribbed, lobes 1–3-ribbed, bracteoles (1.5–)1.8–5.8(–7.1) × (0.6–)0.9–4.6(–5.2) mm, lanceolate to deltate or ovate to lingulate or elliptic, 1–2 lateral lobes, apically obtuse to subacute, base attenuate, margins entire, ciliolate or eciliate. *Flowers* pedicellate, pedicels (2.1–)5–10(–12) mm long; *calyx* campanulate, 4–5-lobed, tubes 0.3–0.5(–0.6) × (0.6–)0.8–1.2(–1.3) mm, lobes (2.4–)2.5–3.5(–3.8) × (0.5–)1.3–1.9(–2.3) mm, antrorse, elliptic or shortly lingulate, apically obtuse to rounded or subacute, basally attenuate, margins entire, eciliate to ciliolate, ciliolate with (0.1–)0.2–0.6 mm long cilia, adaxially glabrous, abaxially densely to sparsely hirtellous to strigulose, almost all over up to the middle of lobes, 3(–5) ribbed, colleters usually 1(–2) in each sinus, (0.1–) 0.2–0.4 mm long; *corolla* salverform or tubular, tubes 3.2–8 × (1.4–)2.4–2.7 mm, lobes (0.9–)1.1–1.5(–2.3) × 0.9–1.1 mm, ovate, somewhat recurved to antrorse, apically (sub-)acute, margins entire, adaxially the indumentum of orifice extends up to 2.5–2.7(–3) mm inside the tubes, trichomes of orifice (0.1–)0.2–0.3(–0.5) mm long, abaxially densely strigulose to hirtellous with forming cluster near the apices of lobes; *stamens* 5 per flower, attached to corolla tube at (3.2–)3.5–4(–4.2) mm from the base, anthers 1.1–1.4(–1.7) × 0.2–0.4 mm; *style* (1.6–)4.7–5 mm long, stigmatic lobes 1.7–1.9 × (0.1–)0.2 mm; *ovaries* 1.4–1.9 × 1.4–2.4 mm, abaxially almost plain or 5-lobed, densely strigulose to hirtellous, 5-locular, each locule 1–1.2(–1.4) × 0.4–0.7 mm. *Fruits* pink, 3.5–4.1 × 3.2–5 mm when immature, 8 × 9 mm when mature, isolatedly strigulose to hirtellous; *seeds* 0.3–0.4 mm long.

*Phenology, distribution and habitat.* Flowering and fruiting in February and October. Obviously limited to Esmeraldas province of Ecuador (*Sabicea thyrsoiflora* var. *thyrsoiflora*) and

Departamento Del Valle of Colombia (*S. thyrsoiflora* var. *colombiana*). It is found in primary forests or forest along banks of stream; 100–400 m (Fig. 20).

*Discussion.* *Sabicea thyrsoiflora* is characterized by its elongated- and laxly pyramidal- to ovoid-thyrsoid inflorescences, usually strigulose indumentum at branchlets, abaxial surface of stipules, leaves, and external surface of inflorescences including corolla tubes, subinvolucrate bracts, apically obtuse stipules, bracts and calyx lobes, elliptic to widely lingulate, antrorse calyx lobes. *Sabicea thyrsoiflora* appears closely allied to *S. panamensis*, especially *S. panamensis* var. *santanderensis* and *S. pyramidalis*. It is distinct from these two species by its apically obtuse to rounded or (sub-)acute stipules, bracts and calyx lobes, and elliptic or lingulate calyx lobes (Fig. 41F, H). Additionally it differs from *Sabicea pyramidalis* by its subinvolucrate bracts and longer corolla tubes. Andersson (1999) included the length-width ratios and apex-types of leaves in distinguishing this species from *S. pyramidalis*, which cannot be confirmed. It seems close to *Sabicea chocoana* from which it differs in its mostly differentiated and strigulose indumentum of branchlets, abaxial surface of leaves, and inflorescences including corolla tubes, subinvolucrate bracts, longer, wider, antrorse, and elliptic or shortly lingulate calyx lobes, adaxially glabrous upper part or apices of stipules, bracts and calices. *Sabicea thyrsoiflora* var. *colombiana* is considered as a new variety because of its unique combination of characters that are not seen in other Neotropical *Sabicea*.

#### Key to the subspecies:

- 1a. Inflorescences 5–21-flowered, lateral branches < 5-flowered, corolla tube  
6.5–8 mm long.....37a. *S. thyrsoiflora* var. *thyrsoiflora*
- 1b. Inflorescences 32–42-flowered, lateral branches > 5-flowered, corolla tube  
3.2–6.5 mm long.....37b. *S. thyrsoiflora* var. *colombiana*

#### 37a. *Sabicea thyrsoiflora* L. Andersson var. *thyrsoiflora*.

*Additional specimens examined.* **ECUADOR. Esmeraldas:** Approximately 300 m downstream from Río Palaví Awá encampment, *Hoover 4052* (MO); Eloy Alfaro Cantón, Reserva Ecológica Cotachi-Cayapas, Parroquia Luis Vargas Torres, Río Santiago, estero Pote, *Tirado, et al. 554* (MO, NY); San Lorenzo Cantón, Creek pouring into Río Palaví across from Awá camp on west bank, 0°58'N, 78°16'W, *Hoover et al. 3074* (MO), *Hoover 3113* (MO); San Lorenzo, Awá Indigenous Territory, Río Bogotá community, 2 km south of Lita-San Lorenzo road, near Quebrada Pambilar, 00°59'N, 78°35'W, *Neill et al. 13978* (MO).

#### 37b. *Sabicea thyrsoiflora* L. Andersson var. *colombiana* Liede, Meve & Khan, var. nov.

TYPE: Colombia: Departamento Del Valle, Costa de Pacífico, Río Yurumanagui, entre Isla de Golondro y La Amargura, 10–40 m, 07 Feb. 1944 (fl), *J. Cuatrecasas 16050* (holotype, US!).

*Differt de varietate typica inflorescentiis longe thyrsoides de 32–42 flores, pedunculis 35–40 mm longis, bracteis subinvolucratis, tubis corollarum 3.2–6.5 mm longis.*

**38. *Sabicea tillettii*** Steyerl., *Phytologia* 31 (6): 484 (1975). TYPE: Venezuela: Amazonas, Depto Atabapo, near Laja, ca. 1 km inland from mouth of Caño Chamuchina, 2 hours up Río Atabapo from San Fernando de Atabapo, on right bank, 4°2'N, 67°42'W, ca. 130 m, 27 May–03 Jun. 1974, *S. S. Tillett & L. Gutierrez et al. 745–385* (holotype, VEN, not seen, photo VEN!).

Vines, densely arachnose or lanate, and isolatedly sericeous to pubescent. *Stipules* narrowly ovate to triangular, apically acute or acuminate, basally obtuse, margins entire, complanate, eciliate, adaxially sericeous at the base, abaxially densely arachnose or lanate to lanuginose all over, 9–14-veined, colleters not seen. *Leaf blades* lanceolate to narrowly ovate, 4.5–9.5 × 0.8–2.5 cm, apically acuminate, bases obtuse to (sub-)acute, thickly papyraceous, eciliate; adaxially floccose to moderately densely arachnose or lanate, eventually glabrous at lamina, always densely arachnose at costa; abaxially densely arachnose or lanate, secondary veins 12–15 pairs, secondary and tertiary veins plain to slightly sunken adaxially and prominulous abaxially; *petioles* 3–8 mm long, arachnose. *Inflorescences* 1 per node, 7–12-flowered, compact-fascicled or glomerate, sessile, 1.5–2 × 2–2.5 cm (without corolla); *bract* subinvolucrate to exinvolucrate, lobes lanceolate to narrowly ovate, abaxially densely or lanate to lanuginose; *calyx* 4–5-lobed, campanulate, tubes 1.5–3.1 × 2.5–3.5 mm, lobes 4–7 × 0.8–1.6 mm, antrorse, linear or lanceolate, apically sharply acuminate, margins entire, ciliolate with 0.5–1.5 mm long cilia, adaxially glabrous or isolatedly to sparsely arachnose and isolatedly sericeous at the upper part, glabrous at lower part, trichomes 0.5–1.1 mm long, abaxially densely or lanate to lanuginose and isolatedly sericeous to villosulous all over, sericeous-villosulous trichomes 1–2.1 mm long; mature *corolla* not seen, tubes 12 mm, immature corolla hypocrateriform, lobes 1 to 1.3 mm long, lanceolate or ovate, adaxially moniliform at orifice, abaxially sericeous or pubescent, trichomes (1–)1.2–1.6 mm long, (sub-)appressed to ciliate; trichomes of hypanthium (1–)1.5–2.3 mm long, 5-locular, each locule 0.7 × 0.4 mm.

*Phenology, distribution and habitat.* Flowering in February and May–June; known only from Venezuela at 130–200 m (Fig. 14).

*Discussion.* Steyerl (1975) recognized *Sabicea tillettii* based on its rich inflorescences,

narrow and adaxially completely glabrous calyx lobes, short corolla with sericeous external indumentum, short and narrow corolla lobes, and shorter anthers, filaments, and styles. Among these characters, the length of corolla tubes, anthers, filaments, and styles failed to distinguish *Sabicea tillettii* from *S. cinerea*. Nevertheless, we maintain specific status for *Sabicea tillettii* mainly based on the narrow calyx lobes with acuminate apices and the sericeous external indumentum of corolla. *Cerda 2426* (NY) appear an intermediate of *Sabicea cinerea* and *S. tillettii*. *Sabicea tillettii* might be a dubious species unless its distinction from *S. cinerea*, based on calyx lobes with acuminate apices and the sericeous external indumentum of corolla, will be confirmed by additional collections.

*Additional specimens examined.* Venezuela. **Amazonas:** Atabapo. Sabana sobre colinas y planicies aprox. 10 km al E del case Río de Carmelitas, en la ribera S del bajo Río Ventuari, 04°07'N, 66°28'W, *Huber, 3252* (NY).

**39. *Sabicea traillii*** Wernham, Monogr. *Sabicea* 61–62. t. 12. 1914. TYPE: Brazil: R. Amazon, Bank of lower Amazon and territories, Obidos, 22 Jun 1874, *J. W. H. Trail 390* (lectotype, designated here, K!; duplicate, photo F!, NY [2!]). Figure 42A–M.

Terminal flowering branchlets sparsely to moderately densely pilosulous and isolatedly puberulous, eventually glabrescent, (0.1–)0.9–2 mm long. *Stipules* ovate to widely ovate, reflexed, 5.5–9 × 5.5–8 mm, undivided or apically minutely bifid, (sub-)acute, membranous, margins denticulate, complanate, ciliolate with (0.1–)0.4–0.6 mm long cilia, adaxially glabrous excluding the basal part, trichomes (0.8–)1.4–2.1 mm long, abaxially isolatedly to sparsely sericeous to pilosulous at the lower part and at the middle, eventually glabrous, trichomes (0.1–)0.4–2.1 mm long, (9–)12–14-veined, veins plain adaxially, slightly raised abaxially, colleters 9–12. *Leaf blades* narrowly elliptic, (0.8–)2–9 × (0.7–)1–4.5 cm, apically acuminate, papyraceous, ciliolate with (0.1–)0.4–1.1 mm long cilia, sparsely to moderately densely hirtellous to pubescent at secondary veins and lamina, densely, at costa, trichomes (0.2–)0.4–1.3 mm long; abaxially sparsely strigulose to puberulous at lamina, densely strigulose and isolatedly to sparsely puberulous at costa and secondary veins, trichomes (0.1–)0.7–1.5 mm long, secondary veins 7–11 pairs, usually plain adaxially and protruding abaxially, tertiary veins plain or prominulous and quaternary veins distinct abaxially; *petioles* 0–8 mm long. *Inflorescences* 1 per node, 3–5-flowered, loose fascicled, 2–3 × 1–1.5 cm; *peduncles* 0–3 mm long; *bracts* involucrate, papyraceous, 4–6(–8) × 9–14(–15) mm, 3–5-lobed, lobes 1.4–9.5 × (1.4–)2.4–8.5 mm, ovate to deltate or lingulate, apically subacute to obtuse, margins denticulate, ciliolate to ciliate with (0.1–)0.6–1.9(–2.1) mm long cilia, adaxially isolatedly to sparsely pilosulous to sericeous in addition to the densely basal part, trichomes (0.1–)0.7–2.4 mm long, abaxially usually isolatedly to sparsely pilosulous, trichomes (0.1–)0.8–2.2 mm long,



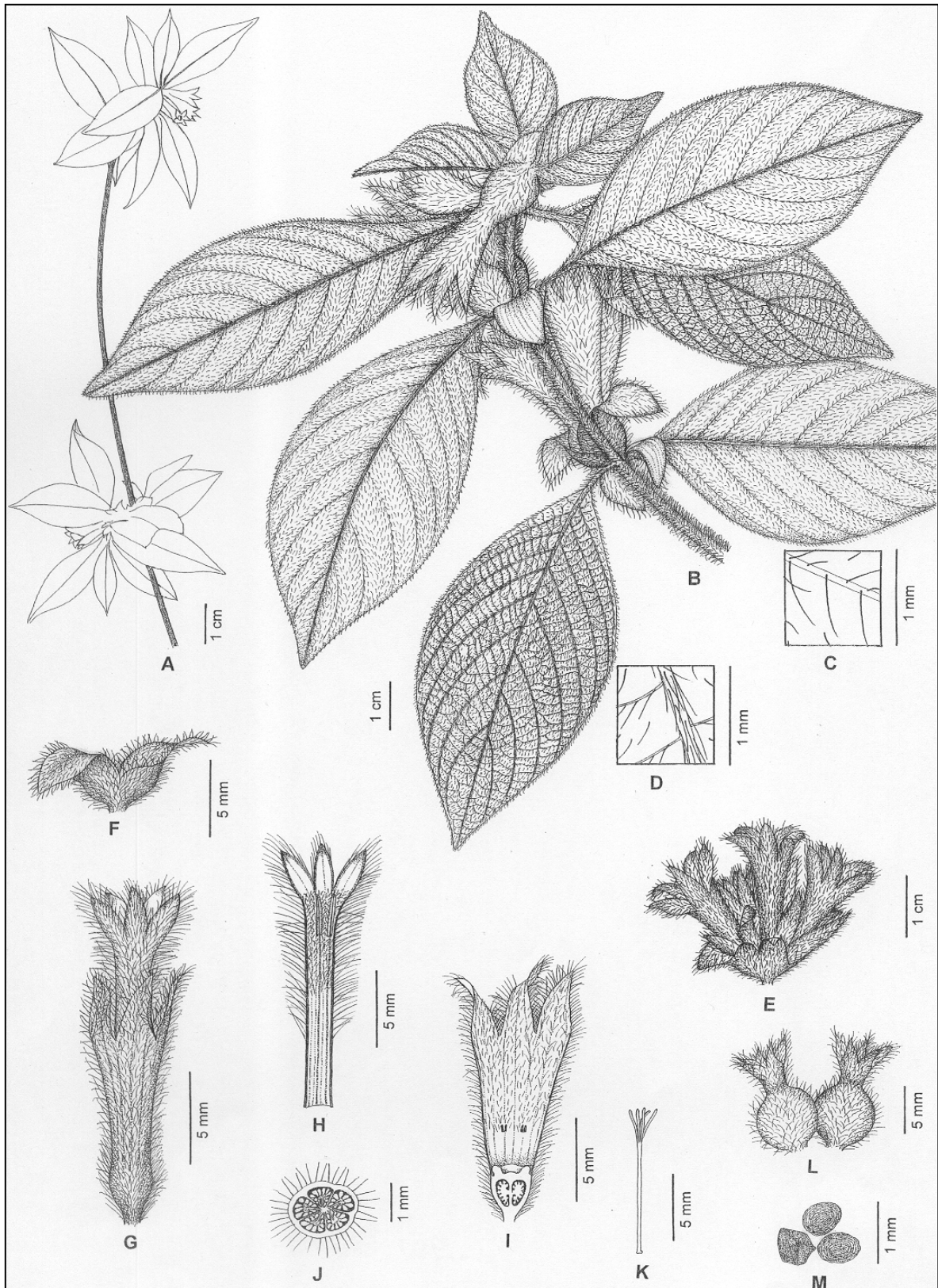


Figure 42. A–M. *Sabicea traillii*. —A. Part of flowering branchlet showing superficially whorled leaves. —B. Part of flowering branchlet with opposite decussate leaves. —C. Indumentum of upper leaf surface. —D. Indumentum of lower leaf surface. —E. Inflorescence. —F. Side view of bract. —G. Flower. —H. Inner corolla surface showing anther's position. —I. Longitudinal section.



16–18-ribbed, 1–5-ribbed, bracteoles 9(–11) × 3.5 mm, colleters 2–7, 0.1–1.2 mm long, *calyx* infundibuliform, 5-lobed, tubes (3.5–)4.1–9.4 × 2.4–5.5(–6.5) mm, lobes (2–)2.5–6 × (1.8–)2–6 mm, antrorse, widely lanceolate to triangular, apically (sub-)acute, margins denticulate, ciliolate to ciliate with (0.6–)0.9–1.9 mm long cilia, isolatedly to sparsely pilosulous at upper part up to the middle of tubes, glabrous at lower part, trichomes (0.2–)0.6–1.5 mm long, abaxially isolatedly to sparsely pilosulous, trichomes (0.3–)0.9–2.1 mm long, tubes 15–18(–21)-ribbed, lobes 3-ribbed, colleters 1–2, usually 4.5–6.8 mm below each sinus and associated with sericeous indumentum, 0.3–1 mm long; *corolla* hypocrateriform, tubes (9–)11–14 × 1–2 mm, lobes 2.6–3.5 × 1.4–1.8 mm, ovate, antrorse, adaxially the indumentum of orifice extends up to 5.5–6.5 mm inside the tubes, abaxially densely pilosulous, trichomes (0.6–)1.2–2.8(–3) mm long; *stamens* 5 per flower, attached to corolla tube at 12.4–12.9 mm from the base, anthers 2.4 × 0.3–0.4 mm; *style* (5.3–)6–8.8 mm long, stigmatic lobes 4, 1.5–1.9 × 0.1 mm; *ovaries* 0.9–1.2 × 0.9–1.2 mm, abaxially densely pilosulous, 4-locular, each locule 0.6–0.8 × 0.5–0.6 mm. *Fruits* deep purple, 6–7 × 6–7 mm when mature, abaxially isolatedly pilosulous; *seeds* 0.6–0.9 × 0.6–0.9 mm.

*Phenology, distribution and habitat.* Flowering and fruiting in June. *Sabicea traillii* seems restricted to central west Pará state of Brazil. It is found in weedy roadside vegetation (Fig. 38).

*Discussion.* *Sabicea amazonensis*, *S. surinamensis*, *S. mollissima*, and *S. traillii* are remarkable for their fascicled inflorescences plus infundibuliform calyces. *Sabicea traillii* is readily distinguished from *S. amazonensis* and *S. mollissima* by its non-arachnoid branchlets, abaxial leaf-surface and outer surface of inflorescences (Fig. 42B, D, C, F, G). It lacks longer trichomes at adaxial surface of leaves that are apparent in *Sabicea amazonensis*. This species does not contain the shaggy indument at external surface of inflorescences or arachnose indument at abaxial surface of corolla tubes like *Sabicea mollissima* (Fig. 42H). *Sabicea traillii* can be set apart from *S. surinamensis* by its shorter corolla tubes, appressed trichomes at adaxial surface of leaves and apparently longer trichomes at abaxial surface of leaves and corolla tubes. The anther- and style-lengths of this species are also shorter than in *Sabicea surinamensis*. It was possible to see only one of two syntypes (*Trail 390*, K, *Trail s.n.*, P) of *Sabicea traillii* that we find in a fairly acceptable condition. We here select it to serve as the lectotype for this species.

*Additional specimens examined.* BRASIL. **Pará:** Oriximiná-Obidos, ca. 20 km from Oriximiná, *Davidson & Martinelli 10061* (MO, US, NY), Cachoeira Porteira, *Davidson & Martinelli CD 10363* (NY).

40. ***Sabicea trianae*** Wernham, Monogr. *Sabicea* 62. 1914. TYPE: Colombia: no date (fl), *J. Triana* 717 (holotype, BM!; isotype, NY!, F [type fragments: inflorescence & leaf!]). Figure 43A–I.

*Terminal flowering branchlets* sparsely to densely arachnose and eventually glabrescent. *Stipules* ovate to oblong, reflexed, 8 × 4–5 mm, papyraceous. *Leaf blades* elliptic to lanceolate, 9–10.5 × 0.9–4.2 cm, apically acute to acuminate, basally acute, ciliolate with 0.2–1.2 mm long cilia, adaxially sparsely arachnose to floccose, 0.5–1.5 mm long; abaxially isolatedly sericeous or strigulose, sparsely arachnose to lanuginose at lamina, and sparsely to densely strigulose or sericeous, and sparsely arachnose to lanuginose at costa and secondary veins, trichomes (0.2–)0.8–2 mm long, secondary veins 9–11 pairs, protruding abaxially, tertiary veins plain or prominulous abaxially; *petioles* 5–7 mm long. *Inflorescences* one per node, 5–7-flowered, compactly umbellate, (1–)1.5–2.5 × 1.5–2.5 cm; *peduncles* 2–4 mm long; *bracts* (sub-)exvolucrate, 11–15 × 6.5–8 mm when subinvolucrate, isolated parts 8–15 × 3.5–5 mm, adaxially glabrous excluding the basal part, trichomes adaxially 0.4–0.9 mm long, abaxially isolatedly to sparsely sericeous and arachnose at the lower part, eventually glabrous near the margins and upper part, bracteoles (1.8–)7–8 × (0.6–)3.5–4.5 mm, colleters 2, 0.3–0.4 mm long. *Flowers* subsessile or pedicellate, pedicels (1.1–)2.4 mm long; *calyx* 4–5-lobed, tubes 1.2 × 1.5 mm, lobes 5.9–9.4 × 1.8–2.9 mm, antrorse, elliptic to lingulate, apically acute, margins entire, ciliolate with 0.1–0.7 mm long cilia, adaxially glabrous, abaxially sparsely to densely or arachnose at the tubes, isolatedly to sparsely at the lower part and middle of lobes, usually glabrous towards the apices and margins, 3(–5)-ribbed, adaxially plain, abaxially gently prominulous, colleters 1 in each sinus; *corolla* salverform, tubes 8–8.6 × 1.5–2.1 mm, lobes 2.9–3.1 × 1.5–1.8 mm, ovate, antrorse, apically (sub-)acute, abaxially densely sericeous at lobes or tubes, trichomes 0.4–1.2 mm long, anthers 1.5–1.7 × 0.2–0.3 mm; *style* 6.4–7.1 mm long, stigmatic lobes 2.6–2.9 mm long; *ovaries* 1.2–1.8 × 1.5–1.9 mm, abaxially 5-lobed or uneven, sparsely to densely arachnose and strigulose. *Fruits* and *seeds* not seen.

*Phenology, distribution and habitat.* The phenology and habitat of this species are unknown. Its distribution is known only in Colombia (Fig. 10).

*Discussion.* *Sabicea trianae* is distinguishable by its adaxially floccose to arachnoid leaves (Fig. 43C), compact-umbellate inflorescences, elliptic to lingulate, apically acute, antrorse, adaxially glabrous and abaxially arachnose ample calyx lobes (Fig. 43F, H), and densely sericeous external indument of corolla tubes. *Sabicea trianae*, known only from the type, is closely allied to *S. boyacana*, *S. cinerea* and *S. grisea*. From *S. boyacana* and *S. mattogrossensis* it differs by its adaxially floccose to arachnose leaves and its compact-

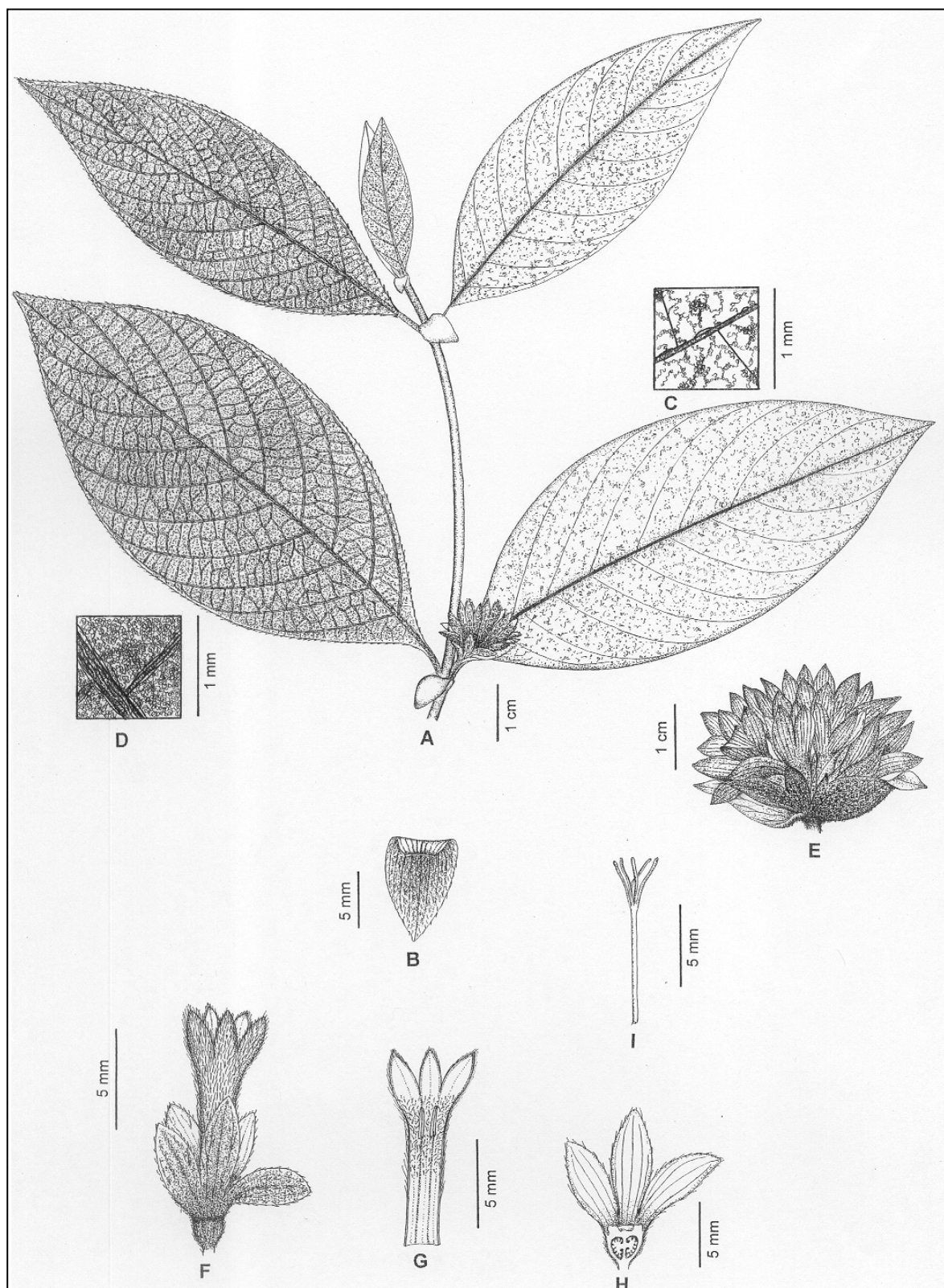


Figure 43. A–I. *Sabicea trianae*. —A. Part of flowering branchlet. —B. Outer stipule surface. —C. Indumentum of upper leaf surface. —D. Indumentum of lower leaf surface. —E. Inflorescence. —F. Flower. —G. Inner corolla surface showing anther's position. —H. Longitudinal section through calyx and ovary. —I. Style and stigmas.

umbellate inflorescences, abaxially arachnose bracts, peduncles, pedicels, hypanthium and calyx lobes, and presence of two colleters at the two margins at the adaxial base of bracts. From *Sabicea cinerea* and *S. grisea* it differ by its elliptic and adaxially glabrous calyx lobes, short peduncles and (sub-)appressed trichomes on abaxial surface of corolla tubes, and *S. grisea* also by its adaxially floccose to arachnoid leaves.

**41. *Sabicea umbellata*** (Ruiz & Pav.) Pers., Syn. i. 203. 1805. Figure A (Ruiz & Pavon 1799).

*Schwenkfelda umbellata* Ruiz & Pav. Fl. Peruv. 2: 55, f. a. 1799. TYPE: Peru. Huanuco: Cochero, Macora & Chinchao, 1778–1788 (fl), *Ruiz & Pavón s.n.* (holotype, BM!; isotype, F!). *Sabicea umbellata* var. *genuina* K. Schum., Fl. Bras. 6(6): 304.1889.

Twining woody vines, stems 1.5–2 m long; *terminal flowering branchlets* sparsely to densely strigulose, eventually glabrescent, trichomes (0.2–)0.6–1.1 mm long. *Stipules* widely lanceolate to triangular, recurved to antrorse, (10–)12–16(–20) × (7–)10–13 mm, apically acute to acuminate, membranous, margins entire, complanate, usually eciliate, occasionally ciliate, adaxially glabrous except the basal part, abaxially sparsely to densely strigulose, glabrous or glabrescent near the margins, trichomes (0.2–)0.5–1.1 mm long, 12–14(–16)-veined, veins slightly raised adaxially, colleters (16–)21–26(–28), (0.7–)1.2–1.6 mm long. *Leaf blades* ovate to elliptic, (9–)13–18 × (4–)6–8.5 cm, apically acuminate, basally acuminate to attenuate, papyraceous, ciliate with 0.2–0.8 mm long cilia; adaxially sparsely strigulose at lamina, usually densely at costa and secondary veins; abaxially isolatedly to sparsely strigulose and puberulous at lamina, and sparsely to densely strigulose at costa and secondary veins, secondary veins (10–)12–14 pairs, costa and secondary veins protruding abaxially and usually plain or sometimes protruding adaxially, tertiary and quaternary veins distinct abaxially; *petioles* (12–)20–40(–50) mm long. *Inflorescences* 2 per node, (22–)36–46(–66)-flowered, subglobose and compact-paniculate with variously branched secondary axes, (1.5–)2.5–4.5(–5.5) × (2–)3.5–6.5(–7) cm, primary axis (2–)5–7(–20) × 0.8–1.5 mm, main secondary axes usually 3, (1–)2–3 mm, simple to compound dichasia, 3–7(–9)-flowered; *peduncles* (2–)6–25(–30) mm long; *bracts* exinvolucrate, usually leafy, incompletely isolated into 2–5 parts, isolated parts 12–16(–18) × 5–7 mm, 1(–3)-lobed, lobes 0.5–5.5 × 1–1.5(–2.5) mm, widely lanceolate or ovate, apically usually acuminate or acute, margins entire, eciliate, adaxially sericeous all over, abaxially sparsely strigulose at the base and middle, 9–12-ribbed, bracteoles (1.5–)3–11(–14) × 1–5.5 mm, linear to lanceolate or ovate. *Flowers* pedicellate, pedicels (1–)2–6(–8) mm long; *calyx* 5-lobed, tubes (0.7–)0.8–1.2 × (1.5–)1.7–2.1(–2.5) mm, lobes (3–)5–7.5 × (0.5–)0.7–1(–1.3) mm, antrorse to spreaded and variously curved to recurved or twisted, lanceolate to linear, apically somewhat aristate or sharply acute, margins entire, ciliate with 0.2–0.5 mm long cilia, adaxially glabrous, abaxially sparsely strigulose at tubes to middle of lobes, glabrous towards the apices, 3–5-ribbed, distinct both abaxially and

adaxially, colleters 1 in each sinus, 0.2–0.4 mm long; *corolla* white, tubes 5–6.5 × 1.4–1.8 mm, lobes (1.9–)2.1–2.5(–3) × (0.7–)1–1.3 mm, ovate to widely lanceolate, antrorse to slightly recurved, adaxially the indumentum of orifice extends up to 2.1–4.2 mm inside the tubes, trichomes 0.2–0.8 mm long, abaxially densely strigulose; *stamens* 5 per flower, attached to corolla tube at 4.1–4.2 mm from the base, anthers (1.4–)1.5–1.7 × (0.2–)0.2–0.3 mm; *style* 6–6.8 mm long, stigmatic lobes 2.5–2.8 × 0.2 mm; *ovaries* (1.1–)1.5–1.8(–2.1) × (1.4–)1.5–1.8(–2) mm, abaxially slightly wavy or plain, 5-locular, each locule 1.2–1.3 × 0.7–0.8 mm. *Fruits* purple, 3.5–5 × 3.2–5 mm when immature, 5.5–7 × 4.5–7 mm when mature, isolatedly strigulose, eventually glabrescent; *seeds* 0.6 × 0.3–0.4 mm .

*Phenology, distribution and habitat.* Flowering from February to April, and September to December, fruiting from November to December. Growing in montane and primary rainforests or forest margins or open thickets, on steep slopes, or sometimes along roadsides; 450–1630m (Fig. 38).

*Discussion.* *Sabicea umbellata* is distinguishable by the combination of its linear to narrowly lanceolate, antrorse to divaricately spreading and shallowly twisted calyx lobes with high length-breadth ratios, and short corolla tubes. *Sabicea umbellata* seems near to *S. panamensis* and *S. mexicana* from which it can easily be distinguished (refer to discussion on *S. panamensis*). Besse, et al. 549 (MO) collected from Cochabamba, Bolivia, seems an intermediate between *Sabicea panamensis* and *S. umbellata*.

*Additional specimens examined.* PERU: Saint Lucia: *Poeppig* 43(F, G); *Poeppig* 1226 (BM, W); *Mathews* 1951, (BM, F, G). **Huánoco:** Cordillera Azul. ca. 39.2 km E of Tingo Maria on the road to Pucallpa, *Jones & Davidson* 9330 (US, NY); La Divisoria, *Woytkowski* 34553 (F,G); 59 km from Tingo Maria on highway to Pucallpa, *Allard* 21245 & 21791(F), 21.8 km east of Puente Pumahausi on road Tingo Maria-Pucallpa, *Plowman & Vigo* 11706 (F); Leoncio Prado, Hermilio Valdizán, Cerca a la Cumbre de la Divisoria, *Vigo*, 11256, (BR, NY), Cochero, *Dombey* 561 (F). **Loreto:** Cornel Portillo, *Ferreyra* 2253 (M, US). **Cuzco:** Paucartambo, Sta. Isabel Kosnipata, *Vergas* 6752 (F).

**42. *Sabicea velutina*** Benth., J. Bot. (Hooker) 3: 219. 1841. TYPE: Guyana: Mount Canaupang, 1838, *R. Schomburgk* s.n. (holotype, K, not seen, photo K!, NY!). Figure 44A–M.

*Sabicea leucotricha* Krause, Notizbl. Bot. Gart. Berlin-Dahlem 6: 202. 1914, Fl. Venez. 532. TYPE: Venezuela: Río Cuquenán, Schaweila Mota, Dec. 1909, *E. Ule* 8779 (lectotype, designated here, photo NY!).

*Sabicea velutina* subsp. *chimantensis* Steyerl., Mem. N.Y. Bot. Gard. 17 (1): 315.1967.

TYPE: Venezuela. Bolívar: Base of southwest-facing escarpment, Chimantá Massif, Amurí-tepuí, 1365 m, 10 Mar. 1955 (fl), J. A. Steyerl. & J. J. Wurdack 1340 (holotype, VEN, not seen, photo VEN!; isotypes, BM!, MO!, NY!, WIS!).

*Sabicea velutina* subsp. *duidensis* Steyerl., Mem. N.Y. Bot. Gard. 17 (1): 315.1967. TYPE:

Venezuela. Amazonas: Cerro Duida, Culebra Peak, 1600 m, 23 Apr 1949 (fl & fr), B. Maguire & B. Maguire Jr. 29137 (holotype, NY!).

Law spreading herbs or suffruticose to scandent, sprawling or trailing shrubby vines, stems (0.3–)0.5–2 m long; *terminal flowering branchlets* densely pilosulous and lanuginose, trichomes 1.1–2.6 mm long. *Stipules* usually ovate to suborbicular, occasionally widely lanceolate, rarely oblong or triangular, usually antrorse and appressed, rarely reflexed, 6–10 × (3.5–)5–9 mm, apically acute or acuminate, papyraceous, ciliolate with (0.2–)0.8–1.7 mm long cilia, adaxially glabrous excluding the basal part, abaxially densely to sparsely lanuginose to floccose and sericeous, usually all over, 12–16-veined, colleters 2–5, (0.3–)0.8–1.2 mm long. *Leaf blades* lanceolate to ovate or elliptic or oblong, (3–)5–12(–16) × (1–)2–2.5(–5.8) cm, apically acute to acuminate, basally subacute to obtuse, occasionally subcordate, thickly papyraceous, cilia 0.2–0.9 mm long; adaxially densely pilosulous to moderately velvety all over, sometimes sparsely arachnose at costa, older leaves usually non-velvety, trichomes (1.5–)2–2.3 mm long; abaxially usually compressed, rarely diffuse arachnose to lanuginose or lanate all over, secondary veins (9–)11–15(–17) pairs, plain to subsulcate adaxially, protruding abaxially, tertiary veins usually prominulous or distinct and quaternary veins occasionally distinct abaxially; *petioles* (3–)5–15 mm long. *Inflorescences* one per node, usually 8–25-flowered, compact-fascicled, 2–2.5 × 1.5–3.5 cm; *bracts* (sub-)exinvolucrate, membranous, usually incompletely isolated into 2–3 parts, 9–15 × 12–15 mm when subinvolucrate, isolated parts 9–15 × 5–9 mm, 1–4-lobed, lobes 0.5–7(–12) × 0.3–8(–10) mm, deltate to ovate or lanceolate or suborbicular, apically acuminate to mucronate or acute, margins entire, ciliolate with (0.5–)0.8–1.8 mm long cilia, adaxially sericeous at upper part, abaxially usually densely lanuginose to floccose or arachnose and sparsely sericeous or pilosulous all over, bracteoles 4.5–10 × 1.5–3(–5) mm, elliptic to lingulate or lanceolate, not lobed, adaxially usually concave, apically acute to acuminate. *Flowers* sessile, *calyx* campanulate gray-green to gray-buff with dull brownish-lavender or brick-red, (4–)5–6-lobed, tubes 0.8–1.5(–1.8) × 1.7–3(–3.5) mm, lobes (1.5–)3–6 × 0.3–1.1 mm, antrorse to spreaded or slightly reflexed, narrowly lanceolate or narrowly triangular, apically acute to acuminate, margins entire, ciliate with (0.8–)1.2–1.8 mm long cilia, adaxially sericeous at the upper part of lobes, glabrous at rest of the surface, abaxially densely lanuginose and sericeous at lobes and tubes, colleters 1–2 in each sinus, (0.1–)0.2 mm long; *corolla* white to pale white or creamy, lobes pale or dull rose-pink, salverform, tubes 8–12(–16) × 1.5–3 mm, lobes 2.5–

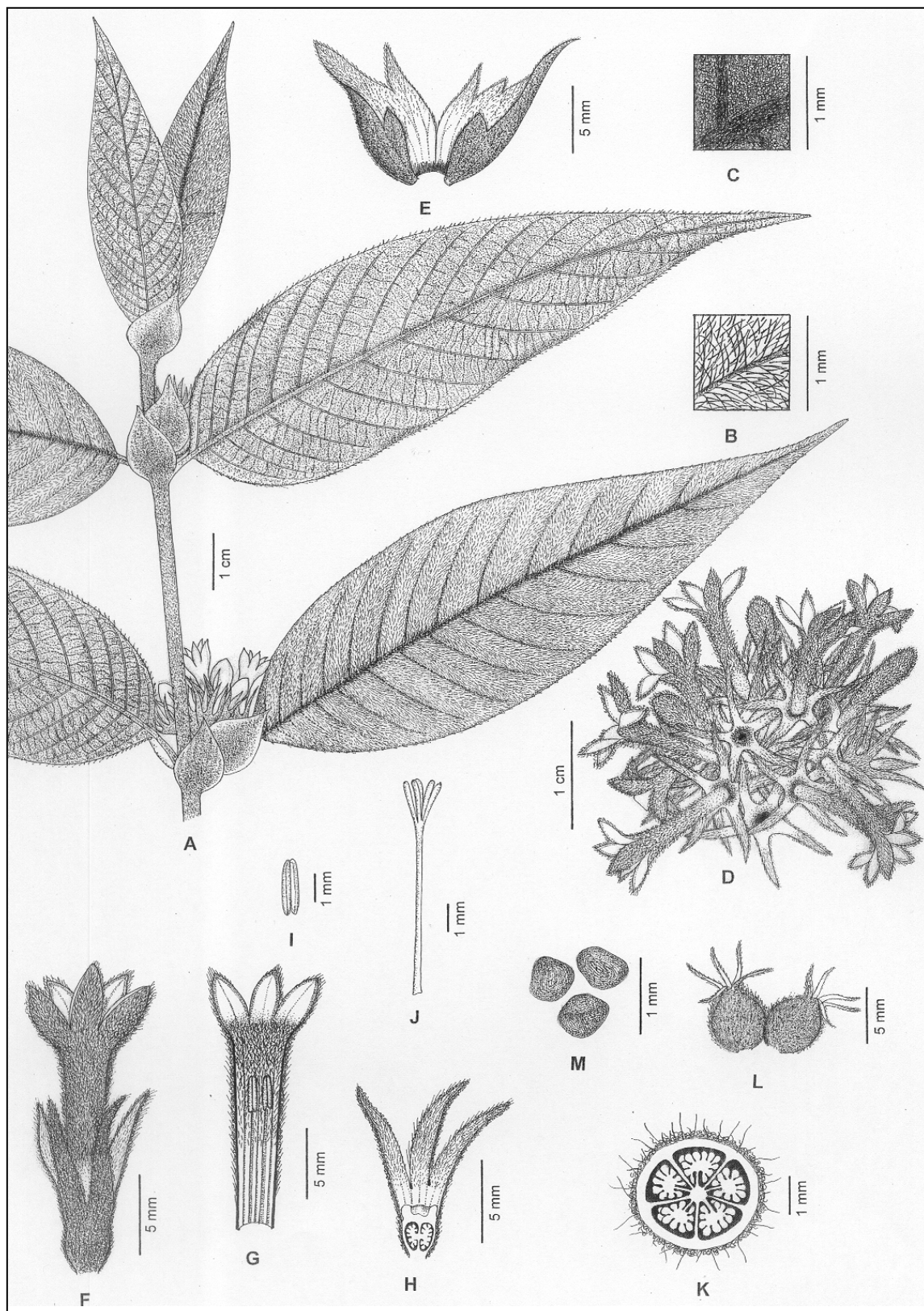


Figure 44. A–M. *Sabicea velutina*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Inflorescence. —E. Part of outer and inner bract surface. —F. Flower. —G. Inner corolla surface showing anther's position. —H. Longitudinal section through calyx and ovary. —I. Face view of Anther. —J. Style and stigmas. —K. Transversal section through ovary. —L. Fruits. —M. Seeds.



3.5(–4) × (1.2–)1.5–2 mm, ovate to widely lanceolate, antrorse to spreaded, adaxially the indumentum of orifice extends up to 2.9–5.3 mm inside the tubes, abaxially sericeous to villosulous or arachnose, trichomes (0.7–)0.8–1.6 mm long; *stamens* 5 per flower, attached to corolla tube at 5.2–6.5 mm from the base, anthers 1.7–2.1(–2.2) × 0.4–0.5 mm; *style* (5.5–)6–7.1 mm long, stigmatic lobes 2.1–2.4 × (0.1–)0.2–0.3 mm; *ovaries* 1.5–3.5(–4.5) × 1.5–3(–3.5) mm, abaxially uneven to 5-lobed, densely sericeous and lanuginose, trichomes (0.9–)1.2–2.8 mm long, 4–5-locular, each locule 1–2.5 × 0.2–0.9 mm. *Fruits* purple red, 4–6 × 4–5 mm when immature, (6–)8–10 × (6–)7–9 mm when mature, isolatedly to sparsely sericeous and lanuginose; *seeds* 0.6–0.8 × 0.4–0.5 mm.

*Phenology, distribution and habitat.* Flowering throughout the year and fruiting in February, April, September and October. *Sabicea velutina* is widely distributed in southern Venezuela, western Guyana, and Roraima state of Brazil. In Venezuela, it extends up to the western boarder with Colombia. It is found in savanna, open scrubs, disturbed grasslands, 15–20 m high canopy forests and forest edges, in woods bordering streams, at burnt or inundated areas and sandstone bluffs or cliff faces or open rocky places; (0–)218–2000 m (Fig. 6).

*Discussion.* Steyermark (1974) recognized three varieties under *Sabicea velutina* based on petiole lengths, length-breadth ratios and base of lamina, number of flowers per inflorescences, and length of corolla. However, these characters failed in characterizing infraspecific taxa sensu Steyermark (1974), because they are too continuous. *Sabicea velutina* is characterized by compact-fascicled inflorescences, usually subinvolucrate bracts, abaxially lanuginose to floccose and sericeous stipules, adaxially very densely pilosulous to moderately velutinous, abaxially arachnose or lanuginose to lanate leaf blades, abaxially densely arachnose to lanuginose and sericeous calyces with lanceolate calyces, sericeous indumentum at upper adaxial surface of bracts and calyx lobes, ciliolate bracts and calyx lobes, and sericeous to villosulous or arachnose corolla tubes.

Few specimens of *Sabicea velutina* with elliptic to oblong leaves might be confused with *S. mollissima* var. *mollissima* that can easily be distinguished by their apparently longer trichomes at the adaxial surface of leaves, narrowly lanceolate calyx lobes, campanulate calyces with very short (usually 0.8–1.5 mm long) and adaxially glabrous tubes (Fig. 44H), and colleter/s located in sinus without the association of trichomes (Fig. 44H), and sericeous to villosulous or arachnose outer surface of corolla (Fig. 44F, G). Some specimens of *Sabicea velutina* with smaller calyx lobes looks like *S. oblongifolia* or *S. camporum* from which they differ by fascicled inflorescences, densely pilosulous to velutinous indumentum of adaxial leaf surface comprised of apparently longer trichomes, lanuginose to arachnose or floccose indumentum at the abaxial stipule surface and inflorescences including corolla, and apparently densely sericeous indument at the upper part of adaxial surface of bracts and



calyx lobes. Additionally these *Sabicea velutina* specimens are distinguishable from *S. oblongifolia* by indumentum lacking rusty-brown to maroon color, whereas, from *S. camporum* by their longer cilia (0.8–1.8 mm long in contrast to 0.1–0.8 mm) at the margins of bracts, bracteoles and calyx lobes. Steyermark (1974) synonymized *Sabicea aspera*  $\beta$  *velutina* K. Schum. under *S. velutina*, although the specimens of Schumann (1889) cited under *S. aspera*  $\beta$  *velutina* belong to *S. oblongifolia*. Therefore, we have included it as a synonym of *Sabicea oblongifolia*, despite Steyermark's placement under *S. velutina*. *Sabicea guianensis* Wernham (non-Aublet; *S. guianensis* (Aubl.) Baill. = *Patima guianensis* Aubl.), is rejected as a legitimate name by Steyermark (1995), as it was based on the holotype of *S. velutina*. Two syntypes were mentioned for *Sabicea leucotricha* Krause- Brazil: Rio Branco, Serra de Mairary am Surumú, 1200 m, Sept, 1909, *E. Ule* 8465 (B, not seen), and Venezuela: Río Cuquenán, Schaweila Mota, Dec., 1909, *E. Ule* 8779 (B, not seen, photo NY!). Both of these syntypes of B are presumably destroyed and could not be located elsewhere except the photo of *E. Ule* 8779 (NY!) that we have selected as the lectotype.

*Selected specimens examined.* BRASIL. **Roraima:** Serra Tepequem, In valley head of Rio Cabosobral, Terr. Do Rio Branco, *Maguire & Maguire* 40165 (HUH, NY), Upper plateau and summit of Serra Tapequém, Vila Tapequém *Prance et al.* 4396 (F, US, NYS, U), Serra dos Surucucus, *Prance et al.* 9883 (F, HUH, NY[2] U), Serra de Tapequém, Alto Alerge, *Hopkins et al.* 974 (F, NY). GUYANA. Pakaraima Mountains, Kamarang River-Wenamou Trail, Samwarakna-tipu (Holitipu), *Maguire & Fanshawe* 32480 (NY); Orindnik Falls, *Harrison* 1458, (NY); Cuyuni-Mazaruni, 0–2 km of Maipuri Falls, Karowrieng River, *Gillespie & Smart* 2730 (NY, U), Utshe campon savanna, *McDowell & Gopaul* 2724A (NY, US, U); Potaro-Siparuni, Pakaraima Mts, upper Ireng river watershed, near base of Malakwalai-Tipiu, *Henkel & Chin* 5510 (NY, US). VENEZUELA. **Amazonas:** Sierra Parima, a lo largo de la frontera Venezolana-Brasilera, a unos 45 km al NE de las cabeceras del río Orinoco, *Steyermark* 105990 (US, NY), Vecindades de Simarawochi, Río Matacuni, a unos 6–7 km al Oeste de la frontera Venezolana-Brasilera, *Steyermark* 107559 (F, NY), aprox, 35 km al NNE de Parima "B", cabeceras del río Ocamo, *Huber* 613 (NY); Amazonas-Atabapo, *Dalgado* 902 (NY); Flanco N del Duida, 2 km al S de la población Culebra, Sustrato de arenisca, *Fernández* 7714 (NY). **Bolívar:** Gran Sabana, between Kun and Uadauraparúta, in valley of Río Kukenán, S of Mount Roraima, *Steyermark* 59037 (NY), Between Kun and Uadauraparúta, in valley of Río Kukenán, south of mount Roraima, *Steyermark* 59037 (F[2]), tributary to Río Kukenán, at base of Mount Roraima, *Steyermark* 58570 (NY[2]), *Steyermark* 58570 (F[2]), La Gran Sabana, Km 145 along hwy, 2 km S of La Ciudadella, *Davidse* 472, (US); Sabana arenosa, Approx, 7 km Oeste de Kavanayen, *Morillo & Rutkis* 7973 (US), 6 km E of Cavanayén, *Kral & Gonzalez* 70513, (NY), Bolívar-Yuruani, San Ignacio, *Liesner* 23029 (NY, U), ca. 10 km SW of Karaurin Tepui at junction of Río Karaurin & Río Asadon (Río Sanpa), *Liesner* 23853 (F); upper slopes of Cerro Toribio, *Maguire et al.* 35932 (NY); Along ridge road

northeast of Morrison-Knudsen Camp, *Wurdack 34470* (F, NY); Chimantá Massif, along base of SE-facing sandstone bluffs of Chimantá-tepuí (Torono-tepuí), from S corner Neward, *Steyermark 75498* (F, US, NY-3); vecindad de Danto en la segunda meseta (hombrillo) arriba del valle de Kamarata, *Steyermark 94116* (NY); Entre la quebrada Los Brasileños, y el camino hacia Playa Blanca y el Río Uaiparu, al suroeste de Icab, *Steyermark 117742* (F); Roscio, selva ribereña a lo largo de la Quebrada Saunay (Pozo Negro), afluente del río Uairén, 6 km al Oeste de Santa Elena de Uairén, *Steyermark & Liesner 127329*, (NY), Sabanas sobre cerros ondulados a aprox, 3 km al NW de San Ignacio de Yuruani, *Huber & Alarcon 7517* (NY), al S de Cantarana, aprox, 20 km al NE de Ikabarú (aprox, 95 km al W de Santa Elena de Uairén), *Huber & Alarcon, 9639* (NY), 2 km S of El Pauji, 1000m, *Holst & Liesner 2340*, (NY, U), Uairén, Santa Elena de Uairén, en selvas, *Lasser, 1621*, (F, US, NY); Mount Auyan -Tepui, *Tate, 1190*, (NY); extensas sabanas secundarias sobre las faldas inferiores SW Cerro Kukená, *Huber & Alarcon 7688* (NY); Piar, cumbre del Cerro Auyan-tepui, sector central del brazo occidental, Estación Edelca Auyantepui, *Huber & Alarcon 7769* (NY); Cerro Kurún-tepui, aprox, 17 km al este de Canaima, *Huber et al. 8210* (NY), cumbre meridional del Cerro Venado, aprox, 20 km al E de Canaima, *Huber & Huber 10849* (NY); Sabana de Arekuna, E margin of lower Río Caroni, *Prance & Huber 28307* (NY, U); 0 to 6 km SE of El Pauji, Nov 09, 1985, (fl), *Liesner 19777* (NY); Sifontes, sector "La Hoyada", 7 km al NW del Caserío "El Pílon", 58 km al W de Sta, Elena de Uairén, *Aymard 4662*, (NY); Piar-Río Acaná, Río Acanán, Guarumo, 5 km W of Amaruay-tepui, 0 to 1 km S of base camp at Guadeguen, *Liesner & Host 20566* (NY); a la cuenca media del río Paragua (Hoja NB20-6), *Stergios 10273* (NY); Raul Leoni Zona minerea Aza Karón, Piedra Pintada (F2), *Diaz 832* (NY). Isla del Espuezo, *Croizat 554*(F, NY); Campo Claro, On Río Chicanan South of El Dorado, *Dressler 2999* (US, NY, U); Elena, Mata Cutia, Campo natural de terra firm, *Rosa & Nascimento 3328* (NY).

**43. *Sabicea villosa*** Willd. ex Roem. & Schult., Syst. Veg. 5: 265. 1819. TYPE: Venezuela: Río Orinoco, *F. W. H. A. Humboldt & A. J. A. Bonpland s.n.* (holotype, B, presumably destroyed, photo F!, NY!). Figure 45A–M.

Creeping, scandent, sprawling or twining vines, stems 0.5–8(–15) m long, richly branched; *terminal flowering branchlets* sparsely to densely pilosulous or villosulous to strigulose and additionally sometimes puberulous, trichomes (0.07–)0.8–2(–2.3) mm long. *Stipules* ovate to deltate, antrorse to reflexed, 5–9(–12) × 3–11 mm, not fided, apically (sub-)acute to acuminate, rarely bifid, membranous, ciliolate with (0.3–)0.7–1.5 mm long cilia, adaxially glabrous excluding the basal part, abaxially isolatedly to sparsely strigulose or pilosulous all over, trichomes (0.3–)0.7–1.5(–1.8) mm long, 7–9-veined, veins plain adaxially, slightly raised abaxially, colleters 5–9, 0.6–1.2 mm long. *Leaf blades* elliptic to oblong or ovate, (2.5–)4–12.5(–16.5) × (1.2–)2–6(–8) cm, apically acuminate, basally acute or obtuse, membranous or

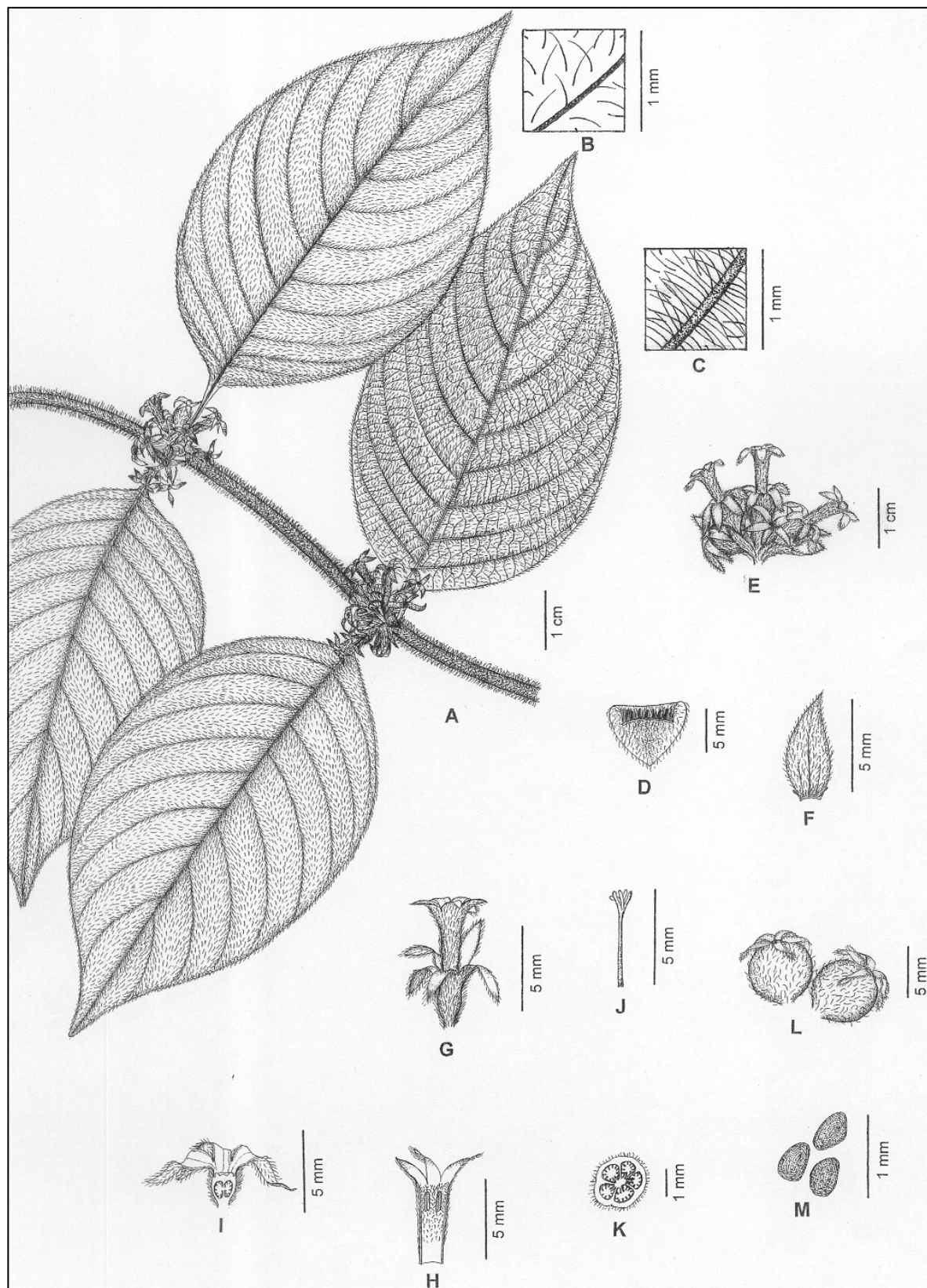


Figure 45. A–M. *Sabicea villosa* var. *villosa*. —A. Part of flowering branchlet. —B. Indumentum of upper leaf surface. —C. Indumentum of lower leaf surface. —D. Outer and base of inner stipule surface. —E. Inflorescence. —F. Outer bract surface. —G. Flower. —H. Inner corolla surface. —I. Longitudinal section through calyx and ovary. —J. Style and stigmas. —K. Transversal section through ovary. —L. Fruits. —M. Seeds.

papyraceous, cilia 0.4–1(–1.2) mm long; adaxially isolatedly to sparsely strigulose to pilosulous and puberulous at lamina, sparsely to densely at costa, trichomes (0.07–)0.6–1.6(–2.1) mm long; abaxially isolatedly to sparsely pilosulous or strigulose and puberulous at lamina, sparsely to densely pilosulous or strigulose, and rarely isolatedly lanuginose at costa and secondary veins, trichomes 0.07–1.8(–2.1) mm long, secondary veins 9–14(–16) pairs, costa and secondary veins usually protruding abaxially and plain adaxially or usually plain or sometimes protruding adaxially, tertiary veins prominulous and quaternary veins distinct, sometimes prominulous abaxially; *petioles* 0.5–18(–38) mm long. *Inflorescences* 1 per node, 2–7(–12)-flowered, verticillate, 1–1.5 × (1–)1.5–2.5 cm; *peduncles* 0(–2) mm long; *bracts* usually exinvolucrate, leafy papyraceous, incompletely isolated into 2–3 parts, isolated parts (3.5–)4–6(–8) × 2–4(–5) mm, 0(–3)-lobed, usually lanceolate to ovate, apically acute or acuminate, margins usually entire, sometimes shallowly wavy or sparsely denticulate, adaxially glabrous excluding the basal part, trichomes 1–1.2(–1.5) mm long, abaxially isolatedly to sparsely pilosulous to strigulose, 3–5-ribbed, bracteoles 2–3.8(–4.1) × 0.5–1.2(–1.4) mm, narrowly elliptic to lingulate or lingulate to lanceolate, apically acute, colleters 2, 0.2–0.7(–1) mm long. *Flowers* usually sessile, occasionally subsessile, pedicels 0(–1.5) mm long; *calyx* campanulate, 4–5(–10)-lobed, tubes (0.2–)0.8–1.8 × 1.1–2.1(–2.7) mm, lobes (0.6–)3–5(–6) × (0.3–)1–1.5(–2.1) mm, usually reflexed, sometimes antrorse, usually narrowly lingulate to lanceolate, occasionally narrowly ovate, apically acute to acuminate, margins usually entire, sometimes the upper part shallowly wavy or denticulate, ciliolate with 0.1–0.6 mm long cilia, adaxially glabrous, rarely isolatedly puberulous at the upper part, glabrous at lower part, abaxially sparsely pilosulous to strigulose, at tubes and lobes, eventually glabrescent, trichomes 1 mm long, colleters 1–2(–3) in each sinus, 0.2–0.5(–0.8) mm long; *corolla* white to cream, salverform, tubes 3–5.5(–7) × 1–1.5 mm, 4–5-lobed, lobes 1.4–2.1(–2.4) × 0.7–1.2 mm, ovate, antrorse to reflexed, adaxially glabrous, adaxially the indumentum extends up to 1.8–2.4(–2.9) mm inside the tubes, trichomes 0.1–0.6 mm long, abaxially moderately densely strigulose, trichomes (0.5–)0.8–1.1 mm long; *stamens* 4–5(–10), attached to corolla tube at 4.1–4.4 mm from the base, anthers 1.1–2(–2.4) × 0.2–0.3 mm; *style* (3–)4–5.3 mm long, stigmatic lobes usually 5, rarely up to 10, 1.8–2 × 0.2–0.3 mm; *ovaries* 1.8–3 × 1.8–3 mm, abaxially shallowly 5-lobed or uneven, densely strigulose to pilosulous to occasionally puberulous, trichomes (0.5–)1.2–1.8 mm long, 5(–6)-locular, each locule 1.1–1.8 × 0.3–0.6 mm. *Fruits* maroon to pink, 4–8 × 3–6 mm when immature, (8–)10–12(–14) × (8–)9–11(–12) mm when mature, abaxially strigulose to pilosulous; *seeds* 0.4–0.6 × 0.3–0.5 mm.

*Phenology, distribution and habitat.* Flowering throughout the year. Fruiting usually throughout the year in *Sabicea villosa* var. *adpressa*, in February, April, August, and November to December in *S. villosa* var. *sellowii*, and in March to May and September to November in *S. villosa* var. *villosa*. In Mesoamerica, all three varieties are commonly

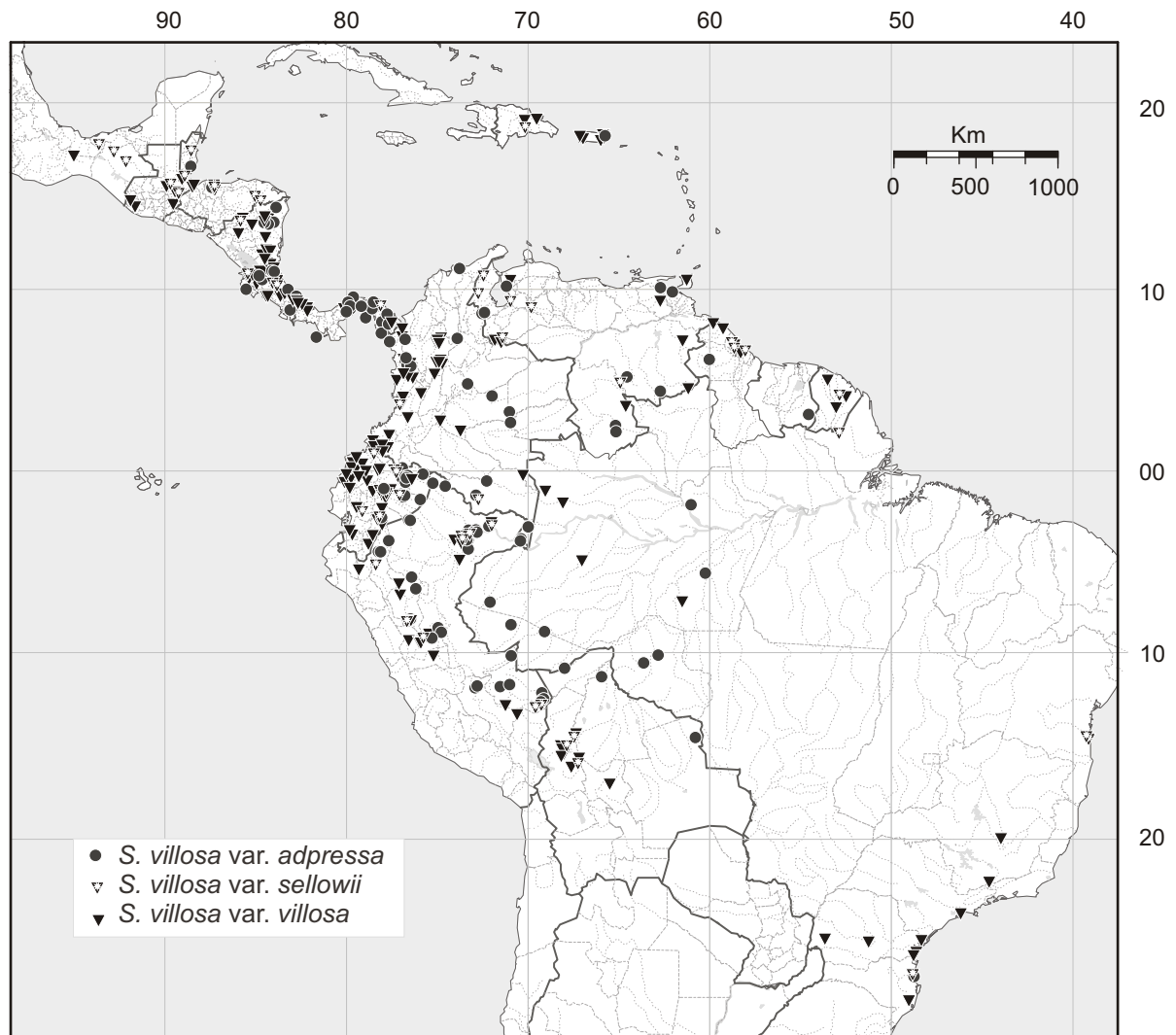


Figure 46. Map of central and southern Mesoamerica and South America (in part), showing the distribution of *Sabicea villosa*.

distributed in Costa Rica, Nicaragua, and Panama. Additionally, *Sabicea villosa* var. *adpressa* is found in Honduras, *S. villosa* var. *villosa* in Mexico and Guatemala, and *S. villosa* var. *sellowii* in Mexico, Belize and Guatemala. In South America, all varieties extend from Colombia to Bolivia, Guyana and southwest Brazil, with short and long disjunction. In addition, *Sabicea villosa* var. *adpressa* is found in Suriname, and *S. villosa* var. *sellowii* and *S. villosa* var. *villosa* in French Guiana. *Sabicea villosa* var. *adpressa* and *S. villosa* var. *villosa* are common in northwest Brazil. In the Caribbean Islands, *Sabicea villosa* var. *adpressa* is found only in eastern Puerto Rico, and *S. villosa* var. *sellowii* in southeast Dominican Republic, whereas, *S. villosa* var. *villosa* in central east Dominican Republic, southern and eastern Puerto Rico and northern Trinidad. All varieties of this species grow in primary and secondary, (sub-)tropical forests, clearings or agricultural fields, swamps, roadsides, and riverbanks. *Sabicea villosa* var. *adpressa* and *S. villosa* var. *villosa* are also found in non-inundated and seasonally inundated or pluvial to selectively logged and lowland

to (sub-)montane forests, along streams, scrubs, pastures or savanna, base of hills or hillsides. *Sabicea villosa* var. *adpressa* is also collected from the vegetation dominated by ferns and monocots, and *S. villosa* var. *villosa* from rocky walls. All varieties commonly grow on sandy loam or lateritic to clayey soil; 0–2000 m (*Sabicea villosa* var. *adpressa*), 0–1300 m (*S. villosa* var. *sellowii*), 0–3200 m (*S. villosa* var. *villosa*) (Fig. 46).

*Discussion.* *Sabicea villosa* is distinguishable by the combination of its indumentum lacking curled or tortuous trichomes, 2–7(–12)-flowered verticillate inflorescences (Fig. 45A, E), usually reflexed, narrowly lingulate to lanceolate, or narrowly ovate and apically acute to acuminate calyx lobes (Fig. 45E, G), and short corolla tubes (3–5.5[–7]) and lobes (1.4–2.1[–2.4]), externally covered with moderately strigulose indumentum. *Sabicea villosa* var. *adpressa* seems very close to *S. aspera* with compact inflorescences due to its closely appressed trichomes of the stems (Standley, 1938) and leaves. It can be distinguished by its shorter corolla tubes and the appressed indumentum at abaxial surface of corolla tubes (Fig 45G, H). *Sabicea villosa* seems closely allied to *S. parva* from which it can be set apart by its usually narrowly lingulate to lanceolate, occasionally narrowly ovate, and usually reflexed calyx lobes, shorter calyx tubes, colleter's location in the sinus of calyces, shorter corolla tubes externally covered with appressed indument.

At vegetative stage, *Sabicea villosa* var. *villosa* can not be distinguished from *S. cochabambensis*, *S. hirta*, and *S. pearcei* with smaller leaves and indumentum exclusively comprised of long, soft, straight and erecto-patent trichomes, though it can be set apart from *S. liesneri* and *S. novo-granatensis*, merely by its adaxially glabrous stipules (excluding the common densely sericeous base), whereas, from *S. chocoana* and *S. noelii* by its longer, usually differentiated and erecto-patent trichomes (in contrast to usually erect, short, and uniform), and adaxially glabrous stipules. On the other hand, at the vegetative stage, *Sabicea villosa* var. *adpressa* cannot be differentiated from *S. aspera*, *S. mattogrossensis*, *S. panamensis*, *S. pyramidalis*, and *S. thyrsoiflora* with smaller leaves and, *S. parva* containing appressed indumentum and lacking curled or tortuous trichomes. However, all of these species are readily distinguishable at the flowering stage. *Sabicea villosa* var. *sellowii* seems as a sympatric group from *S. villosa* var. *villosa* and *S. villosa* var. *adpressa*. We find it better to maintain the existing varieties of *Sabicea villosa* because the variation in the trichome orientation within this species seems consistent.

Wernham (1914) included 11 syntypes of *Sabicea hirsuta* var. *adpressa*: Brasil. Jurua R., Nov. 1900, *Ule 5118* (syntype, B, BM, K, G!, P, F!), Maynas, Yrimagaus, *Poeppig s.n.* (syntype, B, BM, K, G, P, NY!). Costa Rica. Limón: *Kuntze 1995* (syntype, B, BM, K, G & P not seen, NY!), Puntarenas, Jan, 1893, 300 m, Mar 1896, *Tonduz 9955[7055]* (syntype, B, BM!, K, G[2]!, P, F!); Panama. Isthmus of Panama, Chagres, Aug 1862, (fl), *Hayes s.n.* (syntype, B, BM!, K, G, P, HUH!), no date, *Seemann 1073* (syntype, B, BM!, K, G, P), Jan-Mar 1850, (fl), *A. Fendler 180*, (syntype, B, BM!, K, G, P, HUH!, MO!, W!); Portobello, *Billberg*

*s.n.* (B, BM, K, G, P, not seen), Trinidad. *Broadway* 3338 (syntype, B, BM, K, G, P, not seen), St. Thomas Is., *Friedrichstal s.n.*, (syntype, B, BM, K, G, P, not seen). We select *A. Fendler 180* (F) as the lectotype for *Sabicea villosa* var. *adpressa*, as we find it in better condition among the flower bearing syntypes. Wernham (1914) cited ten syntypes of *Sabicea hirsuta* var. *sellowii* (Brazil: Rio de Janeiro, 1833, *M. Gaudichaud 622* (syntype, B, BM, K, G!, P, US!) & *s.n.* (not seen), *S. Hilaire 980* (not seen), Minas Gerais: Tombador, near Diamantina, *Glaziou 1935a* (syntype, not seen), Bahia, *Sello 223, 299, 381, 732 & 1072* (syntypes, B, BM, K, G, P, not seen), Ilheos, *Blanchet 3004* (syntype, BM!, K, B, G! P, W!). We select *M. Gaudichaud 622* (G) for *Sabicea villosa* var. *sellowii*, as we observed it in good condition with flowers

Schumann's (1889) *Sabicea aspera* var. *scandens* is a heterogenous taxon representing both *S. villosa* and *S. parva*. We have seen eight of ten syntypes of *aspera* var. *scandens*. Among these eight syntypes, five [Guiana Gallica, *Poiteu s.n.* G!, Pillao, ad Pillao, *Ruiz s.n.* (F!), montibus ad flumen Mayo, *Spruce 4837* (BR!), Sao Paulo, *Burchel 3155* (HUH!) & *3475* (BR!)] belong to *Sabicea villosa* var. *villosa*. *Poeppig 2515* (NY!, W!) belong to *S. parva* var. *adpressa*, *Poeppig 1821* (F!, NY!), collected from Peruvia orientale ad ripas fluminis Huallaga prope Tocache), belong to *S. villosa* var. *adpressa*, and *Blanchet 3004* (BM!, G-2!) collected from Bahia prope capitalem, belong to *S. villosa* var. *sellowii*. *Müller s.n.* and *Schnek 430*, are the two syntypes, collected from Santa Catharina in silvis prope Blumenau, that we have not seen. However, as it is mostly comprised of *Sabicea villosa* var. *villosa*, therefore, we have merged it with *S. villosa* var. *villosa* and selected *Poiteu s.n.* (G) as the lectotype as it is well-preserved in good condition with flowers.

Wernham (1914) cited *Tonduz 6712* as one of the 11 syntypes of *Sabicea hirsuta* var. *adpressa*, and on the other hand, *Pittier 6712* as a syntype of *S. costaricensis*. The collections of BM, G, and F are same. These collections are not any *Sabicea hirsuta* (= *S. villosa*), rather, *S. costaricensis* (= *S. panamensis*) but *S. panamensis*. We are not confirmed about *Tonduz 6712* (US) due to the erecto-patent indumentum of branchlets, and immature inflorescences. Its erecto-patent indumentum of branchlets and appressed indumentum of leaves support its inclusion to *Sabicea villosa* var. *sellowii*, whereas its calyx lobes indicate it as *S. panamensis* or *S. aspera*.

#### Key to the varieties:

- 1a. Trichomes erecto-patent at terminal branchlets, secondary veins and costa of lower side of leaf.....43a. *S. villosa* var. *villosa*  
 1b. Trichomes erecto-patent or (sub-)appressed at terminal branchlets and (sub-)appressed at secondary veins and costa of lower side of leaf.  
 2a. Trichomes (sub-)appressed at terminal branchlets.....43b. *S. villosa* var. *adpressa*  
 2b. Trichomes erecto-patent at terminal branchlets.....43c. *S. villosa* var. *sellowii*

**43a. *Sabicea villosa*** Willd. ex Roem. & Schult. var. **villosa**. *Schwenkfelda villosa* Willd. ex Spreng., Syst. i. 765. 1825.

*Sabicea hirsuta* Kunth., Nov. Gen. Sp. 3: 417. 1820. *Schwenkfelda hirsuta* (Kunth) Spreng. Syst.Veg.1: 765. 1825. TYPE: Crescit in ripa Orinoci fluminis, Floret Majo, specimens not cited, supposed to be based on the holotype of *S. villosa* Willd. ex Roem. & Schult.

*Sabicea aspera* ð *scandens* K. Schum., Fl. Bras. 6(6): 307. 1889. TYPE: Guiana Gallica, 1819-1821, *M. Poiteu s.n.* (lectotype, designated here, (G!)).

*Selected specimens examined.* BOLIVIA. **Beni:** Rurrenabaque, Cwaum, 1151, (NY), Gegen von Reyes, Rurrenabaque am Río Beni, *Fleischmann*, 381(S). **Cochabamba:** Carrasco, Guacharos, *Altamirano and Altamirano*, JA1877 (MO). **La Paz:** Charopampa bei Mapiri, *Buchtien* 1487 (F, G, US), Mapiri region, São Carlos, *Buchtien*, 1451 (F, NY); Sud Yungas, Alto Beni, Colonia San Pedro, *Seidel and Vaguaiata*, 7523 (MO), Concesión de la cooperativa Sapaecho, 15°30'S, 67°20'W, *Seidel*, 2836 (MO, NY). Cordillera Real, Río Chimate, *Tate*, 549 (NY). *Buchtien* 1450 (MO). BRASIL. **Amazonas:** Cerauari, cerca de 3 km norte de Cidade, *Silva et al.* 619 (NY), Rio Popeyaca *Schultes & Cabrera* 15614 (HUH). **Meta:** Morro da Fazenda, Itajaí, *Klein* 1321 (U). **Minas Gerais:** Sabará, *Cluza & Jùnia* 102 (MO). **Paraná:** Guaratuba, *Dusén* 13765 (HUH, S); Guaraqueçaba, 25°19'S, 48°19'W, *Cervi et al.* 6923 (NY). **Rio de Janeiro:** **Santa Catarina:** Três Barras, Garuva, S, Francisco do Sul, *Reitz & Klein* 6224 (NY, S, US). **São Paulo:** Santos, *Mosén* 3416 (F, S), *Lindbery* 718 (S). COLOMBIA. **Amazonas:** Amazonas-Vaupés, Río Apaporis, entre el río Pacoa y el Río Kananari, *Schultes & Cabrera* 12582 (BM, F, HUH, NY, U). **Vaupés:** cuenca del río Apaporis, río Piraparaná, *García-Barriga* 14207 (NY). **Antioquia:** Vicinity of Planta Providencia, 26 kms S & 23 kms W (Air) of Zaragoza, in valley of Río Anorí between Dos Bocas & Anorí, *Denslow* 308 & 2526 (WIS), Anorí, Corregimiento de Providencia, Valle del río Anorí, entre Dos Bocas y Anorí, *Ponnegra, et al.* 474 (MO), on west side Río Anorí, vic. Planta Providencia 28 km SW of Zaragoza, approx, 3 km upriver from Planta Providencia, *Alverson et al.* 121 (WIS), *Alverson et al.* 192 (MO, NY), valley of Río Anorí between Dos Bocas and Anorí, Planta Providencia and vicinity, near Caño Tirana, 7°21'N, 75°03'W, *Zarucchi* 3289 (MO, NY); Mutatá, Vereda Oquendo, Mutatá-Pavarandó Grande, Orilla de la carretera, km 4, 76°27'N, 07°14'W, *Roldán et al.* 609 (MO, NY). **Caldas:** Nariño: Vereda Puente Linda, margen izquierda del río Samaná, 5°34'N, 75°03'W, *Fonnegra* 4999 (MO). **Chocó:** Río Tolo, Guayabal, al SE de Acandí, 0–50, *Ordoñez & Valencia* 26 (MO), 5 horas a pie al SE de Acandí, *Forero et al.* 990 (MO, NY); Carretera San José del Malmar-Nóvita, Campamento Curundé, Río Ingará, Fin de la carretera en, *Forero et al.* 2339 (MO, NY); base del Cerro Torrá, Camino a lo largo del río Surama, *Forero, et al.* 3072 (MO); Quibdó, Carretera Quibdó-Tutunendo, Titio Los Etancos, 10 km de Quibdó, *Forero & Jaramillo* 2524 (MO), Quibdó-Tutunendo Road, 14 km E of Quibdó, *Gentry & Renteria*, 24143 (NY), along road between Quibdó and Medellín at km 207.5, *Croat* 52250 (MO). **Meta:** El Pato, SE of San Antonio



Fortalecillas, Huila, *Little Jr.* 7977 (MO, US); Sierra de La Macarena, Vereda El Tablazo, *Carcía et al.* 398 (MO), La Macarena, *Ohba et al.* 1221 (MO). **Nariño:** Mongon, on Río Telembi, 21 km ESE of Barbacoas, *Fosberg* 21201 (NY, US); vicinity Ricaurte, along Río Imbí, km NW of Ricaurte, along trail to Ramos, 1°08'N, 77°56'W, *Croat* 71508 (MO). **Valle Del Cauca:** *Fosberg* 20506 (S, US); *Killip* 5080 (F), *Cuadros* 1003 (MO); *Gentry & Monsalve* 53196 (MO); 4°07'N, 76°51'W, *Taylor & Adarve* 12002 (MO). COSTA RICA. WSW of Arenal Volcano, *Funk* 10394 (US); **Alajuela:** Los Niños, Río Penas Blancas Valley, Laguna Poco Sol, *Haber & Zuchowski* 11169 (F, MO); 4 km SE of Fortuna, then 2.5 km SW on jeep road, 10°29'N, 84°43'W, *Liesner, et al.* 15220 (MO). **Cartago:** Las Vueltas, Tucurrique, *Tonduz* 13363 (BM, F, M); La Selva, ca. 1 km N La Suiza, 9°50'50"N, 83°35'50"W, *Kiehn & Veiman* MK-880321-2/1 (MO); vicinity of Pejivalle, *Standley & Valerio* 46796 & 46829 (US). **Guanacaste:** NNE slopes of Volcan Orosi, Pitilla along trail, 10°59'N, 85°27'W, *Taylor & Gereau* 9835 (F, MO); P. Nac. Rincón de la Vieja Cerro Chato, Colonia Libertad, *Rivera* 851 (MO). **Heredia:** En socola vecina al Río Sarapiquí, *Jiménez* 3619 (F, HUH); La Selva, near Puerto Viejo, *Opler* 248 (F), Finca La Selva, E of Río Puerto Viejo-Río Sarapiquí the junction, *Smith* 79 (F), *McDowel & Santana* 168 (F, MO), S of Hwy, *McDowel* 789 (F, MO), *Hammel* 12600 (MO), *Chacon* 653 (MO, NY), Estacion Biologico, La Selva, 10°24'N, 84°02'W, *Smith & Frost* 480 (F, WIS); Canton de Sarapiquí, Rara Avis, ca. 15 km al SO de Horoquetas, 10°17'N, 84°02'W, *Vargas & Frazee* 27 (F, MO). **Limón:** Talamanca, 200m, *Tonduz* 9419 (BR, US); Mountain range inland from Cahuita *Gentry* 1312 (MO); S of Limón, along the road inland through Penhurst, *Taylor & Skotack* 4498 (MO); Cerro coronel, E of Río Zapote, 10°40'N, 83°40'W, *Stevens* 23942 (MO); Cantón de Talamanca, *Mora* 97 (MO), Cuenca del Sixoala, San Miguel de Sixoala, 9°33'60"N, 82°38'20"W, *Alfaro*, 2071 (MO). **Puntarenas:** Corcovado National Park, 8°30'N, 83°37'W, *Liesner* 3018 (MO); Reserva Indígena Guaymí Alto Laguna, Osa, *Cordero* 68 (MO); Cantón de Golfito P. N. Corcovado peninsula de Osa, *Maas*, 48 (MO); along the banks of the Río Sonador, 23 mile east of San Isidro, *Webster et al.* 12411 (F, HUH); La Gamba, Parque Nacional Esquinas, 8°41'N, 83°13'W, *Will* 55 (MO). **San Jose:** Reserva Biológica Caraca. Sector Caraca, 9°45'05"N, 84°32'00"W, *Zúñiga* 300 (MO); El sur de Turrubares, 9°45'N, 84°35'W, *Biesmeijer et al.* 334 (U). DOMINICAN REPUBLIC. De Samana, Civ. Santo Domingo, Hispaniola, Los Banaderos Prietos, *Ekman* 15126 (S), Samana, Leguna, *Ekman* 14966 (S); Jayaco, Bonaio, *Liogier* 20370 (F, HUH, NY). ECUADOR. San Lorenzo, *Gilmartin* 261 (HUH). **Cañar:** Guayaquil, Cuenca Road, ca. 10 km E of Cochencai, *Gentry, et al.* 30809 (MO). **Carchi:** Chical, 0°56'N, 78°11'W, *Thompson et al.* 1067 (MO, F); stream by Rafeal Quindís Finca flowing into Río Verde, Above Untal, along road to Charchi, 0°53'N, 78°8'W, *Hoover & Wirmley* 1508 (MO); montanas al Sur de Maldonado, *Delprete & Verduga* 6396 (NY, UPS). **El Oro:** 11 km west of Pinas on new road to Sta. Rosa, *Dodson* 9233 (MO); Limón-Playa, 3°29'S, 79°45'W, *Cornejo* 368 (MO). **Esmeraldas:** San Lorenzo, *Játiva & Epling* 591 (NY, S), San Lorenzo Cantón, Reserva Etnica Awá, Centro Recourte, 0°10'N, 78°32'W, *Tpaz et al.* 2143 (MO); Río Onzole,

upstream from San Francisco de Onzole, 0°52'N, 79°30'W, *Holm-Nielsen et al.* 25781 (NY); San José, Km 321 along railroad from Ibarra to San Lorenzo, 1°0'N, 78°00'W, *Boom* 1356 (MO, NY); Frutos rojados, 1°8'N, 78°33'W, *Aulestia et al.* 587 (MO). **Los Ríos:** Hacienda Climentina, between Babahoyo and Montalve, *Sparre* 17896 (NY, S); Río Palenque Biological Station, Km 56, Quevedo-Santo Domingo, *Dodson* 5736 (MO, US), 0°37'S, 79°22'W, *Dodson & Duke* 7643 (MO). **Morona-Santiago:** valley of the ríos Negro and Chupianza, on the trail from Sevilla de Oro to Méndez, *Camp E-1523* (NY, S), Méndez, *Harling* 938 (S); Mera, *Asplund* 18494 (G, NY, S); Environs of Pan de Azucar, along road Indanza-Don Bosco, *Harling & Stahl* 26856 (MO, S). **Napo:** Tena, *Asplund* 8881 (G, S); Road Coca, Auca oilfields, along the road to Yucca, *Holm-Nielsen et al.* 19637 (NY). **Pastaza:** Oriente, valley of Río Pastaza, south of Shell-Mera, Parroquia Mera, *Steere & Camp* 8277 (F, US, NY); Río Puyo, near the village Puyo, *Fagerlind & Wiborn* 1218II (S), *Prescott* 905 (NY), Puyo, road to Tena, ca. 2 km from Puyo, *Harling* 3238 (S). **Pichincha:** Santo Domingo de los Colorados, *Fagerlind & Wiborn* 1660 (MO, S); 20 km West of Santo Domingo de los Colorados, *Cazalet & Pennington*, 5278 (NY); Road along Santo Domingo, Toachi, *Sparre* 13855 (S); in Cooperativa Santa Marta 2, along Río Verde, 2 km southeast of Santo Domingo de Los Colorados, *Dodson et al.* 7587 (MO), 3 km south of Santo Domingo, *Dodson & Gentry* 10370 (MO). **Tungurahua:** Between Hacienda La Victoria and Río Topo, *Penland & Summers* 232 (F, HUH). **Zamora-Chinchipe:** Zumbi, on the northern border of Río Zamora, *Sparre* 16481 (S); El Pangui, 3°31'33''S, 78°26'52''W, *Montenegro et al.* 145 (MO). PERU. **Huánuco:** Tingo Maria, *Asplund* 12183 (G, S); Monzón, *Ferreira* 10064 (MO); Leoncio Prado, Rupa Rupa, Este de Tingo Maria, cerca al Cerro Quemado, *Vigo* 9938 (F, MO, NY, US, U), *Vigo*, 10114 (F, MO). **Loreto:** Vicinity of Iquitos, San Juan, *Asplund* 14438 (BR, NY, S), Maynas, Iquitos, Prolongacion Yavarí, Versalles (Paina), *Rimachi* 936 (MO, NY), Quebrada Orejon, Purma, *Ayala et al.* 2805 (F), Allpahuayo, 04°10'S, 73°30'W, *Vásquez* 16723 (MO); Santa Ana on the upper Río Nanay, *Williams* 1227 (F, S). **Pasco:** Oxapampa in vicinity of Proyecto Palcazu camp in Iscozacín Río Iscozacín, tributary of Río Palcazu, 10°12'S, 75°13'W, *Knapp et al.* 7842 (MO, NY). **San Martín:** Mariscal Cáceres, Tocache Nuevo, *Vigo* 8271 (MO); San Roque, *Williams* 7469 (F); Rioja, *Woytkowski* 6114 (G, HUH, MO). **Tungurahua:** Between Hacienda La Victoria and Río Topo, *Penland & Summers* 232 (F, HUH). **Zamora-Chinchipe:** Zumbi, on the northern border of Río Zamora, *Sparre* 16481 (S); El Pangui, 3°31'33''S, 78°26'52''W, *Montenegro et al.* 145 (MO). FRENCH GUIANA. **Saint-Laurent-Du-Maroni:** Vicinity of Saül, along road to airstrip, 3°38'N, 53°12'W, *Andersson et al.* 2028 (S). **Cyenne:** Piste de Bélizon, *Billiet et al.* 6258 (MO); Camp Eugène, Bassin de Sinnamary, 4°51'N, 53°4'W, *Granville & Cremers* 12816 (MO). GUATEMALA. *Türckheim s.n.* (M). **Alta Verapaz:** Cubilquitz, *Türckheim*, 7749 (HUH, M, NY); **Chiquimula:** Eastern portions of Vera Paz and Chiquimula, *Watson* 4 (HUH, US). **Izabal:** Near Puerto Barrios, *Standley* 72119 & 72575 (F); Mariscos, bordering Lake Izabal, Playa Dorada, *Conteras* 7609 (F); El Estor, *Contreras* 11455 (F, S). **Retalhuleu:** Río Talculán, 5 km west of Retalhuleu, *Standley* 87335 (F). GUYANA. **E.**

**Islands-W. Demerara Region:** Along west bank of the canal between St. Lawrence and Hubu, 6°49'N, 58°28'W, *Kelloff, et al. 648* (MO); Naamryck Canal, nearly 3.5 km SW of Parika, 6°50'N, 58°27'W, *Gillespie & Gopaul 1013* (MO, NY, U); Barima-Waini, upper Sebai River, 8 km upriver from Sebai village, 7°51'N, 59°17'W, *Hoffman et al. 659* (MO, NY); Barabina hill, 2 km SE of Mabaruma, 8°13'N, 59°48'W, *Reinders & Torres 172* (NY, U).

**MEXICO. Oaxaca:** Ubero, *Williams 9370* (F). **Chiapas:** MO); En el Vértice del río Chixoy a 100 km al S de Boca Lacantum, Ocosingo, *Martínez 18950* (MO); Santa Rita, Cacahoatan, *Ventura & López 2106* (G, HUH, U).

**NICARAGUA. Atlántico Norte:** Bridge over (Caño) Shilam Wasito, ca. 6 km E of first suspension bridge E of Rosita on road to Bonanza, 14°00'N, 85°31'W, *Stevens 12530* (MO), along road from Bonanza to Constancia, *Stevens 12505* (MO), on road from Bonanza to El Salto Grande, *Pipoly 3617* (MO), 0.5–1.5 km from Plantel El Salto along road to Bonanza, 14°03'N, 84°37'W, *Stevens 18868* (MO). **Atlántico Sur:** Route 7, near El Recreo, *Hamblett 329* (MO), Estacion Experimental El Recreo, SE de Río Mico, 12°10'N, 84°18'W, *Sandino 1603* (MO), ca. 1.5 km al S de la Estación Experimental El Recreo, *Soza et al. 337* (MO), SW de Estación Experimental El Recreo, 12°10'N, 84°18'W, *Sandino, 2681* (MO), on the Río Mico, 12°10'N, 84°18'W, *Devidse et al. 30716* (MO); Monkey point, Caño El Pato, 1.5 km sobre la ribera del Caño, 11°35'N, 83°42'W, *Moreno 12381* (MO); Río Punta Gorda, en el Caño El Guineo, *Jellez et al. 4893* (MO), Atlanta, La Richard, 11°32'N, 84°05'W, *Moreno & Sandino 13078 & 22978* (MO), *Moreno & Sandino* (MO). **Matagalpa:** ca. 5.9 km E Río babasca and 2.7 km W of Río Mancera, ca 54 NE of El Tuma, 13°16'N, 85°31'W, *Stevens et al. 19231* (MO). **Río San Juan:** En Santa Marta a 30 km al W de San Juan del Norte, 11°06'N, 83°54'30''W, *Martínez & Riviere 1990* (MO); Buenos Aires en la Ribera del río Sábalo, 11°02'N, 83°28'W, *Moreno 22978* (MO); Sobre el Río San Juan, a lo largo del Río Bartola, 10°58'N, 84°40'W, *Rueda et al. 1960* (MO); Reserva Indio-Máiz, Castillo, Estación Experimental La Lupe, 11°07'N, 84°22'W, *Rueda & Velaásques 15117* (MO).

**PANAMA. Bocas Del Toro:** Region of Almirante, *Cooper 149* (F); Vicinity of Chiriqui lagoon, *Wedel 1497* (HUH, MO), *Wedel 1590* (HUH, MO), *Wedel 1782* (MO); Shepherd Island, *Wedel 2681* (HUH, MO); Punta Peña, *Lewis et al. 2161* (HUH, MO); Alrededor de IRHE, *Carrasquilla & Mendoza 1198* (F, MO); Al SE y NE de Changuinola del IRHE, *Correa et al. 3391* (MO, NY). **Darién:** Río Cocalito, *Whitefoord & Eddy 157* (BM).

**PERU. Huánuco:** Tingo Maria, *Asplund 12183* (G, S); Monzón, 700–750, *Ferreyra 10064* (MO); Leoncio Prado, Rupa Rupa, Este de Tingo Maria, cerca al Cerro Quemado, *Vigo 9938* (F, MO, NY, US, U), *Vigo 10114* (F, MO). **Loreto:** Vicinity of Iquitos, San Juan, *Asplund 14438* (BR, NY, S), Maynas, Iquitos, Prolongacion Yavarí, Versalles (Paina), *Rimachi 936* (MO, NY), Quebrada Orejon, Purma, *Ayala et al. 2805* (F), Allpahuayo, 04°10'S, 73°30'W, *Vásquez 16723* (MO). **Pasco:** Oxapampa in vicinity of Proyecto Palcazu camp in Iscozacín Río Iscozacín, tributary of Río Palcazu, 10°12'S, 75°13'W, *Knapp et al. 7842* (MO, NY). **San Martín:** Mariscal Cáceres, Tocache Nuevo, *Vigo 8271* (MO); San Roque, *Williams 7469* (F); Rioja, *Woytkowski 6114* (G, HUH, MO).

**PUERTO RICO. Maricao,**

Ad ripam Fluminis, *Sintenis* 263 (BM, G, HUH, M, S); Guavate, *Woodbury* s.n. (NY); Mayaguez, *Hess* 1046 (NY); South of Aihruito, *Britton & Britton* 9994 (NY); Along highway 988, 18°20'N, 65°45'W, *Boom & Marshall* 7094 (NY); Naguabo, Río Blanco, along Rt 191, *Axelrod & Chavez* 2975 (MO). TRINIDAD. Isle de la Trinité, *Sieber* 324 (G); Siera de Luguillo, *Urban* 1819 (L), *Broadway* 5863 (MO, S); Melajo, *Adams* 14044 (NY), at Asa Wright Nature Centre, on the Blachisseuse Road, north of Arima, *Harriman* 17466 (NY). VENEZUELA. **Monagas**: Morichal el Esfuerzo, *Jsepín*, 9°32'N, 62°43'W, *Heredia* 58 (MO). **Apure**: Paéz, Parcela 3, E of El Nula, *Werff & Gonzáles* 4815 (F). **Bolívar**: Tumeremo, alrededores del caño Botanamo, camino Tumeremo-Bochinch, *Stergios et al.* 3717 (MO), 7°18'N, 61°30'W, *Stergios et al.* 3683 (MO, NY). **Zulia**: Camino desde la casa de Diego Coronel a torre de Observación de la Guardia Nacional, de la casa próximo al Río Miranda, 10°27'N, 70°49'W, *Zambrano & Alfonso* 1403 (VEN).

**43b. *Sabicea villosa*** Willd. ex Roem. & Schult. **var. *adpressa*** (Wernham) Standl., Publ. Field Columbian Mus., Bot. Ser.7: 52. 1930. *Sabicea hirsuta* var. *adpressa* Wernham, Monogr. *Sabicea* 55. 1914. TYPE: Panama. Isthmus of Panama, Chagres, Jan.-Mar. 1850 (fl), *A. Fendler* 180 (lectotype, designated here, F!; duplicates, BM!, HUH!, MO!, W!).

*Selected specimens examined.* BOLIVIA. **Beni**: Vaca Diez, 18,4 km E of Riberalta, the 1 km NE on old road to Cachuela Esperanza, *Solomon* 7795 (MO, NY). **Cochabamba**: Carrasco, *Smith et al.* 12954 (MO). **Pando**: Manuripi, Humaitá. Río Madre Dios, *Moraes* 404 (MO). **Santa Cruz**: Velasco, Parque Nacional Noel Kempff Mercado, El Ecanto, 14°39'S, 60°43'W, *Solidas et al.* 2750 (F, MO, NY). BRASIL. **ACRE**: Manoel Urbano, Rio Chandless *Daly et al.* 11500 (MO, NY); Tarauacá, basin of Rio Muru, Cajazeira, ca. 50–60 km upstream from Tarauacá, 08°31'S, 70°53'W, *Delprete et al.* 8250 (NY, U); Highway Abuna to Rio Branco, km 242–246, vicinity of Campinas, *Forero et al.* 6318 (NY, S). **Amazonas**: Scrinoyal S, Fransisco, Rio Acre, *Ule* 9858 (G), basin of Rio Negro, between Ilha Jacaré & Airão, *Prance et al.* 15060 (MO, NY, U). **Rondônia**: Rondônia-Ariquemes, Mineracao Mibrasa, Setor Alto Candeias, km 128, Sudoeste de Ariquemes, 10°35'S, 63°35'W, *Teixeira et al.* 421, (MO, NY). Seringal São Luis, *Santos et al.* 306 (HUH, MO, NY). **Santa Catarina**: Cunhas, Itajai, *Klein* 1126 (U, US). COLOMBIA. Santa Marta, near the coast, *Smith* 2653 (BM, F, G, HUH, MO, NY, S, WIS, U). **Amazonas**: Río Caqueta, Araracuara, 0°37'S, 72°15'W, *Dulman & Wijninga* 63a (U); Río lagara-Paraná 17 km en aval de La Chorrera, Parcelle 108 *Gasche & Desplats* 72 (G); Leticia, Puerto Narino at Loreto Yacu River, 3°46'13''S, 70°22'59''W, *Soejarto & Cardozo* 785 (F, HUH, US), Leticia, Río Cotuhé entre la Cabaña Lorena y Caña Brava, en el margen izquierdo del río, 03°01'S, 70°02'W, *Rudas et al.* 2179 (MO). **César**: Rincón Hondo, Magdalena valley, *Allen* 442 (MO). **Chocó**: Km 226 on the road from Quibdo to Munquirri, *Cutrecasas & Llano* 24038 (US); Between Camp Curiche and

Q. Changame, 3.7 miles S of Camp Curiche, *Duke 11540(2)* (MO); Near Río Truando, 3–5 km above airport at Teresita, *Duke 11198(4)* (MO); Río Truando, between Río Cucio and La Nueva, *Duke 9816* (MO). **Meta:** Altilanuras, cerca de Morichal, Hato Horizontes, *Blydenstein 994* (NY). **Santander:** Puerto Wilches, *Killip & Smith 14929* (F). **Valle Del Cauca:** Buenaventura, *Killip 11684* (F, HUH, NY), near highway bridge over Río Dagua, ca. 20 km E of Buenaventura, *Killip & Garcia, 33302*, (BM, F), Bocas del Tigre, quebrada Mondoyá, *Cuadros 958* (MO), San Isidro, along unpaved road from San Isidro to Juanchao, 3°59'N, 76°57'W, Rooden et al. 294 (F[2] MO, NY-2); Cali, Villa Carmello, *Murphy 395* (US). COSTA RICA. **Alajuela:** 4 km SE of Fortuna, then 2,5 km SW on jeep road, 10°29'N, 84°43'W, *Liesner et al. 15208* (WIS). **Limón:** Bosque llovisoso, Suerre y Dos Bocas, Drenajes de los Rios Parismina y Reventazon, *Shank & Molina 4209 4217* (HUH); Puerto Limón, 10°0'N, 83°02'W, *Kuntze 1995* (NY). **Puntarenas:** Along the banks of the Río Sonador, 23 mile east of San Isidro, *Webster et al. 12411* (F, HUH), Cantón de Golfito R.F. Golfo Dulce, Serranias de Golfito, estacion Río Bonito, *Fletes 335* (MO). ECUADOR. **Los Ríos:** Continela Ridg area, 12,5 km E of Patricia pilar, *Hansen et al. 7744* (MO, U). **Napo:** Río Aguarrico, Santa Cecilia, border of Río Aguarrico, *Sparre 13194* (MO, S); Mishuallí, in the surroundings of the junction Río Mishuallí-Río Napo, 1°3'S, 77°41'W, *Holm-Nielsen 19323* (MO, NY); Road Coca-Auca Oil fields, 3 km along the road to Yocca, 0°28'S, 76°55'W, *Nolm-Nielson et al. 196543* (NY); Orellana, Parque Nacional Yasuní, Pozo petrolero Daimí, 0°55'S, 76°11'W, *Cerón & Hurtado 4200* (MO, NY). **Pastaza:** Curaray, Northern Bank, 01°22'S, 76°58'W, *Holm-Nielsen et al. 21881* (MO, NY), Río Curaray, about 10 km upstream from the military camp, 1°36'S, 75°59'W, *Brabdyge and Asanza 31439* (MO), Finca El Valle de Muerte on Río Curaray, ca. 10 km E of Curaray (Jesús Pitishka), 1°23'S, 76°50'W, *Harling & Andersson 17664* (MO), Lorocachi, A2 horas en deslizador uaro y Curaray, S, *Miller et al. 231* (F, MO, NY). **Pichincha:** Tiputini, Lagartococha, *Fagerlind & Wibom 2327* (S). **Morona Santiago:** Santiago-Zamora ("Oriente"), near Méndez, *Camp E-964* (NY). **Sucumbios:** Road from Lago Agrio-Coca, Proyecto Payamino (IERAC), edge of pasture S of River Payamino, 265 km, *Sobel & Strudwick 2382* (MO, NY), Río Pucino, above bridge at Aguarico, near Lago Agrio, *Gentry 9760* (HUH). FRENCH GUIANA. **Cayenne:** *Jaquemín 1521* (US). GUYANA. Cuyuni-Mazaruni: Along road from Ariching airstrip to Mazaruni river, 6°10'N, 60°07'W, *McDowell 4045* (MO). HONDURAS. **Atlántida:** Orillas Río Piedras Gordas, 10 km E. Tela, *Segovia 55* (MO); Tela, orilla del río Piedras Gordas, *Nelson 7758* (MO, US). NICARAGUA. **Atlántico Norte:** Comarca de El Cabo, El matorral de Quebrada Cuyu, *Molina 15048* (NY); Nera Río Okanwas, 12 km east of Rosita, *Neil 4451* (MO); Between 0.3 and 1.9 km N of Limbaica, 13°29'N, 84°13'W, *Stevens 19487* (MO); Siuna, Wany, *Ortiz 28* (MO), Finca La Manzana, *Ortiz 2049* (MO). **Río San Juan:** Río Sábalo, *Araquistain 3236* (MO); San Juan del Norte, *Araquistain 3405* (MO); Reserva Indio-Máiz, Juan del Norte, caño Negro, ramal del río Indio, 11°02'N, 83°54'W, *Rueda et al. 4734* (MO). PANAMA. **Bocas Del Toro:** Along RR track near station at Milla 5, *Croat & Porter 16494* (MO, NY). **Colón:** Gatun Station, on Panama

Railroad, *Hayes 66* (HUH), *Hayes 241* (NY). **Darién:** Along Río Pirre, *Duke 4963* (HUH, MO); Río Uruti, *Bristan 231a* (MO); Choco village, Piji vassal, *Folsom 4575* (MO); Río Cocalito, *Whitefoord & Eddy 157* (BM). **De Veraguas:** Isla de Coiba, *Aranda et al. 2245* (MO), Los Pozos, *Cuadras et al. 7963* (MO). **Panamá:** Barro Colorado Island, Canal Zone, *Aviles 22* (F, MO), Barbour Point, *Shattuck 704* (F, MO), Gigante Bay, *Shattuck 1130* (F, MO), Canal Zone, Military Road K-9, *Ebinger 521* (F, MO), Fairchild Point, *Ebinger 281* (F, MO), *Croat 6703 & 11725* (MO); near Arraiján, *Woodson et al. 1353* (F, HUH, MO, NY); San José Island, Pearl Archipelago, in vicinity of Naval Station, *Erlanson 479* (G, HUH, NY). **San Blas:** *Cooper 275* (F, NY); Isla Ailigandi, *Dwyer 6840* (MO); mainland opposite to Ailigandi, from mouth of Ailigandi River to 2.5 miles inland, *Lewis et al. 160* (MO); Hills southeast of Puerto Obaldia, *Croat 16708* (MO); Playon Chico and Vicinity, Molia, *Stier 42* (MO); Comarco De San Blas, Playon Chico and vicinity, 9°18'N, 78°13'60"W, *Stier 232* (MO); Around Puerto Armila, *D'Arcy and McPherson 16131* (MO). PERU. **Amazonas:** Río Cenepa, ridge 10–12 km SW of Huampami, 298.70. *Berlin 106* (HUH); Al lado de Huampami, *Kayap 1471* (HUH); Quebrada Wampusik entsa, Chacra, *Ancuash 721* (HUH, MO), Condorcanqui, Huampami, Río Cenepa, 198–213 mBoster 6 (MO); Huambisa, 1 km atrás de La Poza, *Tonqui 27* (MO, F), quebrada Caterpiza, 03°50'S, 77°40'W, *Tunqui 605* (MO). **Cuzco:** Camisea, Campamento San Martín, 11°47'08"S, 72°41'57"W, *Smith 8966* (G, MO, NY, U), Campamento Malvinas, 11°52'12"S, 72°56'28"W, *Acevedo-Rodriguez & Ramirez 9896* (MO, US). **Huánoco:** Pachitea, Comunidad Nativa Santa Marta, 9°20'S, 75°15'W, *Smith 1249* (MO), Honoria, Bosque Nacional de Iparia, a lo largo del río Pchitea cerca del Miel de Abeja, 1 km arriba del pueblo de Tournavista, *Vigo 1671* (F, HUH, NY). **Loreto:** Alto Amazonas, Andoas, *Ayala 2111* (HUH, MO, NY), Río Pastaza near Ecuador border, 2°48'S, 76°28'W, *Gentry et al. 29855* (F, MO); Caballo-Cocha on the Amazon River, *Williams 2203* (F, S); Between Yurimaguas and Balsapuerto, *Killip & Smith 28263* (NY, US); Maynas, Iquitos, *Killip & Smith 27211* (F), *Asplund 14740* (S), *McDaniel & Rimachi 18818* (BR, MO), Río Nanay below Bellavista, *McDaniel & Rimachi 188818* (NY), Carretera Iquitos-Nauta, km 3 de Quisto Cocha, cerca Peña Negra, *Rimachi 10061* (MO, NY), La carretera de Momonillo near Río Momon, *McDaniel & Rimachi 16996* (F, NY), Río Yubineto, Santa Rita, 1°00'S, 74°20'W, *Haxaire 2431* (MO), Río Yaguasyacu, affluent of Río Ampiyacu, Brillo Nuevo and Vicinity, 2°40'N, 72°00'W, *Balik, et al. 1054 & 1055* (MO), Sanangal, margen derecha del río Itaya, cerca de Yanayaco, 4°10'S, 73°20'W, *Vásquez et al. 318* (F, G, MO, NY). **Madre De Dios:** Small tributary of Río Madre de Dios, below Puerto Maldonado, *Gentry et al. 19635* (MO); Manu Parque Nacional, Río Manu, Río Cumerjali, 11°49'S, 71°32'W, *Foster & d'Achile 11935* (F, MO), Cocha Cashu Uplands, 11°45'S, 71°00'W, *Núñez 5855* (F, MO); SE bank of Río Tambopata, ca. 30 air km or 70–80 river km SSW Puerto Orbigny, 12°49'S, 69°17'W, *Barbour 5097* (MO), Tambopata Wildlife Reserve, 30 km S of Puerto Maldonado, 12°15'S, 69°17'W, *Young & Stratton 114* (MO, NY), en la quebrada Julia, al Oeste de Las Pampas, Río Heath, *Núñez 9813* (MO, NY), Las Piedras, Cusco Amazónico, *Timaná & Jaramilo 3131*

(MO). **San Martín:** Chazuta, Río Huallaga, *Klug 4110* (BM, F, MO, NY-left part, WIS, S); Tocache Nuevo, Mariscal Caceres, *Vigo 6400* (HUH, MO). **Ucayali:** Purús, Río la Novia, 10°12'S, 70°57'W, *Vigo & Graham S14814* (MO, NY); Ivita, 59 km Pucallpa-Tingo Maria road, *Gentry et al. 18616* (F, G, MO). PUERTO RICO Luquillo Mountains, *Wilson 232* (NY); Naguabo, Río Blanco, *Axelrod & Chavez 3229* (NY). SURINAME. Oelemari, circa portum aeronaut, *Boer 931* (NY, U). VENEZUELA. **Amazonas:** Alto Orinoco, Indios Guaicas, (Yanomano), 65°11'W, 2°8'N; *Aristeguieta & Lizot 7385* (MO, NY), entre Ocamo y Mavaca, a lo largo del río Orinoco, 65°11'W, 2°30'N, *Aristeguieta & Lizot 7385* (NY). **Bolívar:** Raul Leoni, alto Río Paragua, 4°27'N, 62°48'W, *Fernandez 2685* (MO); Cedeño, along tributary of the Río Erebató, 5°09'N, 64°34'W, *Boom & Marin 10369* (NY). **Delta Amacuro:** Antonio Díaz, along Cano Araguao, 9°50'N, 61°60'W, *Steyermark et al. 114822* (MO, NY); Vegas del Guayo, Cerca de la Misión, *Ferrari 1898* (F, M). **Monagas:** Reserva Forestal de Guarapiche, Caño Colorado, 10°5'N, 62°40'W, *Aristeguita et al. 7193* (NY, US). **Zulia.** Colón, sector West-Tarra, Machiques-La Fría, en Alcabala La Redima, 8°39'N, 72°35'W, *Bunting & Alfonzo 6921* (NY), alrededores de Casigua El Cubo, sector West-Tarra, 8°44'N, 72°30'W, *Bunting & Fucci 8439* (NY), Casigua El Cubo y Km 8 de la vía rumbo a Palmira, y en el sector Puerto Tigre, 8°44'N, 72°30'W, *Bunting & Fucci 7744* (NY); Cuenca del Embalse Burro Negro (Pueblo Viejo), sector Quirós-El Pensado y el pie de Cerro, 10°10'N, 71°04'W, *Bunting 9594* (NY).

**43c. *Sabicea villosa*** Willd. ex Roem. & Schult. var. ***sellowii*** (Wernham) Steyerem., Mem. New York Bot. Gard. 17: 314. 1967. *Sabicea hirsuta* var. *sellowii* Wernham, Monogr. *Sabicea* 56. 1914. TYPE: Brazil: Río de Janeiro, 1833 (fl), *M. Gaudichaud 622* (lectotype, designated here, G!; duplicate, US!).

*Sabicea domingensis* I. Urban & E. L. Ekman., Arkiv Bot., Stockh. 24A (4): 45. 1932. TYPE: Dominican Republic: Santo Domingo, 05 Feb. 1929 (fl), *E. L. Ekman H11441* (holotype, S!; isotype, US!).

*Selected specimens examined.* BELIZE. Toledo, *Pec, 481* (HUH, NY), Woods bank, Sibun River, *Gentle 1441* (F, HUH, MO, NY, S, WIS). BOLIVIA: **Beni:** Rurenabaque, *Cárdenas 1151* (F, HUH). **La Paz:** Sud Yungas, Alto Beni, San José de Popoy, *Seidel & Schulte 2210* (MO); Franz Tamayo, Parque Madidi, orilla izquierda del río Quendeque, 14°57'40''S, 67°47'59''W, *Quintana et al. 295* (NY). BRASIL. **Bahia:** Rodovia para Itacaré, entrada ca. 1 km E da BR 101, 14°18'35''S, 39°16'22''W, *Sant'Ana et al. 657* (MO, NY); Iihéus, Castelo Novo, 14°38'S, 39°12'W, *Jardim et al. 2003* (G, NY). **Santa Catarina:** Cunhas, Itajai, *Klein 1310* (NY, U, US). **Paraná:** Bank of Várzea of Rio Paraná, just south of Porto Byington, *Lindeman & Haas 1713* (MO, U). GUYANA. Pomeroon, Pomeroon River, *Cruz 3155* (F, HUH, MO, NY), *Cruz 3038* (F, HUH, MO, NY). COLOMBIA. **Nariño:** Recaurte, *Sneidern 471* (MO,

S). **Valle**: Cordoba, *Sneidern 4600* (S). **Amazonas**: Río Iagara-parana, affl, Río Putumayo, corr, La Chorrera, *Sastre 3074* (G). COSTA RICA: **Heredia**: 1,4 km NW of Puerto Viejo, *Anderson & Mori 39* (F, WIS). **San José**: Parque Nac, Braulio Carrillo, 10°09'N, 83°50'W, *Delprete 5102* (NY). **Guanacaste**: Parq, Nacion, Guanacaste ascending the NNE slopes of Volcan Orosi, 10°59'N, 85°27'W, *Taylor 9815* (F, MO). DOMINICAN REPUBLIC. **Hispaniola**: Santo Domingo, Cordillera Central, La Cumbre, *Ekman 14346* (G, HUH, S), near a brook, *Ekman H11441* (US). ECUADOR: **Guayas**: Junction of Guayas, Cañar, Chimborazo & Bolívar, *Camp, E-3719* (NY). **Morona-Santiago**: Pumpuentza, *Brandbyge & Asanza 32288* (MO); **Santiago-Zamora**: near Méndez, *Camp E-856* (NY), *Camp, 856* (US). **Napo**: Tena, *Asplund 8997* (S); Coca (Puerto Francisco de Orellana), *Lugo 2817* (NY); Estación Biologica Jatun Sacha, 01°4'S, 77°36'W, *Rueda 1107* (MO); Parque Nacional Sumaco, Río Paushiyacu, 00°21'S, 77°19'W, *Tirado 1957* (MO, NY). FRENCH GUIANA: **Cayenne**: Riviere Oyapock, face a Zidoaville, 1 km en aval de Trois Sauts, *Oldeman 3321* (NY, U); Saut Deux Roros, 4°22'N, 52°53'W, *Hoff 7436* (MO). GUATEMALA. **Izabal**: Vicinity of Quiriguá, *Standley 23875 & 24206* (HUH, NY), Cadenas, on bank of Sarstun River, *Contreras 9056* (F, MO, S). HONDURAS. **Atlántida**: Lancetilla Valley, vicinity of Tela, *Standley 55115* (F, HUH), near Tela, *Pfeifer 2031* (US), *Standley 53582* (F, HUH), *Standley 52882* (F), ca. 3 mile south of Tela, *Webster et al. 12613* (F, HUH, MO). **Gracias A Dios**: Ahuras Bila, 200 km S.O. de Puerto Lempira, orilla del río Wankí, *Nelson & Cruz, 9239* (MO), La Mosquitia, Ahua Bila, 200 km S.O. de Puerto Lempira, *Nelson & Cruz 9239* (MO). **Yoro**: E of Cerro Guan Guan, S of San José, 15°29'N, 87°27'W, *McDougal et al. 3210* (F, MO). MEXICO. **Chiapas**: Ocosingo, a 50 km al S de Boca Lacantum, *Martínez 1900* (BM, BR, MO). **Chihuahua**: a 33 km del Vertice del río Chixoy camino a Chajul, *Martínez 16202* (BR, F, MO). **Tabasco**: Tacotalpa, *Ramos & Cowan 2717* (MO, NY), Huimanguillo, *Cowan 3330* (MO, NY). 1km north of Teapa, at Rancheria Morelia, *Gilly & Hernandez 238* (HUH). NICARAGUA. **Atlántico Sur**: area de la Bahía de Bluefield, Río Escondido, Molina, 2075 (F). **Atlántico Norte**: Vicinity of Wani including Río Uli, 13°41'–42'N, 85°50'–51'W, *Stevens 7364* (MO). PANAMA. Western Panama, *Stork 108* (US). PERU. **Amazonas**: Imaza, Yamayakat, 5°3'6''S, 78°20'14''W, *Pino et al. 238* (MO); Al lado de Quebrada Sasa, *Kayap 997* (HUH, MO). **Cuzco**: Río Tambopata, 2 km E from the Colpa de Guacamayos, *Núñez 6513* (MO). **Loreto**: Cornel Portillo, *Ferreyra 13025* (MO, US); Maynas, Iquitos, *Simpson & Vigo 642* (F, G, NY), 12.5 km SW of Iquitos, *Croat 8281* (MO), Carretera de Pena Negro, Km 13, en Purma, *Rimachi 6117* (BR, MO), Puerto Almendras, Río Nanay, *Ruíz 1322* (F, MO). **Madre De Dios**: Tambopata, ca. 30 air km or 70–80 river km SSW Puerto Maldonado 12°49'S, 69°17'W, *Barbour 4828* (MO, NY). **San Martín**: Tocache Nuevo, Mariscal C áceres, *Vigo 7423* (HUH, MO), Cerro Sin Sin, cerca a Bambamarca, *Vigo 11961* (MO). VENEZUELA. **Bolivar**: Sucre, alrededores de Santa María de Erebató, 200 m 4°59'N, 64°49'W, *Sanoja 2540* (MO, NY, VEN). **Mérida**: Arzobispo Chacón, La Florida, a 1 km al SO de Santa María de Chaparo, 7°43'N, 71°28'W, *Aymard, et al. 4506* (MO). **Portuguesa**: Guanare, 9°40'N, 69°49'W, *Stergios & Aymard 8559*



(MO, NY), *Stergios & Aymard*, 9305 (MO). **Trujillo**: La Ceiba, *Pittier 10894* (F, G, HUH, NY). **Zulia**: Serrania de Perijá, southwest of Guasare, 10°52'N, 72°29'W, *Luteyn 9249* (NY), al S de la Misión de Los Angeles de Tokuku, al SO de Machiques, 9°50'N, 72°48'W, *Steyermark 99976* (G, NY, U).

**Dubious or insufficiently known names/ taxa:**

***Sabicea aspera* var. *rotundifolia*** K. Schum., Bull. Soc. Bot. France 56, Mem. 3d: 339. 1909.

TYPE: *Minas, 19420* (holotype, P, not seen; isotype B, K, not seen). Quartel do Biribiry, prés Diamantina, Arbuste sarmenteux, fl. Blanchâtres, Février-mars. R.

We could not locate its type. The original description is insufficient to recognize this taxon.

***Sabicea flagenioides*** Wernham, Monogr. *Sabicea* 57. 1914. TYPE: Yucatan:

Chichankanab, *Gaumer 1432* (holotype, F, not seen).

Wernham (1914) characterized this species by its subulate-setaceous stipules, which is contrasting to the Neotropical *Sabicea*. We could neither observe the holotype Gaumer 1432 (F) nor any other specimen showed this characteristic stipule. Lorence (1999) recognized the status of *Sabicea flagenioides* as "uncertain". It is probably based on a species of *Chiococca* P. Browne (C. M. Taylor, pers. comm.).

***Sabicea pumila*** Bartl. ex DC., Prodr. 4: 440, 1830. TYPE: Peru. montibus Huanoccensibus (G-DC).

It was not possible to locate its type. Wernham (1914) suggested *Hoffmannia* Sw. to included this taxon.

***Sabicea pratensis* var. *glaberrima*** Bremek., Rec. Trav. Bot. Neerl. 33: 707. 1936. TYPE:

Suriname, *Rombouts, 223* (holotype: U).

It appears *Sipanea pratensis* var. *glaberrima*.

***Sabicea stenantha*** K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem. TYPE: Ecuador.Oriente,

Pacapaca, stark gelichteter Regenwald mit primären Resten, ca. 200 m u. M, 28 April 1937, *Schultze-Rhonhof 2371* (holotype, herbarium not cited, presumably destroyed in B).

It seems to differ from *Sabicea villosa* by its very few or missing hairs. However, its original description indicates that it is either *Sabicea villosa* var. *adpressa* or *S. aspera*.

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**Appendix 1. Aligned ITS and *trnT-F* data matrices used in the combined ITS-*trnT-F* analysis (Chapter 6.1)**

**ITS Matrix (670 bp)**

**ITS1**

	▶	90
<i>S._angolensis</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._amazonensis</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGTTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._aspera</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGTTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._brevipes</i>	TCGAATCC-TG-CAAAGTAGACGACC-GCGAACTTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._caminata</i>	TCGAATCC-TG-CAAAGTAGACGACC-GCGAACTTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._cana</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGTTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._capitellata</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CGGGTT-GGGATAGTA-CC	
<i>S._chocoana</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGTTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._cinerea</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGTTGTCGGC--AGGTG-CGGGTT-GGKATAATA-CC	
<i>S._congensis</i>	TCGAATCC-TG-CAAAGTAGACGACC-GCGAACTTGTGTTATTA-----CACGGCTGTCGGT--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._dewevrei</i>	TCGAATCC-TG-CAAAGTAGACCACC-GTGAACCTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._dinklagei</i>	TCGAATCC-TG-CAAAGTAGACGACC-GCGAACTTGTGTTATTA-----CACGGATGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._discolor</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._diversifolia</i>	TCGAATCC-TG-CAAAGTAGACGACC-GCGAACTTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._effulenensis</i>	TCGAATCC-TG-CAAAGTAGACGACC-GCGAACTTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._exellii</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTAATA-----CACGGATGTTGCC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._ferruginea</i>	TCGAATCC-TG-CAAAGTAGACGACT-GCGAACTTGTGTTATTA-----CACGGGCGTCGGT--AGGTG-CGGGTT-GGGATAATA-TC	
<i>S._fulva</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._gilletii</i>	TCGAATCC-TG-CAAATAGACGACC-GCGAACTTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CGGGTT-GGGATAC----C	
<i>S._glabrescens</i>	TCGAATCC-TG-CATAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGTTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._harleyae</i>	TCGAATCC-TG-CAAAGTAGACGACC-GCGAACTTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._humilis</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGTTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._ingrata</i>	TCGAATCC-TG-CAAAGTAGACGACC-GAGAACTTGTGTTATTA-----CACGGCTGTCGGT--AGGTG-CGGGTT-GGGATAGTA-CC	
<i>S._johnstonii</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CGGGTT-GGGATAAGTA-CC	
<i>S._mattogrossensis</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGTTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._mexicana</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTAATA-----CACGGTTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._najatrix</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGCTGTCGGG--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._orientalis</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGCTGTCGGG--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._panamensis</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGTTGTCGGC--AGGTG-CGAGTT-GGGATAATA-CC	
<i>S._pyramidalis</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGTTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._rosea</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGATGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._seua</i>	TCGAATCC-TG-CAAAGTAGACGACC-GCGAACTTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._speciosa</i>	TCGAATCC-TG-CAAAGTAGACGACC-GCGAACTTGTGTTATTA-----CACGGATGTAGGC--AGGTG-CGGGTT-GGGATAACA-CC	
<i>S._thomensis</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTAATA-----CACGGATGTTGCC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._venezuelensis</i>	TCGAATCC-TG-CATAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGTTGTCGGT--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._velutina</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATCA-----CACGGTTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._venosa</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGCTGTCGGG--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._villosa1</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGTTGTCGGG--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._villosa2</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGTTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._vogelii</i>	TCGAATCC-TG-CAAAGTAGACGACC-GCGAACTTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CGGGTT-GGGATA-TA-CC	
<i>S._xanthotricha</i>	TCGAATCC-AG-CAAAGTAGACGACC-GCGAACTTGTGTTATTA-----CACGGTTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>P._aurifodinae</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGCTGTCGGG--AGGAG-CGGGTT-GGGATAATA-CC	
<i>P._mildbraedii</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGCTGTCGGG--AGGAG-CGGGTT-GGGATAATA-CC	
<i>P._nobilis</i>	TCGAATCC-TG-CAAAGTAGACGACC-GCGAACTTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CTGATT-GGGATAATA-CC	
<i>P._segregata</i>	TCGAATCC-TG-CAAAGTAGACGACC-GCGAACTTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CTGATT-GGGATAATA-CC	
<i>P._medusula</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGCTGTCGGG--AGGAG-CGGGTT-GGGATAATA-CC	
<i>P._batesii</i>	TCGAATCC-TG-CAAAGTAGACGACC-GTGAACCTGTGTTATTA-----CACGGCTGTCGGG--AGGAG-CGGGTT-GGGATAATA-CC	
<i>P._proseltyta</i>	TCGAATCC-TG-CAAAGTAGACGACC-GCGAACTTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CTGATT-GGGATAATA-CC	
<i>P._arborea</i>	TCGAATCC-TG-CAAAGTAGACGACC-GCGAACTTGTGTTATTA-----TACGGCTGTCGGC--AGGAG-CGGGTT-GGGATAATA-CC	
<i>P._becquetii</i>	TCGAATCC-TG-CAAAGTAGACGACC-GCGAACTTGTGTTATTA-----TACGGCTGTCGGC--AGGAG-CGGGTT-GGGATAATA-CC	
<i>E._hucniana</i>	TCGAATCC-TG-CAAA-TAGACGACT-GCGAACTTGTGTTATTA-----CACGGCTGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>H._minutiflora</i>	TCGAATCC-TG-CAAAGCAGACGACC-GCGAACTCGTGACACCG-----CACGGGTGCCGGT--GGGAG-CGGGTT-GGGACAAAA-CC	
<i>S._hirsutum</i>	TCGAATCC-TG-CAAAGTAGACTACC-GCGAACTTGTGTTATAA-----CACGGATGTCGGC--AGGTG-CGGGTT-GGGATAATA-CC	
<i>S._elliptica</i>	TCGATCC-TG-CAAAGCAGACGACC-GCGAACTTGTGTGATTA-----CACGGTTGCCGAC--AGGAA-CGGGTT-GGGATAATA-CC	
<i>T._capsulifera</i>	TCGAATCC-TG-AAAACAGACCACT-GTGAACCTCGTATCAATA-----CACGGGTGCCGGT-----	
<i>V._multiflora</i>	TCGAATCC-TG-AAAAGCAGACCACT-GTGAACCTCGTGTACC-----CACGGCCGTGGTGTGGAG-CGGGTT-GGATTAATA-CC	
<i>V._procumbens</i>	TCGAATCC-TG-AAAAGCAGACCACT-GTGAACCTCGTGTACC-----AACGGGCGTTGGT--GGGAG-CGGGTT-GGATTAATA-CC	
<i>C._coromandelicum</i>	GCGAACCCTTCCAAGACCCGCGCCGCGGGGAAGGGAAGGGCGCGCGCGCGGAGCCCGTTCC-TCCCC--GTCGCCCGCCCT	
<i>H._zanzibarica</i>	TCGAATCC-TG-CAAAGCAGACGACC-GCGAACTCGTCAACTG-----C-CGGGCGTCGGG--GAACG-GGGG-A-GGCGAAAGC-CT	
<i>I._coccinea</i>	TCGAATCC-TG-CAAAGCAGACGACC-GCGAACTTGTGTAAGT-----C-CGGGCGTCTGGG-AAACGAGCGGGGTGACTTACC-GT	
<i>W._coccinea</i>	TCGAATCC-TG-CGAGACGGACGACC-CGGAACACGTTAACC-----C-CGGGCGTCGGG--GAACG-GCGG-A-GACTCAACC-CT	

<i>S._angolensis</i>	C-TCTCGTTGCC----TCACCCGGCACCACC-GCGTGTCTGA---CACGCGGACAGATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._amazonensis</i>	C-TCTCGTTGCC----TCACCCGGCACCACC-GCGTGTCTGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._aspera</i>	C-TCTCGTTGCC----TCACCCGGCACCACC-GCGTGTCTGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._brevipes</i>	C-TCTCGTTGCC----TCACCCGGCACCACC-GCGTGTCTGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._caminata</i>	C-TCTCGTTGCC----TCACCCGGCACCACC-GCGTGTCTGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._cana</i>	C-TCTCGTTGCC----TCACCCGGCACCACC-GCGTGTCTGA---CACGCGGAAA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._capitellata</i>	CCTCTCGTTGCC----TCACCCGGCACCACC-GCGTGTCTGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._chocoana</i>	C-TCTCGTTGCC----TTACCGGACCCATC-GCGTGTCTGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._cinerea</i>	C-TCTCGTTGCC----TCACCCGGCACCACC-GCGTGTCTGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._congensis</i>	C-TCTCGTTGCC----TCACCCGGC-CCCACC-GCGTGTCTGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA

<i>S._dewevrei</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._dinklagei</i>	C-TCTCGTTGCC----TCACCGGC-CCCACC-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._discolor</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGTGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._diversifolia</i>	C-TCTTGTGGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._effulenensis</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._exellii</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGTGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._ferruginea</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GGTGTCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._fulva</i>	C-TCTCGTTGCC----TCACCGGC-CCCACC-GCGTGCTCGA---CACGTGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._gilletii</i>	C-TCTCGTAGCC----TCACCGGCATCCACT-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._glabrescens</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._harleyae</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGTGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._humilis</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCAA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._ingrata</i>	CCTCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._johnstonii</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._mattogrossensis</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._mexicana</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._najatrix</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._orientalis</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGTGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._panamensis</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGTGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._pyramidalis</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-ACGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._rosea</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._seua</i>	C-TCTTGTGGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._speciosa</i>	C-TCTCGTTGCC----TCGCTGGCACCCACC-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._thomensis</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGTGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._venezuelensis</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._velutina</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._venosa</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGTGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._villosa1</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-ACGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._villosa2</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-ACGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._vogelii</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACGTGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._xanthotricha</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CGCGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>P._aurifodinae</i>	C-TCTCGTTGCC----TGACCGGCGCCTACC-GCGTGCTCGA---CGTGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>P._mildbraedii</i>	C-TCTCGTTGTC---TGACCGGCGCCTACC-GCGTGCTCGA---CGTGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>P._nobilis</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACACGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>P._segregata</i>	C-TCTCGTTGCC----TCACCGGCACCCACT-GCGTGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>P._medusula</i>	C-TCTCGTTGCC----TGACCGGCGCCTACC-GCGTGCTCGA---CGTGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>P._batesii</i>	C-TCTCGTTGCC----TGACCGGCGCCTACC-GCGTGCTCGA---CGTGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>P._proseltya</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTCGA---CACACGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>P._arborea</i>	C-TATCGTTGCC----TCACCGGCGCCTACC-GCGCGCTCGA---CGTGCGGACA-ATAACTTAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>P._becquetii</i>	C-TATCGTTGCC----TCACCGGCGCCTACC-GCGCGCTCGA---CGTGCGGACA-ATAACTTAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>E._hierniana</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCTTGA---CACGTGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGC
<i>H._minutiflora</i>	C-TCCCGTCCCA---GCGCGCGCGCCCCC-GCGCGCTCGT---CGCGCGGACA-CTAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._hirsutum</i>	C-TCTCGTTGCC----TCACTGGCACCCACC-GCGCGCTCGA---CACGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>S._elliptica</i>	C-TCTCGTTGCC----TCACCGGCACCCACC-GCGTGCCCGA---TGCGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>T._capsulifera</i>	-----GCC---TCACCGGCGCCACC-GCGTGCTCGT---CGCGTGGACC-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>V._multiflora</i>	C-TCCCGTTGTC---ACACCAGCGTCCATC-GTGCACCTTT---TTGGTGCACC-AAAACCTAA-CTCCGGCGCGGAAAGCGCCAAGGA
<i>V._procumbens</i>	C-TCCCGTTATC---ACACCGGCGTCCATC-ATGCACCCAT---TGGGTGCACC-ATAACTAAA-CTCCGGCGCGGAAAGCGCCAAGGA
<i>C._coromandelicum</i>	CTCCCTCCCTCGGCGCGGAAGCGCGGCGGCGGAGAGTGTCTCGCCCGGGCGAACCTCACAAACCCCGGCGGAAAGCGCCAAGGA
<i>H._zanzibarica</i>	C-CCC-TCCTTC---CCCGGCGCTCCCC---GCGCC--C---CGCGCGGACA-ATAACTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>I._coccinea</i>	CCCTTGCTCCTTTTT-CCTGGCGCTCCCC---GTGCGCTCGT---CGCACGGACCAACAACCTCAA-CCCCGGCGCGGAAAGCGCCAAGGA
<i>W._coccinea</i>	C-CCC-TCCTTC---CCCGACGCCCCCC---GCGCGCACGT---CGCGCGGACG-ACAACCTCAA-CCCCGGCGCGGAAAGCGCCAAGGA

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**S5.8 gene**



<i>S._angolensis</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGATGTG-G-CTTCTRTTGT-AACCAA
<i>S._amazonensis</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGATGTG-G-CTTCTGTTGT-AACCAA
<i>S._aspera</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGATATG-G-CTTCTGTTGT-AACCAA
<i>S._brevipipes</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTATTGT-AACCAA
<i>S._caminata</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA
<i>S._cana</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGATGTG-G-CTTCTGTTGT-AACCAA
<i>S._capitellata</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGTTGTG-G-CTTCTGTTGT-AACCAA
<i>S._chocoana</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGATGTG-G-CTTCTGTTGT-AACCAA
<i>S._cinerea</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGATGTG-G-CTTCTGTTGT-AACCAA
<i>S._congensis</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA
<i>S._dewevrei</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA
<i>S._dinklagei</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA
<i>S._discolor</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GG-GTGATGTG-G-CTTCTGTTGT-AACCAA
<i>S._diversifolia</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA
<i>S._effulenensis</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA
<i>S._exellii</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA
<i>S._ferruginea</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA
<i>S._fulva</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA
<i>S._gilletii</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTATTGT-AACCAA
<i>S._glabrescens</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGATGTG-G-CTTCTGTTGT-AACCAA
<i>S._harleyae</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA
<i>S._humilis</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGATGTG-G-CTTCTGTTGT-AACCAA
<i>S._ingrata</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGTTGTG-G-CTTCTGTTGT-AACCAA
<i>S._johnstonii</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA
<i>S._mattogrossensis</i>	AAACTA-AAATTGGATAGCCTG----CCTCCCCGTTTCGC-GG-----GGGGTGATGTG-G-CTTCTGTTGT-AACCAA



S.\_mexicana AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGGTGATGTG-G-CTTCTGTTGT-AACCAA  
 S.\_najatrix AACTA-AAATTGGATAGCCTG----CTCCCTCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA  
 S.\_orientalis AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGGTGATGTG-G-CTTCTGTTGT-AACCAA  
 S.\_panamensis AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGAGTGATGTG-G-CTTCTGTTGT-AACCAA  
 S.\_pyramidalis AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGATGATGTG-G-CTTCTGTTGT-AACCAA  
 S.\_rosea AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA  
 S.\_seua AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGGTGATGTG-G-CTTCTGTTGT-AACCAA  
 S.\_speciosa AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA  
 S.\_thomensis AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA  
 S.\_venezuelensis AACTA-AAATTGGATAGCCTA----CTCCCGTTTCGC-GG-----GGGGTGATGTG-G-CTTCTTTTGT-AACCAA  
 S.\_velutina AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGGTGATGTG-G-CTTCTGTTGT-AACCAA  
 S.\_venosa AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGGTGATGTG-G-CTTCTGTTGT-AACCAA  
 S.\_villosa1 AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGGTGATGTG-G-CTTCTGTTGT-AACCAA  
 S.\_villosa2 AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGGTGATGTG-G-CTTCTGTTGT-AACCAA  
 S.\_vogelii AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA  
 S.\_xanthotricha AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTATTGT-AACCAA  
 P.\_aurifodinae AACTA-AAATTGGATAGCCG----CTCCCGTTTGTG-GG-----GGGGTGATATG-G-CTTCTGTTGT-AACCAA  
 P.\_mildbraedii AACTA-AAATTGGATAGCCG----CTCCCGTTTGTG-GG-----GGGGTGCTATG-G-CTTCTATTGT-AACCAA  
 P.\_nobilis AACTA-AAATTGGATAGCCTG----CTCCCATTCGC-GG-----GGGGTACTGTG-G-CTTCTGTTGT-AACCAA  
 P.\_segregata AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA  
 P.\_medusula AACTA-AAATTGGATAGCCG----CTCCCGTTTGTG-GG-----GGGGCCTATG-G-CTTCTGTTGT-AACCAA  
 P.\_batesii AACTA-AAATTGGATAGCCG----CTCCCGTTTGTG-GG-----GGGGTGCTATG-G-CTTCTGTTGT-AACCAA  
 P.\_proselya AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA  
 P.\_arborea AACTA-AAATTGGATAGCCG----CTCCCGTTTGTG-GG-----GGGGTGCTGTG-G-CTTCTATTGT-AACCAA  
 P.\_becquetii AACTA-AAATTGGATAGCCG----CTCCCGTTTGTG-GG-----GGGGTGCTATG-G-CTTCTATTGT-AACCAA  
 E.\_hierniana AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA  
 H.\_minutiflora AACTG-AAATTGGATGGCCG----CTCCCGTTTCGC-GG-----GGGGTGCCCG-G-CGTCTGTCGT-AACCAA  
 S.\_hirsutum AACTA-AAATTGGATAGCCTG----CTCCCGTTTCGC-GG-----GGGGTGCTGTG-G-CTTCTGTTGT-AACCAA  
 S.\_elliptica AACTA-AAATTGGATAGCCG----CTCCCGTTTCGC-GG-----GAGGTACTGTG-G-CTTCTATTGT-AACCAA  
 T.\_capsulifera TAACTA-AAATTGGATTGCCG----TCTCCCGTTTCGC-GG-----GGT-TCGTGTG-G-CATCTGTCGT-AACTAA  
 V.\_multiflora AAACAA-AAATTGGATTGCCG----TTACTTCCCGTTTCGC-GG-----GGGGTATCATG-G-CATCTGTCGT-AATCTA  
 W.\_procumbens AAACAA-AAATTGGATTGCCG----CTACCTTTCGTTCGC-GT-----GGGGTGCTGTG-G-CTTCTGTTGT-AATCTA  
 C.\_coromandelicum AAATC-GAAACG-ATTGCCCGCTCCCGA--CTGCCCG-GTGCCTGCGCGC-AGGGAGGGGCTCCGCGCATCCGTCGT-AACCAA  
 H.\_zanzibarica AACTG-AAAAA--A-GGATTG-----CCC-GCCTCCCC-----GTGCGC--GGGGGTGCCGTG-G-CGTCTGTCGT-AACCAA  
 I.\_coccinea AAATTTGAAAATG-ATCGCTCGC--TCCCGC-TTTCGCCG-GTTCGCGGTGCGCAACGGGGATGTCGCA-G-CGTCTGTCGT-AACCAA  
 W.\_coccinea AAATC-AAAGTG-ACGGCCCG--TCCCGCCCGGAGCGC-GTTCGCGGAGCGC-AGGCGGGAGCCGCG-G-CGTCTGTCGTTAACCTA

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S.\_angolensis AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_amazonensis AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_aspera AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_brevipes AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_caminata AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_cana AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_capitellata AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_chocoana AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_cinerea AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_congensis AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_dewevrei AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_dinklagei AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_discolor AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_diversifolia AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_effulensensis AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_exellii AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_ferruginea AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_fulva AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_gilletii AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_glabrescens AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_harleyae AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_humilis AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_ingrata AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_johnstonii AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_mattogrossensis AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_mexicana AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_najatrix AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_orientalis AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_panamensis AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_pyramidalis AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_rosea AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_seua AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_speciosa AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_thomensis AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_venezuelensis AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_velutina AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_venosa AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_villosa1 AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_villosa2 AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_vogelii AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 S.\_xanthotricha AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA  
 P.\_aurifodinae AACGACTCTCGACAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGA



C.\_coromandelicum ACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCCGAGGGCACGTCTGCCTGGGCGTCACGCATCGCGTCGCCGCCCTC  
H.\_zanzibarica ACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCCGAGGGCACGTCTGCCTGGGCGTCACGCATCGCGTCGCCGCCCTC  
I.\_coccinea ACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCCGAGGGCACGTCTGCCTGGGCGTCACGCATCGCGTCGCCGCCCTC  
W.\_coccinea ACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATTAGGCCGAGGGCACGTCTGCCTGGGCGTCACGCATCGCGTCGCCGCCCTC

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S.\_angolensis GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_amazonensis GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_aspera GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_brevipes GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_caminata GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_cana GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_capitellata GT---TCATTTCRGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_chocoana GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_cinerea GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_congensis GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_dewevrei GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_dinklagei GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_discolor GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_diversifolia GT---TCATTTCGCGGGG---TA-CGGATAATGGCCTCCCGTACCAC--AGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_effulenensis GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_exellii GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CGGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_ferruginea GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTAGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_fulva GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_gilletii GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_glabrescens GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_harleyae GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_humilis GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_ingrata GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_johnstonii GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_mattogrossensis GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_mexicana GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_najatrix GT---TCATTTCGCGGGG---TA-CGGATAATGGCCTCCCGTACCAC--AGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_orientalis GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_panamensis GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-TAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_pyramidalis GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_rosea GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CGGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_seua GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC--AGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_speciosa GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_thomensis GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CGGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_venezuelensis GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_velutina GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_venosa GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_villosa1 GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_villosa2 GT---TCATTTCATGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGATGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_vogelii GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_xanthotricha GT---TCATTTCGAGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
P.\_aurifodinae GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
P.\_mildbraedii GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
P.\_nobilis GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
P.\_segregata GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
P.\_medusula GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
P.\_batesii GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
P.\_proselita GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
P.\_arborea GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
P.\_becquetii GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
E.\_hierniana GT---TCATTTCGAGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
H.\_minutiflora AT----C----GCGGG---CGGCGGAAATGGCCTCCCGTCCCG-GAGGCGCGGCGGCCAAACCGCAGTCTCTCGGCGAGGGACGTC  
S.\_hirsutum GT---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
S.\_elliptica GC---TCATTTCGCGGGG---TAGCGGATAATGGCCTCCCGTACCAC-CAGGCGCGGCTGGCCTAAATGCGAGTCTCTCGGCGAGTGACTTC  
T.\_capsulifera A-----ATTTCGAGGG---TGGCGGATAATGGCCTCCCGTTCGT-GAGGAGCGGCGGCCAAATGCGAGTCTCTGGTGAGGGACGTC  
V.\_multiflora AC---CTAT---GGGG---TGGCGGATAATGGCCTCCCGTACCAC-GAG-AGTGGCTGGCCTAAATGCGAGTCTCTGGTGAGGGACGTC  
V.\_procumbens AC---CT---GCGGG---CGCAGAGAATGGCCTCCCGTACCAC-CAGGAGTGGCTGGCCTAAATGCGAGTCTCTGGTGAGGGACGTC  
C.\_coromandelicum CCCCCATCTCGGGCGGGG-CGGCGGAGATTGGCCCTCCCGTCCCGTTCGGGCGGCGGCCCTAAATGCGAGTCTCTCGGCGAGGGG-CGTC  
H.\_zanzibarica CC----T---CTCGCGGGG-CGGCGGATACTGGCCTCCCGTACCACAGTTCGGCGCGGCCCTAAATGCGAGTCTCTCGGCGAGGGACGTC  
I.\_coccinea CC---ATCT---CGGGGGG---CGGCGGAGATTGGCTTCCCGTCCCG-TAGGCGCGGCGGCCCTAAATGCGAGTCTCTCGGCGAGGGACGTC  
W.\_coccinea CC---AT---CGCGGGG---CGGCGGATACTGGCCTCCCGTACCAC-GAGGCGCGGCGGCCCTAAATGCGAGTCTCTCGGCGAGGGACGTC

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S.\_angolensis ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACTCCGCCGTTA-----ACTCCCTTTACCCTACA--  
S.\_amazonensis ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAAACC-CGCCGTTA-----ACTCCCTTTACCCTACA--  
S.\_aspera ATGACAACGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACT-CGCCGTTA-----ACTCCCTTTACCCTACA--  
S.\_brevipes ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
S.\_caminata ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGTTGGCAAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
S.\_cana ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAAACC-CACCCTTA-----ACTCCCTTTACCCTACA--  
S.\_capitellata ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
S.\_chocoana ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAAACC-TGCCGTTA-----ACTCCCTTACCCTACA--  
S.\_cinerea ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAAACC-CGCCGTTA-----ACTCCCTTTACCCTACA--  
S.\_congensis ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
S.\_dewevrei ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--

S.\_dinklagei ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_discolor ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_diversifolia ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_effulenensis ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_exellii ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_ferruginea ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_fulva ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_gilletii ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_glabrescens ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_harleyae ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_humilis ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_ingrata ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_johnstonii ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_mattogrossensis ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_mexicana ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_najatrix ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_orientalis ACACAAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_panamensis ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_pyramidalis ATGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_rosea ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_seua ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_speciosa ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_thomensis ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_venezuelensis ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_velutina ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_venosa ACACAAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_villosa1 ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_villosa2 ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_vogelii ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_xanthotricha ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 P.\_aurifodinae ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 P.\_mildbraedii ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 P.\_nobilis ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 P.\_segregata ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 P.\_medusula ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 P.\_batesii ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 P.\_proseltyta ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
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 E.\_hierniana ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 H.\_minutiflora ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGCCGGCAATCC-CCCGTTGTCTCGGACTCCCACGACCCACG--  
 S.\_hirsutum ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-TGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 S.\_elliptica ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGTTGGCAAACC-CGCCGTTA-----ACTCCCTTGACCCTACA--  
 T.\_capsulifera ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGCCGATGAGTCC-CCCATATATCT-GGACTCCTATGACCCTGCA--  
 V.\_multiflora ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGTTGACGAACT--CCCGTTACTT-GGACTTAGTTGACCCTATT--  
 V.\_procumbens ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGTTGACGAACT--CCCGTTACTT-GGACTCTGTTGACCCTATA--  
 C.\_coromandelicum ACGACCCTGGTGGTTGATTTCTTCGACTCGATTCTCGT-CGTGCCGTTTCCCC-CGTGCTTCC-GGACTCGATCGACCCCGAAGA  
 H.\_zanzibarica ACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCT-GT-CGTGTTGCTGCCT-CGCAGTTTCTCGGG-CTCCCT-GACCCTTTATA  
 I.\_coccinea ACGACTAGTGGTGGTTGAATGCCTCAACTCGAGTCCTGTTGTTGCTGACGGCAGACCCCAACCGTAAATCGCG-CTCCAACGACCCTCAA--  
 W.\_coccinea ACGACAAGTGGTGGTTGAATGCCTCAACTCGATTCTCT-GT-CGTGCCCGCACCACC-CGCCGTTTCTC-GG-CTCCCC-GACCCTTCA--

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S.\_angolensis -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_amazonensis -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_aspera -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_brevipes -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_caminata -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_cana -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_capitellata -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_chocoana -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_cinerea -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_congensis -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_dewevrei -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_dinklagei -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_discolor -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_diversifolia -GCATGCACCTTGGT--CCGA-CCTCGAC-GCG-CC--A  
 S.\_effulenensis -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_exellii -GCACGACCCCTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_ferruginea -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_fulva -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_gilletii -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_glabrescens -ACATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_harleyae -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_humilis -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_ingrata -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_johnstonii -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_mattogrossensis -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_mexicana -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_najatrix -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA  
 S.\_orientalis -GCATGCACCTTGGT--GCAAGCCTCGACCGGACC-CA

S.\_panamensis -ACATGCACCTTGGT---GCAAGCCTCGACCGCGACC-CA  
 S.\_pyramidalis -GCATGCACCTTGGT---GCAAGCCTCGACCGCGACC-CA  
 S.\_rosea -GCACGCACCTTGGT---GCAAGCCTCGACCGCGACC-CA  
 S.\_seua -GCATGCACCTTGGT---GCAAGCCTCGACCGCGACC-CA  
 S.\_speciosa -GCATGCACCTTGGT---GCAAGCCTCGACCGCGACC-CA  
 S.\_thomensis -GCACGCACCTTGGT---GCAAGCCTCGACCGCGACC-CT  
 S.\_venezuelensis -ACATGCACCTTGGT---GCAAGCCTCGACCGCGACC-CA  
 S.\_velutina -GCATGCACCTTGGT---GCAAGCCTCGACCGCGACC-CA  
 S.\_venosa -GCATGCACCTTGGT---GCAAGCCTCGACCGCGACC-CA  
 S.\_villosa1 -GCATGCACCTTGGT---GCAAGCCTCGACCGCGACC-CA  
 S.\_villosa2 -GCATGCACCTTGGT---GCAAGCCTCGACCGCGACC-CA  
 S.\_vogelii -GCATGCACCTTGGT---GCAAGCCTCGACCGCGACC-CA  
 S.\_xanthotricha -GCATGCACCTCGGT---GCAAGCCTCGACCGCGACC-CA  
 P.\_aurifodinae -GCATGTACCTTGGT---ACAAGCCTCGACCGCGACC-CA  
 P.\_mildbraedii -GCATGCACCTCGGT---GCAAGCCTCGACCGCGACC-CA  
 P.\_nobilis -GCATGCACCTTGGC---GCAAGCCTCGACCGCGACC-CA  
 P.\_segregata -GCATGCACCTTGGC---GCAAGCCTCGACCGCGACC---  
 P.\_medusula -GCATGCACCTCGGT---GCAAGCCTCGACCGCGACC-CA  
 P.\_batesii -TCATGCACCTCGGT---GCAAGCCTCGACCGCGACC-CA  
 P.\_proselyta -GCATGCACCTTGGC---GCAAGCCTCGACCGCGACC-CA  
 P.\_arborea -GCATGCACCTCGGT---GCAAGCCTCGACCGCGACC-CA  
 P.\_becquetii -GCATGCACCTCGGT---GCAAGCCTCGACCGCGACC-CA  
 E.\_hierniana -GCATGCACCTTGGT---GCAAGCCTCGACCGCGACC-CA  
 H.\_minutiflora -GCGCGCTCACGGC---GCRAGCCTCGACCGCGACC-CA  
 S.\_hirsutum -GCATGCACCTTGGT---GCAAGCCTCGACCGCGACC--A  
 S.\_elliptica -GCATGCGCCTCGGT---GCAAGCCTCGACCGCGACC-CA  
 T.\_capsulifera -GCATGCGTCTTGAC---GTAAGCCTCGACTGCGACC-CA  
 V.\_multiflora -GCGCACGTCTTGAC---GTGAGCATCAATTGCGACC-CA  
 V.\_procumbens -GCGCACGTCTTGAC---GTGAGCATCAATTGCGACC-CA  
 C.\_coromandelicum GGCGCGAGCCTCGACC-----  
 H.\_zanzibarica TGCCCGCTCTCGACG--CGA-GCCTCGACCGCGACCCCA  
 I.\_coccinea -GCTCGCGTCTCGACT--CGA-GCCTCGACC-----  
 W.\_coccinea -GCTCGCGTCTTGACGGCGTAGGCTCGACCGCGACCAGT

**trnT-F Matrix (1928 bp)**  
**trnT-L spacer**

►

S.\_angolensis -----AGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_amazonensis -----TCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_aspera TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_brevipes TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_caminata TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_cana -----GTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_capitellata TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_chocoana TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_cinerea -----CTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_congensis TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_dewevrei TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_dinklagei TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_discolor GAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_diversifolia TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_effulenensis TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_exellii TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_ferruginea TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_fulva TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_gilletii TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_glabrescens TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_harleyae TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_humilis TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_ingrata TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_johnstonii TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGATAAGGAATAAAAATA  
 S.\_mattogrossensis TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_mexicana -----AGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_najatrix TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATACCATAATCGATATAAAATACAGA-AAGGAATAAAAATA  
 S.\_orientalis -----TAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_panamensis TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_pyramidalis TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_rosea TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_seua TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_speciosa TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_thomensis TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_venezuelensis TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_velutina -----TCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_venosa TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_villosa1 TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_villosa2 TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA  
 S.\_vogelii TAGTTAGTAACTAGTATTTCT-----TATCCATTCATAATCGATATAAAATA-----CAGA-AAGGAATAAAAATA

S.\_xanthotricha TAGTTAGTAAGTACTAGTATTTCT-----TATCCATTTCATAATCGATATAAATA-----CAGA-AAGGAATAAAAATA  
P.\_aurifodinae TAGTTAGTAAGTACTAGTATTTCT-----TATCCATTTCATAATCGATATAAATA-----CAGA-AAGGAATAAAAATA  
P.\_mildbraedii TAGTTAGTAAGTACTAGTATTTCT-----TATCCATTTCATAATCGATATAAATA-----CAGA-AAGGAATAAAAATA  
P.\_nobilis TAGTTAGTAAGTACTAGTATTTCT-----TATCCATTTCATAATCGATATAAATA-----CAGA-AAGGAATAAAAATA  
P.\_segregata TAGTTAGTAAGTACTAGTATTTCT-----TATCCATTTCATAATCGATATAAATA-----CAGA-AAGGAATAAAAATA  
P.\_medusula TAGTTAGTAAGTACTAGTATTTCT-----TATCCATTTCATAATCGATATAAATA-----CAGA-AAGGAATAAAAATA  
P.\_batesii TAGTTAGTAAGTACTAGTATTTCT-----TATCCATTTCATAATCGATATAAATA-----CAGA-AAGGAATAAAAATA  
P.\_proselyta TAATTAGTAAGTACTAGTATTTCT-----TATCCATTTCATAATCGATATAAATA-----CAGA-AAGGAATAAAAATA  
P.\_arborea TAGTTAGTAAGTACTAGTATTTCT-----TATCCATTTCATAATCGATATAAATA-----CAGA-AAGGAATAAAAATA  
P.\_becquetii TAGTTAGTAAGTACTAGTATTTCT-----TATCCATTTCATAATCGATATAAATA-----CAGA-AAGGAATAAAAATA  
E.\_hierniana TAGTTAGTAAGTACTAGTATTTCT-----TATCCATTTCATAATCGATATAAATA-----CAGA-AAGGAATAAAAATA  
H.\_minutiflora -----  
S.\_hirsutum TAGTTAGTAAGTACTAGTATTTCT-----TATCCATTTCATAATCGATATAAATA-----CAGA-AAGGAATAAAAATA  
S.\_elliptica TAGTTAGTAAGTACTAGTATTTCT-----TATCCATTTCATAATCGATATAAATA-----CAGA-AAGGAATAAAAATA  
T.\_capsulifera -----TCATAATCAATATAAATA-----TAGA-AAGGAATAAAAATA  
V.\_multiflora -----AACTAGTATTTCTTATCCATTTCATAATCGATATAAATA-----GAGA-AAAGAATAAAAATA  
V.\_procumbens -----TCAGAAAT-TCTATAAATA-----GAGA-AAGGAATAAAAATA  
C.\_coromandelicum TAGTTAGTAAGTACTAGTATTTCT-----TATCTATTTCATAATCGATATGGATC-----TAGA-AAAGAATAAAAATA  
H.\_zanzibarica TAGTTAGTAAGTACTAGTATTTCT-----TATCTATTTCATAATCGATATGAATA-----TAGA-ATGGAATAAAAATA  
I.\_coccinea TAGTTAGTAAGTACTAGTATTTCT-----TATCTATTTCATAATCGATATGGATC-----TAGA-AAAGAATAAAAATA  
W.\_coccinea TAGTTAGTAAGTACTAGTATTTCT-----TATCTATTTCATAATCGATATGGATA-----TAGA-AAAGAATAAAAATA

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S.\_angolensis GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGACCTAATATAGCGATATAGAATTTTCGATTTATTATCA  
S.\_amazonensis GAGTTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_aspera GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAAAGGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_brevipes GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_caminata GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_cana GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_capitellata GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_chocoana GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_cinerea GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_congensis GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_dewevrei GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_dinklagei GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_discolor GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_diversifolia GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_effulensensis GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_exellii GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATATAATTTTCGATTTATTATCA  
S.\_ferruginea GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_fulva GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_gilletii GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_glabrescens GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_harleyae GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_humilis GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_ingrata GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_johnstonii GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_mattogrossensis GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_mexicana GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_najatrix GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_orientalis GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_panamensis GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_pyramidalis GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_rosea GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_seua GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_speciosa GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_thomensis GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_venezuelensis GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_velutina GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_venosa GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_villosa1 TAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_villosa2 TAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_vogelii GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_xanthotricha GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
P.\_aurifodinae GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
P.\_mildbraedii GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
P.\_nobilis GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
P.\_segregata GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
P.\_medusula GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
P.\_batesii GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
P.\_proselyta GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
P.\_arborea GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
P.\_becquetii GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
E.\_hierniana GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
H.\_minutiflora -----  
S.\_hirsutum GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
S.\_elliptica GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
T.\_capsulifera GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
V.\_multiflora GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGAC-TAATATAGCG-ATATAGAATTTTCGATTTATTATCA  
V.\_procumbens GAATTTTAAATAAAATTTATTGAATA-----TTATAGAAGACAA-GGCC-TAAATATAGCG-ATATAGAATTTTCGATTTATTATCA

C.\_coromandelicum TAATTTCAAATAAAATTATTGAATA-----TTATAGAGCACAA-CGAT-TAATATAGCG-ATATAGAATTTTCGATTTTATATCA  
H.\_zanzibarica GAATTTCAAATAAAATTATTGAATA-----TTATAGAACACAA-CAAT-TAATATAGCG-ATATAGAATTTTCGATTTATTTATCA  
I.\_coccinea AAATTTCAAATAAAATTATTGAATAC-----TATAGAACACAA-CGAT-TAATATAGCG-ATATAGAATTTTCGATTT-TTTATCA  
W.\_coccinea GAATTTTAAATAAAATTATTGAATA-----TTATAGAATACAA-CGAT-TAATATAACG-ATATAGAATTTTCGATTTATTTATCA

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S.\_angolensis CTAATA-----GAATTTAGAATTCAAATATTTATTAATTCG-AATTATCATTTAATATT-----  
S.\_amazonensis CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_aspera TTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_brevipes CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_caminata CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_cana CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_capitellata CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_chocoana CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_cinerea CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_congensis CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_dewevrei CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCGAAATATATCATTTAATATT-----  
S.\_dinklagei CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_discolor CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_diversifolia CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_effulnensis CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_exellii CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_ferruginea CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_fulva CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_gilletii CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_glabrescens CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_harleyae CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_humilis CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_ingrata CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_johnstonii CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_mattogrossensis CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_mexicana CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_najatrix CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_orientalis CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_panamensis CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_pyramidalis CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_rosea CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_seua CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_speciosa CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_thomensis CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_venezuelensis CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_velutina CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_venosa CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_villosa1 CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_villosa2 CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_vogelii CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
S.\_xanthotricha CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
P.\_aurifodinae CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
P.\_mildbraedii CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
P.\_nobilis CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
P.\_segregata CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
P.\_medusula CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
P.\_batesii CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
P.\_proseltya CCAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
P.\_arborea CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
P.\_becquetii CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
E.\_hierniana CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
H.\_minutiflora -----  
S.\_hirsutum CTAATA-----GAATTTAGAATTCAAATATTTATTAATTCG-AATTATCATTTAATATT-----  
S.\_elliptica CTAATA-----GAATTTAGAATTCAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
T.\_capsulifera CTAATC---TATTTATCACTAATAAGAAATTCGAATTCGAAATATT-ATTAATTCG-AATTATCATTTAATATT-----  
V.\_multiflora CTAATAATTTATTTATCACTAATAAAATTTAGAATTCGAAATATT-AGTAACTTCG-AATTATCATTTACTAGT-----  
V.\_procumbens CTAATAATTTATTTATCACTAATAAGAAATTTAGAATTCGAAATATT-ATTAATTCG-AATTATCATTTACTAGT-----  
C.\_coromandelicum CT-----CGAATAGT-ATTAATTCG-AATTATCATCTAGTATT-----  
H.\_zanzibarica CTAATAG-----AATTCGAATATT-ATAATATTCG-AATTCTAATTTAGTATTAGATTAGATTAGTATT-----  
I.\_coccinea CT-----CGAATAGT-ATTAATTCG-AATTATCATCTACTATT-----  
W.\_coccinea CTAATA-----TAATTCGAATATT-ATTAATTCG-AATTATCATTTAGTATT-----

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S.\_angolensis -----CGAATTAGATAGTAAATAGTTTTAGATAGTTAAATAGTTAAATTTTTTCATTTTGAATTC-AAA-TG  
S.\_amazonensis -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATAGTTAAATTTTT-CATTTTGAATTC-AAA-TG  
S.\_aspera -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATAGTTAAATTTTT-CATTTTGAATTC-AAA-TG  
S.\_brevipes -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATAGTTAAATTTTT-CATTTTGAATTC-AAA-TG  
S.\_caminata -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATAGTTAAATTTTT-CATTTTGAATTC-AAA-TG  
S.\_cana -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATAGTTAAATTTTT-CATTTTGAATTC-AAA-TG  
S.\_capitellata -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATAGTTAAATTTTT-CATTTTGAATTC-AAA-TG  
S.\_chocoana -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATAGTTAAATTTTT-CATTTTGAATTC-AAA-TG  
S.\_cinerea -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATAGTTAAATTTTT-CATTTTGAATTC-AAA-TG  
S.\_congensis -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATAGTTAAATTTTT-CATTTTGAATTC-AAA-TG  
S.\_dewevrei -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATAGTTAAATTTTT-CATTTTGAATTC-AAA-TG

S.\_dinklagei -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_discolor -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_diversifolia -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_effulenensis -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_exellii -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_ferruginea -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_fulva -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_gilletii -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_glabrescens -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_harleyae -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_humilis -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_ingrata -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_johnstonii -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_mattogrossensis -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_mexicana -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_najatrix -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_orientalis -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_panamensis -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_pyramidalis -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_rosea -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_seua -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_speciosa -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_thomensis -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_venezuelensis -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_velutina -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_venosa -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_villosa1 -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_villosa2 -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_vogelii -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_xanthotricha -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 P.\_aurifodinae -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 P.\_mildbraedii -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 P.\_nobilis -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 P.\_segregata -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 P.\_medusula -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 P.\_batesii -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 P.\_proseltyta -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 P.\_arborea -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 P.\_becquetii -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 E.\_hierniana -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 H.\_minutiflora -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_hirsutum -----TCGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 S.\_elliptica -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 T.\_capsulifera -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 V.\_multiflora -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 V.\_procumbens -----CGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 C.\_coromandelicum -----AGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-AATTTTTGAATTC-AAA-TG  
 H.\_zanzibarica -----AGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG  
 I.\_coccinea -----AGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-AATTTTTGAATTC-AAA-TG  
 W.\_coccinea -----AGA-TTAGATAGTAAATAGTTTTAGATAGTTAAATTAGTTAAATTTTT-CATTTTTGAATTC-AAA-TG

S.\_angolensis ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_amazonensis ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_aspera ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_brevipes ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_caminata ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_cana ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_capitellata ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_chocoana ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_cinerea ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_congensis ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_dewevrei ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_dinklagei ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_discolor ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_diversifolia ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_effulenensis ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_exellii ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_ferruginea ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_fulva ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_gilletii ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_glabrescens ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_harleyae ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_humilis ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_ingrata ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_johnstonii ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_mattogrossensis ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_mexicana ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_najatrix ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA  
 S.\_orientalis ACATTTGAAATTTTTTTT-----ACACTT-----ATA-----GTATATATATTTTTATACTATTTGATTCATATCATAATCA



S.\_panamensis ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 S.\_pyramidalis ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 S.\_rosea ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 S.\_seua ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 S.\_speciosa ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 S.\_thomensis ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 S.\_venezuelensis ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 S.\_velutina ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 S.\_venosa ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 S.\_villosa1 ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 S.\_villosa2 ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 S.\_vogelii ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 S.\_xanthotricha ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 P.\_aurifodinae ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 P.\_mildbraedii ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 P.\_nobilis ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 P.\_segregata ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 P.\_medusula ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 P.\_batesii ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 P.\_proselyla ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 P.\_arborea ACATTTGAAATTTTTTACT-----TTTACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 P.\_becquetii ACATTTGAAATTTTTTACT-----TTTACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 E.\_hierniana ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 H.\_minutiflora -----  
 S.\_hirsutum ACATTTGAAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 S.\_elliptica ACATTTGAAATTTTTTACTTTT-----TTTACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 T.\_capsulifera ACATTTGAAATTTTTTCCACTTTCTTACTA-----AT-CTTATAG--TATATATTTTTTATACTATTGGATTCATATCATAATCA  
 V.\_multiflora ATATTTGAAATTTTTT-----ACACTT-----ATACTTATAGTATATATTTTTTATACTATTGGATTCATATCATAATCA  
 V.\_procumbens ACATTTGCAATTTTTT-----ACACTT-----ATAGTATATATATTTTTTATACTATTGGATTCATATCATAATCA  
 C.\_coromandelicum ACATTTGAAATTTTTT-----TTTACTTCTATATTTTACTTATGTATATATTTTTTACTATTGGATTCATATCATAATCA  
 H.\_zanzibarica ACATTTGAAATTTTTT-----TTTACTTCTAT-----TATATATATTTTTTACTATTGGATTCATATCATAATCA  
 I.\_coccinea ACATTTGAAATTTTTTACTT-----TATATTT--ATA--CTA--TGTATATAT--TTTACTATATTTGGATTCATATCATAATCA  
 W.\_coccinea ACATTTGAAATTTTTT-----TTTACTTCTAT-----TATATATA--TTTATATTTACTTGGATTCATATCATAATCA

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S.\_angolensis TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_amazonensis TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_aspera TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_brevipes TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_caminata TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_cana TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_capitellata TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_chocoana TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_cinerea TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_congensis TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_dewevrei TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_dinklagei TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_discolor TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_diversifolia TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_effulensensis TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_exellii TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_feruginea TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_fulva TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_gilletii TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_glabrescens TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_haleyae TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_humilis TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_ingrata TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_johnstonii TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_mattogrossensis TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_mexicana TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_najatrix TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATT-----CATTTCATAAAG-----  
 S.\_orientalis TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_panamensis TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_pyramidalis TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_rosea TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_seua TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_speciosa TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_thomensis TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_venezuelensis TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_velutina TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_venosa TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_villosa1 TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_villosa2 TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_vogelii TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 S.\_xanthotricha TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 P.\_aurifodinae TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 P.\_mildbraedii TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 P.\_nobilis TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----  
 P.\_segregata TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCCTCCGCTTTCATTCATAAAG-----

P.\_medusula TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCTCCGTTTCATTATAAAG-----  
P.\_batesii TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCTCCGTTTCATTATAAAG-----  
P.\_prosellyta TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCTCCGTTTCATTATAAAG-----  
P.\_arborea TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCTCCGTTTCATTATAAAG-----  
P.\_becquetii TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCTCCGTTTCATTATAAAG-----  
E.\_hierniana TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCTCCGTTTCATTATAAAG-----  
H.\_minutiflora -----  
S.\_hirsutum TATA-TTTCTAATTTAAATTAGGATTAATTAGGAATGATTAGTTCTAACTAATGAGACATTCTCCGTTTCATTATAAAG-----  
S.\_elliptica TATA-TTTCTAAT-----TAAATTAGGAATGATTAGTTCTAACTAATGAGACATTCTCCGTTTCATTATAAAG-----  
T.\_capsulifera TATA-TATCTAAT-----TAGGAATGATTAGTTCTAACTAATGAGACATTCTCCGTTTCATTATAAAGCATAAAT--  
V.\_multiflora TATA-TTTTGAAT-----TAGGAATGATTAGTTCTAACTAATGAGACATTCTCCGTTTCATTATAAAGCATAAAG--  
V.\_procumbens TATA-TTTTGAAT-----TAGGACTGATTAGTTCTAACTAATGAGACATTCTCCGTTTCAGTCATAAAGCATAAAG--  
C.\_coromandelicum TATAATTTATAAT-----TAGGAATATTAGTTCTAACTAATGAGACATTCTCCGTTTCATTATAA--GATGGAATGT  
H.\_zanzibarica TATA-TTTCTAAT-----TAGGAATAATTAGTTCTAACTAATGAGACATTCTCCGTTTCATTATAAAG-----  
I.\_coccinea TATA-TTTCTAAT-----TAGAAATGATTAGTTCTAACTAATGAGACATTCTCCGTTTCATTATAA--GATGTA-----  
W.\_coccinea TATA-TTTCTAAT-----TAGGAATGATTAGTTCTAACTAATGAGACATTCTCCGTTTCATTATAAAG-----

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S.\_angolensis ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_amazonensis ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_aspera ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_brevipes ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_caninata ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_cana ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_capitellata ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_chocoana ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_cinerea ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_congensis ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_dewevrei ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_dinklagei ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_discolor ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_diversifolia ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_effulensensis ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_exellii ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_ferruginea ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_fulva ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_gilletii ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_glabrescens ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_harleyae ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_humilis ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_ingrata ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_johnstonii ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_mattogrossensis ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_mexicana ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_najatrix ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_orientalis ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_panamensis ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_pyramidalis ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_rosea ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_seua ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_speciosa ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_thomensis ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_venezuelensis ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_velutina ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_venosa ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_villosa1 ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_villosa2 ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_vogelii ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_xanthotricha ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
P.\_aurifodinae ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
P.\_mildbraedii ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
P.\_nobilis ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
P.\_segregata ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
P.\_medusula ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
P.\_batesii ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
P.\_prosellyta ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
P.\_arborea ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
P.\_becquetii ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
E.\_hierniana ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
H.\_minutiflora -----  
S.\_hirsutum ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
S.\_elliptica ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
T.\_capsulifera ----ATGTAATGTAATA---ATGAAGGCC-----GAAATTAAGACGACAAAAAAA--GAATCGTCCGTTCAAGTATT-CAAAATTG  
V.\_multiflora ----GTGTAATGTAATA---GTAAGGCC-----GAAATTAAGACGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG  
V.\_procumbens ----ATGTAATGTAATA---GTAAGGCC-----GAAATTTAAGACGACAAAAAAA--GAATCGACCGTTCAAGTATTCAAAATTG  
C.\_coromandelicum TGTAAATGTAAGTAAATAAAAAATAAAGGCTAAATTAAGAAATTAAGACGACAAAAAAA--GAATCGACCGTTCAACCTTTCAAAATTG  
H.\_zanzibarica ----ATATGATGTAATA---GTAAGGCC-----GAAATTAAGACGACAAAAAGA--GAATCGACCGTTCAAGTATT-CAAAATTG  
I.\_coccinea ----ATGTAAGTAAATAAATAAATAAAGGCC-----AAAATTAAGACGACAAAAAAA--GAATCGACCGTTCAACTATT-CAAAATTG  
W.\_coccinea ----ATGTAATATAAATA---GTAAGGCC-----GAAATTAAGATGACAAAAAAA--GAATCGACCGTTCAAGTATT-CAAAATTG

<i>S._angolensis</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._amazonensis</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._aspera</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._brevipes</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._caminata</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._cana</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._capitellata</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._chocoana</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._cinerea</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._congensis</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._dewevrei</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._dinklagei</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._discolor</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._diversifolia</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._effulenensis</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._exellii</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._ferruginea</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._fulva</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._gilletii</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._glabrescens</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._harleyae</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._humilis</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TGT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._ingrata</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._johnstonii</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._mattogrossensis</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._mexicana</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._najatrix</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._orientalis</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._panamensis</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._pyramidalis</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._rosea</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._seua</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._speciosa</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._thomensis</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._venezuelensis</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._velutina</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._venosa</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._villosa1</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._villosa2</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._vogelii</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._xanthotricha</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>P._aurifodinae</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>P._mildbraedii</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>P._nobilis</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>P._segregata</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>P._medusula</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>P._batesii</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>P._proseltyta</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>P._arborea</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>P._becquetii</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>E._hierniana</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>H._minutiflora</i>	-----
<i>S._hirsutum</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>S._elliptica</i>	TATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>T._capsulifera</i>	CATCGGAAAGCTAACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>V._multiflora</i>	CATCGGAAAGCTAACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>V._procumbens</i>	CATCGGAAAGCTAACAGGGAGATATATATATTCTTAAGATATATATCCATCTATATTGAATTGCGGATACGGAAAATGATAAAAATTCATA
<i>C._coromandelicum</i>	CATTTGAAAGCTGACAGGGAGATATATATA-TCT-AAAATATATATTCATCTATATTGAATTGGGGATACAGAAA-TGATAAAAAT-CATA
<i>H._zanzibarica</i>	CATCGGAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATCCCTCTATATTGAATTGCGGATACGGAAA-TGATAAAAAT-CATA
<i>I._coccinea</i>	CATTTGAAAAGCTGACAGGGAGATATATATA-TCT-AAGATATATATTCATCTATATTGAATTGGGGATACAGAAAG-TGATAAAAAT-CATA
<i>W._coccinea</i>	CATCGGAAAGCTGACAGGGAGATATATATC-T-T--AGATATATATTCATCTATATTGAATTGCGGATACAGAAA-TGATAAAAAT-CATA

<i>S._angolensis</i>	TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAA-
<i>S._amazonensis</i>	TTGGATTGG-ACCAATAGAAAATTGTTGGTCTCCTCTATAGAA-----GTTAA-GTATGAAAG-CAAAGAAAA-
<i>S._aspera</i>	TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAG-CAAAGAAAA-
<i>S._brevipes</i>	TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAA-
<i>S._caminata</i>	TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAA-
<i>S._cana</i>	TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAG-CAAAGAAAA-
<i>S._capitellata</i>	TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAA-
<i>S._chocoana</i>	TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAG-CAAAGAAAA-
<i>S._cinerea</i>	TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAG-CAAAGAAAA-
<i>S._congensis</i>	TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAA-
<i>S._dewevrei</i>	TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAA-
<i>S._dinklagei</i>	TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAA-
<i>S._discolor</i>	TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAA-
<i>S._diversifolia</i>	TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAA-
<i>S._effulenensis</i>	TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAA-
<i>S._exellii</i>	TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAA-

S.\_ferruginea TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAATCTATTATAGAATCTATAGAAGATAA-GTAAGAAAT-CAAAGAAAAG  
S.\_fulva TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
S.\_gillettii TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
S.\_glabrescens TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAG-CAAAGAAAAG  
S.\_harleyae TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----TCTATAGAAGATAA-GTAAGAAAT-CAAAGAAAAG  
S.\_humilis TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GTTAA-GTATGAAAG-CAAAGAAAAG  
S.\_ingrata TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
S.\_johnstonii TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
S.\_mattogrossensis TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAG-CAAAGAAAAG  
S.\_mexicana TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAAAGTAAGAAAT-CAAAGAAAAG  
S.\_najatrix TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
S.\_orientalis TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
S.\_panamensis TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAG-CAAAGAAAAG  
S.\_pyramidalis TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAG-CAAAGAAAAG  
S.\_rosea TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
S.\_seua TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
S.\_speciosa TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----TCTATAGAAGATAA-GTAAG-AT-CAAAGAAAAG  
S.\_thomensis TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
S.\_venezuelensis TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAG-CAAAGAAAAG  
S.\_velutina TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
S.\_venosa TTGGATTGG-ACCAATAGAAAT-AGGGGTCTCCTCTATAGAA-----GTTAA-GTAGGAAAT-CAAAGAAAAG  
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S.\_villosa2 TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAG-CAAAGAAAAG  
S.\_vogelii TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----TCTATAGAAGATAA-GTAAGAAAT-CAAAGAAAAG  
S.\_xanthotricha TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
P.\_aurifodinae TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
P.\_mildbraedii TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
P.\_nobilis TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
P.\_segregata TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
P.\_medusula TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
P.\_batesii TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----TCTATAGAAGATAA-GTAAGAAAT-CAAAGAAAAG  
P.\_proselyla TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
P.\_arborea TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
P.\_becquetii TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
E.\_hierniana TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
H.\_minutiflora -----  
S.\_hirsutum TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
S.\_elliptica TTGGATTGG-ACCAATAGAAAATTAGGGGTCTCCTCTATAGAA-----GATAA-GTAAGAAAT-CAAAGAAAAG  
T.\_capsulifera TTGGATTGG-ACCAAT-----AGGGGTCTCCTCTA--GAA-----GATAA-GTAAGAAAT-GAAAGAAAAG  
V.\_multiflora TTGGATTGG-ACCAGAT-----AGGGGTCTCCTCTATAGAG-----GATAA-GTAAGAAAG-CAAAGAAAAG  
V.\_procumbens TTGGATTGG-ACCAGAT-----AGGGGTCTCCTCTATAGAG-----GATAA-GTAAGAAAGGCAAAGAAAAG  
C.\_coromandelicum TTGGATTGG-ACCAATG-----GGGGTCTCCT--ATAGAA-----GATAG-ATAAGAACT-CAAAAACAAG  
H.\_zanzibarica TTGGATTGG-ACAAAAT-----AGGGGTCTCCT--ATAGAA-----GATAG-GTAAGAAAT-CAAAGAAAAG  
I.\_coccinea TTGGATTGG-ACCAACG-----GGGGTCTCCT--ATAGAA-----GATAG-ATAAGAACT-CAAAAACAAG  
W.\_coccinea TTGGATTGG-ACCAAT-----AGAGGTCTCCT--ATAGTA-----GATAG-GTAAGAAAT-CAAAAAGAA-

900

S.\_angolensis ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_amazonensis ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_aspera ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_brevipes ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_caminata ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_cana ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_capitellata ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_chocoana ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_cinerea ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_congensis ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_dewevrei AAAACCGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_dinklagei ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_discolor ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
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S.\_gillettii ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_glabrescens ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
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S.\_humilis ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_ingrata ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_johnstonii ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_mattogrossensis ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
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S.\_najatrix ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
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S.\_panamensis ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_pyramidalis ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_rosea ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_seua AAAACCGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACAAATTT-CAGTATAAAT-----GAAAGA-AAAAAAGA  
S.\_speciosa AAAACAGTTTTTCGAGATAGGAATCGGTATATAATGAATTCACAAATTT-CAGTATAAAT-----AAAAGA-AAAAAAG-

S.\_thomensis ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACCAATTTTCAGTATAAAT-----GAAAGA-AAAAAAGA  
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 S.\_velutina ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACCAATTTTCAGTATAAAT-----GAAAGA-AAAAAAGA  
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 S.\_villosa1 ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACCAATTTTCAGTATAAAT-----GAAAGA-AAAAAAGA  
 S.\_villosa2 ----CAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACCAATTTTCAGTATAAAT-----GAAAGA-AAAAAAGA  
 S.\_vogelii AAAACAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACCAATTTTCAGTATAAAT-----GAAAGA-AAAAAAGA  
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 P.\_segregata AAAACAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACCAATTTTCAGTATAAAT-----GAAAGA-AAAAAAGA  
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 P.\_batesii AAAACAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACCAATTTTCAGTATAAAT-----GAAAGA-AAAAAAGA  
 P.\_proseliya AAAACAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACCAATTTTCAGTATAAAT-----GAAAGA-AAAAAAGA  
 P.\_arborea AAAACCGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACCAATTTTCAGTATAAAT-----GAAAGA-AAAAAAGA  
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 E.\_hierniana AAAACAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACCAATTTTCAGTATAAAT-----GAAAGA-AAAAAAGA  
 H.\_minutiflora -----  
 S.\_hirsutum AAAACAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACCAATTTTCAGTATAAAT-----GAAAGA-AAAAAAGA  
 S.\_elliptica AAAACAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACCAATTTTCAGTATAAAT-----GAAAGA-AAAAAAGA  
 T.\_capsulifera AAAACAGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACCAATTTTCAGTATAAAT-----GAAAGA-AAAAAAGA  
 V.\_multiflora AAAACCGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACCAATTTTCAGTATAAAT-----CAAAGA-AAAAAAGC  
 V.\_procumbens AAAACCGTTTTTCGAGATAGGAATCGGTATCTAATGAATTCACCAATTTTCAGTATAAAT-----GAAAGA-AAAAAAGC  
 C.\_coromandelicum AAAACACTTTTTCAAGATAGGAATCGGTATCTAATGCATTCACGATTTTCAGTATAAATATAAAATAAAATAAAGGAGAGAAAGAAAAGC  
 H.\_zanzibarica AAAAGACTTTTTTCGAG-----CGGTATCTAATGAATTCACCAATTTTCAGTAGAAGT-----GAAAGG--AAAAAGC  
 I.\_coccinea AAAGCACTTTTTCAAGATAGGAATCGGTATCTAATGCATTCACGATTTTCAGTATAAAA-----AAAGGAAAGA-AAAAAAGC  
 W.\_coccinea ----CAGTTTTTCGAGATAGGAATCAAATATCTAATGAATTCACCAATTTTCAGTATAAAT-----GAAAGA-AAAAAAGC

**trnL spacer**



990

S.\_angolensis -CCGACATCACA-ATGAAATCCTAATCT-AAAAAAGAAAAA-G-AAGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTG  
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 S.\_aspera ACCGACATCACA-ATGAAATCCTAATCTCAAAAAGAAAAA-GGAAGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTG  
 S.\_brevipes ACCGACATCACA-ATGAAATCCTAATCTCAAAAAGAAAAA-GGAAGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTG  
 S.\_caminata ACCGACATCACA-ATGAAATCCTAATCTCAAAAAGAAAAA-GGAAGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTG  
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 S.\_congensis ACCGACATCACA-ATGAAATCCTAATCTCAAAAAGAAAAA-GGAAGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTG  
 S.\_dewevrei ACCGACATCACA-ATGAAATCCTAATCTCAAAAAGAAAAA-GGAAGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTG  
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 S.\_seua ACCGACATCACA-ATGAAATCCTAATCTCAAAAAGAAAAA-GGAAGGGG-----  
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 S.\_xanthotricha ACCGACATCACA-ATGAAATCCTAATCTCAAAAAGAAAAA-GGAAGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTG  
 P.\_aurifodinae ACCGACATCACA-ATGAAATCCTAATCTCAAAAAGAAAAA-GGAAGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTG  
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 P.\_nobilis ACCGACATCACA-ATGAAATCCTAATCTCAAAAAGAAAAA-GGAAGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTG  
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P.\_becquetii ACCGACATCACA-ATGAAATCCTAATCTCAAAAACAAAAGAAAA-GGAAGGGGG-ATATGGCGAAATTGGTAGACGCTACGGACTTAATTG  
E.\_hierniana ACCGACATCACA-ATGAAATCCTAATCTCAAAAACAAAAGAAAA-GGAAGGGGG-ATATGGCGAAATTGGTAGACGCTACGGACTTAATTG  
H.\_minutiflora -----  
S.\_hirsutum ACCGACATCACA-ATGAAATCCTAATCTCAAAAACAAAAGAAAA-GGAAGGGGG-ATATGGCGAAATTGGTAGACGCTACGGACTTAATTG  
S.\_elliptica ACCGACATCACA-ATGAAATCCTAATCTCAAAAACAAAAGAAAA-GGAAGGGGG-ATATGGCGAAATTGGTAGACGCTACGGACTTAATTG  
T.\_capsulifera ACCGACATCACA-ATGAAATCCTAATCTCAAAAACAAAAGAAAA-GGAAGGGGG-ATATGGCGAAATTGGTAGACGCTACGGACTTAATTG  
V.\_multiflora ACCGACATCACA-ATGAAATCCTAATCTCAAAAACAAAAGAAAA-GGAAGGGGG-ATATGGCGAAATTGGTAGACGCTACGGACTTAATTG  
V.\_procumbens ACCGACATCACA-ATGAAATCCTAATCTCAAAAACAAAAGAAAA-GGAAGGGGGGATATGGCGAAATTGGTAGACGCTACGGACTTAATTG  
C.\_coromandelicum AACGACATCACA-ATGAAATCCTAATCTCAAAAACAAAAGAAAA-GGAAGGGGG-GTATGGCGAAATCGGTAGACGCTACGGACTTAATTG  
H.\_zanzibarica AACGACATCACA-ATGAAATCCTAATCTCAAAAACAAAAGAAAA-GGAAGGGGG-ATATGGCGAAATCGGTAGACGCTACGGACTTAATTG  
I.\_coccinea AACGACATCACA-ATGAAATCCTAATCTCAAAAACAAAAGAAAA-GGAAGGGGG-ATATGGCGAAATCGGTAGACGCTACGGACTTAATTG  
W.\_coccinea AACGACATCACA-ATGAAATCCTAATCTCAAAAACAAAAGAAAA-GGAAGGGGG-ATATGGCGAAATCGGTAGACGCTACGGACTTAATTG

1080

S.\_angolensis GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_amazonensis GATCGGGCCCTGGTATGAAAACCCGCTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_aspera GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_brevipes GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_caminata GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
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S.\_discolor GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_diversifolia GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
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S.\_ferruginea GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
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S.\_harleyae GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_humilis GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_ingrata GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_johnstonii GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_mattogrossensis GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_mexicana GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_najatrix GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_orientalis GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_panamensis GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_pyramidalis GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_rosea GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_seua GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_speciosa -----ATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_thomensis GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_venezuelensis GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
S.\_velutina GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAA-----  
S.\_venosa GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
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S.\_villosa2 GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
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T.\_capsulifera GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
V.\_multiflora GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
V.\_procumbens GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
C.\_coromandelicum AATTGAGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
H.\_zanzibarica GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
I.\_coccinea AATTGAGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CCC-TGGAATTAATAAAAAGGGGCAATCCTGAGCC  
W.\_coccinea GATTGGGCCCTTGGTATGAAAACCCACTAAGTGATAACTTTCAAATTCAGAGAAA-CTC-CGGAATTAATAAAAAGGGGCAATCCTGAGCC

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S.\_amazonensis AAATCC-TGTTTTCCGAAA-C-CAAAGGTTCA-GAAAGTGAAGAAA---GGGATAGG-TGCAGAAGACTCAAC-GGGACTGTTCTAAC-AA

S.\_aspera AAATCC-TGTTTTCCGAAA-C-CAAAGGTTCA-GAAAGTGAATAA---GGGATAGG-TGCAG-AGACTCAAC-GGAAGCTGTTCTAAC-A  
 S.\_brevipes AAATCC-TGTTTTCCGAAA-C-CAAAGGTTCA-GAAAGTGAATAA---GGGATAGG-TGCAG-AGACTCAAC-GGAAGCTGTTCTAAC-A  
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 S.\_venosa AAATCC-TGTTTTCCGAAA-C-CAAAGGTTCA-GAAAGTGAATAA-----  
 S.\_villosa1 AAATCC-TGTTTTCCGAAAAC-CAAAGGTTCA-GAAAGTGAATAA---GGGATAGG-TGCAG-AGACTCAACCGAAGCTGTTCTAAC-A  
 S.\_villosa2 AAATCC-TGTTTTCCGAAA-C-CAAAGGTTCA-GAAAGTGAATAA---GGGATAGG-TGCAG-AGACTCAAC-GGAAGCTGTTCTAAC-A  
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 P.\_aurifodinae AAATCC-TGTTTTCCGAAA-C-CAAAGGTTCA-GAAAGTGAATAA---GGGATAGG-TGCAG-AGACTCAACCGAAGCTGTTCTAAC-A  
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 T.\_capsulifera AAATCC-TGTTTTCCGAAA-C-CAAAGGTTCA-GAAAGTGAATAA---GGGATAGG-TGCAG-AGACTCAAC-GGAAGCTGTTCTAAC-A  
 V.\_multiflora AAATCC-TGTTTTCCGAAA-C-CAAAGGTTCA-GAAAGTGAATAA---GGGATAGG-TGCAG-AGACTCAAC-GGAAGCTGTTCTAAC-A  
 V.\_procumbens AAATCC-TGTTTTCCGAAA-CCCAACGGTTCA-GAAAGTGAATAA---GGGATAGG-TGCAG-AGACTCAAC-GGAAGCTGTTCTAAC-A  
 C.\_coromandelicum AAATCC-TGTTTTCCGAAA-C-CAAAGGTTCA-GAAAGTGAATAA---GGGATAGG-TGCAG-AGACTCAAC-GGAAGCTGTTCTAAC-A  
 H.\_zanzibarica AAATCC-TTTTTCCGAAA-C-CAAAGGTTCA-GAAAGTGAATAA---GGATAGG-TGCAG-AGACTCAAC-GGAAGCTGTTCTAAC-A  
 I.\_coccinea AAATCC-TGTTTTCCGAAA-C-CAAAGGTACA-GAAAGTGAATAA---GGGATAGG-TGCAG-AGACTCAAC-GGAAGTGTCTAAC-A  
 W.\_coccinea AAATCC-TGTTTTCCGAAA-C-CAAAGGTTCA-GAAAGTGAATAA---GGATAGG-TGCAG-AGACTCAAC-GGAAGCTGTTCTAAC-A

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 S.\_amazonensis AA-----TGGA-GTTGACTGAGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_aspera AA-----TGGA-GTTGACTGAGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_brevipes AA-----TGGA-GTTGACTGAGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_caminata AA-----TGGA-GTTGACTGAGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_cana AA-----TGGA-GTTGACTGAGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_capitellata AA-----TGGA-GTTGACTGAGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_chocoana AA-----TGGA-GTTGACTGAGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_cinerea AA-----TGGA-GTTGACTGAGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_congensis AA-----TGGA-GTTGACTGAGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_dewevrei AA-----TGGA-GTTGACTGCGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_dinklagei AA-----TGGA-GTTGACTGAGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_discolor AA-----TGGA-GTTGACTGAGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_diversifolia AA-----TGGA-GTTGACTGCGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_effulenensis AA-----TGGA-GTTGAGGAGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_exellii AA-----TGGA-GTTGACTGAGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_ferruginea AA-----TGGA-GTTGACTGCGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_fulva AA-----TGGA-GTTGACTGAGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT  
 S.\_gilletii AA-----TGGA-GTTGACTGAGTTAGTAGAGAAATC-TTTCCATCGAAAATTCAGA-AAGGATAAAGTGAAGGATAAAC----GTATGT





S.\_venosa -----  
S.\_villosa1 ACATACGTATTGAATACTATATCAAATGATTAATGACGACTCGACTGAACTCTGTATTTTTTTTTT-ATATGAAAAACGGGAAGAATTGGTG  
S.\_villosa2 ACATACGTATTGAATACTATATCAAATGATTAATGACGACTCGACTGAACTCTGTATTTTTTTTTT-ATATGAAAAACGGGAAGAATTGGTG  
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P.\_aurifodinae ACATACGTATTGAATACTATATCAAATGATTAATGACGACTCGACTGAACTCTGTATTTTTTT-----ATATGAAAAACGGGAAGAATTGGTG  
P.\_mildbraedii ACATACGTATTGAATACTATATCAAATGATTAATGACGACTCGACTGAACTCTGTATTTTTTT-----ATATGAAAAACGGGAAGAATTGGTG  
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E.\_hierniana -----  
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S.\_elliptica ACATACGTATTGAATACTATATCAAATGATTAATGACGACTCGACTGAACTCTGTATTTTTTT-----ATATGAAAAACGGGAAGAATTGGTG  
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V.\_multiflora ACATACGTATTGAATACTATATCAAATGATTAATGACGACTCGACTGAACTCTGTATTTTTTT-----ATATGAAAAACGGGAAGAATTGGTG  
V.\_procumbens ACATACGTATTGAATACTATATCAAATGATTAATGACGACTCGACTGAACTCTGTATTTTTTT-----ATATGAAAAACGGGAAGAATTGGTG  
C.\_coromandelicum A----CGTATTGAATACTATATCAAATGATTAATGACGACTCGACTGAACTCTGTATTTTTTT-----ATATGAAAA--CGGAAGAATTGGTG  
H.\_zanzibarica ACATACGTATTGAATACTATATCAAATGATTAATGACGACTCGACTGAACTCTGTATTTTTTTAT---ATGAAAAACGGGAAGAATTGGTG  
I.\_coccinea A----CGTATTGAATACTATATCAAATGATTAATGACGACTCGACTGAACTCTGTATTTTTTT-----ATATGAAAA--CGGAAGAATTGGTG  
W.\_coccinea ACATACGTATTGAATACTATATCAAATGATTAATGACGACTCGACTGAACTCTGTATTTTTTTTTT-ATATGAAAAACGGGAAGAATTGGTG

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S.\_aspera TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
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S.\_chinerea TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_congensis TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_dewevrei TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_dinklagei TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_discolor TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_diversifolia TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_effulensensis TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_exellii TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_ferruginea TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_fulva TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_gillettii TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_glabrescens TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_harleyae TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_humilis TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_ingrata TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_johnstonii TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_mattogrossensis TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_mexicana TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCCATAGTCTGATAGATCTTTTCACGAACGGATTA  
S.\_najatrix TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_orientalis TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_panamensis TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_pyramidalis TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_rosea TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_seua -----  
S.\_speciosa TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_thomensis TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_venezuelensis TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_velutina TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_venosa -----  
S.\_villosa1 TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_villosa2 TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_vogelii TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_xanthotricha TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
P.\_aurifodinae TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
P.\_mildbraedii TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
P.\_nobilis TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
P.\_segregata TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
P.\_medusula TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
P.\_batesii TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
P.\_proseliya TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
P.\_arborea TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
P.\_becquetii TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
E.\_hierniana -----  
H.\_minutiflora TGCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA  
S.\_hirsutum TCCTAGATTCCACATTGAAGAAAAGAAATCGAATATTTATTGATCAAATGATTCACTCC-----ATA

S\_elliptica TCACTAGATTCCACATTGAAGAAAGAATCGAATATTTATTGATCAAATGATTCCTCC-----ATA  
T\_capsulifera TCCTAGATTCCACATTGAAGAAAGAATCGAATATTTATTGATCAAATGATTCCTCC-----ATA  
V\_multiflora TGACTAGATTCCACATTGAAGAA- GAATCGAATATTTATTGATCAAATGATTCCTCC-----ATA  
V\_procumbens TGACTAGATTCCACATTGAAGAA- GAATCGAATATTTATTGATCAAATGATTCCTCC-----ATA  
C\_coromandelicum TGAAATAGATTCCACATTGAAGAAAGAATCGAATATTTATTGATCAAATGATTCCTCC-----ATA  
H\_zanzibarica TGAAATAGATTCCACATTGAAGAAAGAATCGAATATTTATTGATCAAATGATTCCTCC-----AGA  
I\_coccinea TGAAATAGATTCCACATTGAAGAAAGAATCGAATATTTATTGATCAAATGATTCCTCC-----ATA  
W\_coccinea TGAAATAGATTCCACATTGAAGAAAGAATCGAATATTTATTGATCAAATGATTCCTCC-----ATA

1530

S\_angolensis GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_amazonensis GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_aspera GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_brevipes GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_caminata GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_cana GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_capitellata GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_chocoana GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_cinerea GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_congensis GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_dewevrei GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_dinklagei GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_discolor GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_diversifolia GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_effulenensis GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
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S\_glabrescens GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
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S\_humilis GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
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S\_mattogrossensis GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_mexicana ATCGGACGAAATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_najatrix GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGANN  
S\_orientalis GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_panamensis GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_pyramidalis GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_rosea GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_seua -----  
S\_speciosa GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_thomensis GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTGNNNNNNNNCAATGTCGGCAACAATGAAATTT  
S\_venezuelensis GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_velutina GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_venosa -----  
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S\_villosa2 GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
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S\_xanthotricha GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
P\_aurifodinae GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
P\_mildbraedii GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
P\_nobilis GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
P\_segregata GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
P\_medusula GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
P\_batesii GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
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P\_arborea GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
P\_becquetii GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
E\_hierniana -----  
H\_minutiflora GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGACAACAATGAAATTT  
S\_hirsutum GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
S\_elliptica GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
T\_capsulifera GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
V\_multiflora GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
V\_procumbens GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
C\_coromandelicum GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
H\_zanzibarica GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCAGCAACAATGAAATTT  
I\_coccinea GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTT  
W\_coccinea GTCTGATAGATCTTTTCACGAACGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAACTT

**trnL-F spacer**

1620

S\_angolensis ATAGTAAGAGGAAAAATCCGTCGACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAG-CCTATTTGACTCCCCAACT-ATT  
S\_amazonensis ATAGTAAGAGGAAAAATCCGTCGACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGGCCATTTGACTCCCCAACTTATT  
S\_aspera ATAGTAAGAGGAAAAATCCGTCGACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAG-CCTATTTGACTCCCCAACT-ATT  
S\_brevipes ATAGTAAGAGGAAAAATCCGTCGACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAG-CCTATTTGACTCCCCAACT-ATT  
S\_caminata ATAGTAAGAGGAAAAATCCGTCGACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAG-CCTATTTGACTCCCCAACT-ATT  
S\_cana ATAGTAAGAGGAAAAATCCGTCGACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAG-CCTATTTGACTCCCCAACT-ATT





S.\_xanthotricha TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGA-TGATTTACAA  
P.\_aurifodinae TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
P.\_mildbraedii TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
P.\_nobilis TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
P.\_segregata TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
P.\_medusula TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
P.\_batesii -----  
P.\_proselyta TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
P.\_arborea TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
P.\_becquetii TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
E.\_hierniana -----  
H.\_minutiflora TCTTATCACAAGTCTATC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
S.\_hirsutum TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
S.\_elliptica TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
T.\_capsulifera TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
V.\_multiflora TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
V.\_procumbens TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
C.\_coromandelicum TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
H.\_zanzibarica TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
I.\_coccinea TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA  
W.\_coccinea TCTTATCACAAGTCTAGC---GTTCTATATGATATACATACAAAATTACCATCTTT-GA-GCAAGAAATCCCATTTGAATGATTTACAA

1890

S.\_angolensis T-CGATATAACTACCTCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_amazonensis TTCGATATAACTAC-TCATACTTGAAGCTTCCAAGTACTCTTTTTTAAAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_aspera T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_brevipes T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_caminata T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_cana T-CGATATAACTAC-TCATACT-GAA-----  
S.\_capitellata T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_chocoana T-CGATATAACTAC-TCATACTTGAAGCTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_cinerea T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_congensis T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_dewevrei T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_dinklagei T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_discolor T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_diversifolia T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_effulenensis T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_exellii T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_ferruginea T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_fulva T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_gilletii T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_glabrescens T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_harleyae T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_humilis T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_ingrata T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_johnstonii T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_mattogrossensis -----  
S.\_mexicana T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_najatrix -----  
S.\_orientalis T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_panamensis T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_pyramidalis -----  
S.\_rosea T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_seua -----  
S.\_speciosa T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_thomensis T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-A-GATCCA-GAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_venezuelensis T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_velutina T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_venosa -----  
S.\_villosa1 T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_villosa2 T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_vogelii T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_xanthotricha T-CGATATAACTAC-TCATACT-GAA-CTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
P.\_aurifodinae T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
P.\_mildbraedii T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
P.\_nobilis T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
P.\_segregata T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
P.\_medusula T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
P.\_batesii -----  
P.\_proselyta T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
P.\_arborea T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
P.\_becquetii T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
E.\_hierniana -----  
H.\_minutiflora T-CGATATAACTAC-TCATACT-GAA-----GTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_hirsutum T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
S.\_elliptica T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
T.\_capsulifera T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
V.\_multiflora T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC  
V.\_procumbens T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAAACCTCGGAAC

C.\_coromandelicum T-CGATATAACTAC-TCATCCT-GAAACTTACAAAGTACT-----GATCCAAGAAATCT-AGTACCTAGATAAAACTTTGTAAT  
H.\_zanzibarica T-CGATATAACTAC-TCATACT-GAAACTTCCAAGTACTCTTTTTT-AAGATCCAAGAAATTC-AGTACCTAGATAAAACTTTGGAAT  
I.\_coccinea T-CGATATAACTAC-TCATACT-GAAACTTACAAAGTACTCTTTTTT-AAGATCCAAGAAATCT-AGTACCTAGATAAAACTTTGTAAT  
W.\_coccinea T-CGATATAACTAC-TCATATT-GAAACTTACAAAGTACTCTTTTTT-AAGATCCAAGAAATTC-ACTACCTAGATAAAACTTTGTAAT

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S.\_angolensis CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_amazonensis CCCCTTTTCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_aspera CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_brevipes CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_caminata CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_cana -----  
S.\_capitellata CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_chocoana CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_cinerea CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_congensis CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_dewevrei CCCCTTTTCTTCTTTTAATTGAC-CGACCCCATTTT  
S.\_dinklagei CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_discolor CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_diversifolia CCCCTTT-CCTTCTTTTAATTGACACAGACC-ATTTT  
S.\_effulenensis CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_exellii CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_ferruginea CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_fulva CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_gilletii CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_glabrescens CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_harleyae CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_humilis CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_ingrata CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_johnstonii CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_mattogrossensis -----  
S.\_mexicana CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_najatrix -----  
S.\_orientalis CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_panamensis CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_pyramidalis -----  
S.\_rosea CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_seua -----  
S.\_speciosa CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_thomensis CCC-----  
S.\_venezuelensis CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_velutina CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_venosa -----  
S.\_villosa1 CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_villosa2 CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_vogelii CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_xanthotricha CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
P.\_aurifodinae CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
P.\_mildbraedii CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
P.\_nobilis CCCCTTT-CCTTCTTTTAATTGACAC-GACCC-ATTTT  
P.\_segregata CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
P.\_medusula CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
P.\_batesii -----  
P.\_proseltya CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
P.\_arborea CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
P.\_becquetii CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
E.\_hierniana -----  
H.\_minutiflora CCCCTTT-CCTTCTTTTAATTGACACAGACCTCATTTT  
S.\_hirsutum CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
S.\_elliptica CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
T.\_capsulifera CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
V.\_multiflora CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
V.\_procumbens CCCCTTT-CCTTCTTTTAATTGACACAGACCCCATTTT  
C.\_coromandelicum CCCCTTT-CCTTCTTTTAATTGACATAGCCCA-CTTT-  
H.\_zanzibarica CCCCTTC-CCTTCTTTTAATTGACATAGACCCCATTTT  
I.\_coccinea CCCCTTT-CCTTCTTTTAATTGACAAAGCCCTTTTT  
W.\_coccinea CCACTTT-CCTTCTTTTAATTGACATAGACCC-ATTTT

**Appendix 2. Aligned ITS, rpoC1, and trnT-F data matrices used in the combined ITS-rpoC1-trnT-F analysis (Chapter 6.2).**

**ITS Matrix (638 bp)**

	ITS1	90
S. hierniana	TCGAATCCTGCAAAT-AGACGACT-GCGAACTTGTGTTATT---ACACGGCTGTCGGCAGGTGCGGGTTGGGAT--AATACCTCTCGT	
H. minutiflora 1	TCGAATCCTGCAAAGCAGACGACC-GCGAACTCGTGACACC---GCACGGGTGCCGGTGGGAGCGGGTTGGGAC--AAAACCTCCCG-	
H. minutiflora 2	TCGAATCCTGCAAAGCAGACGACC-GCGAACTCGTGACACC---GCACGGGTGCCGGTGGGAGCGGGTTGGGAC--AAAACCTCCCG-	
S. becquetii	TCGAATCCTGCAAAGTAGACGACC-GCGAACTTGTGTTATT---ATACGGCTGTCGGCAGGAGCGGGTTGGGAT--AATACCTTATCGT	
S. medusula	TCGAATCCTGCAAAGTAGACGACC-GTGAACTTGTGTTATT---ACACGGCTGTCGGGAGGAGCGGGTTGGGAT--AATACCTCTCGT	
S. mildbraedii	TCGAATCCTGCAAAGTAGACGACC-GTGAACTTGTGTTATT---ACACGGTTCGGGAGGAGCGGGTTGGGAT--AATACCTCTCGT	
S. nobilis	TCGAATCCTGCAAAGTAGACGACC-GCGAACTTGTGTTATT---ACACGGCTGTCGGCAGGTGCTGATTGGGAT--AATACCTCTCGT	
S. aspera	TCGAATCCTGCAAAGTAGACGACC-GTGAACTTGTGTTATT---ACACGGTTCGGCAGGTGCGGGTTGGGAT--AATACCTCTCGT	
S. caminata	TCGAATCCTGCAAAGTAGACGACC-GCGAACTTGTGTTATT---ACACGGCTGTCGGCAGGTGCGGGTTGGGAT--AATACCTCTCGT	
S. mexicana	TCGAATCCTGCAAAGTAGACGACC-GTGAACTTGTGTTATT---ACACGGTTCGGCAGGTGCGGGTTGGGAT--AATACCTCTCGT	
S. venosa	TCGAATCCTGCAAAGTAGACGACC-GTGAACTTGTGTTATT---ACACGGCTGTCGGGAGGTGCGGGTTGGGAT--AATACCTCTCGT	
S. xanthotricha	TCGAATCCTGCAAAGTAGACGACC-GCGAACTTGTGTTATT---ACACGGTTCGGCAGGTGCGGGTTGGGAT--AATACCTCTCGT	
S. hirsutum	TCGAATCCTGCAAAGTAGACTACC-GCGAACTTGTGTTATA---ACACGGATGTCGGCAGGTGCGGGTTGGGAT--AATACCTCTCGT	
S. elliptica	TCGAATCCTGAAAAGCAGACGACC-GTGAACTTGTGTTAAT---ACATGGTTCGGCAGGTGCGGGTTGGGAT--AATACCTCTCGT	
T. capsulifera	TCGAATCCTGAAAACAGACCACT-GTGAACTCGTATCATT---ACACGGGTGCCGGT-G-----CCTCAC--	
V. angustifolia	TCGAATCCTGAAAAGCAGACCACT-GTGAACTCGTGTACC---AAACGGGCGTGGTGGGAGCGGGTT-GGATTA AAAACCTCCCGT	
V. belingana	TCGAATCCTGAAAACAAACCCT-GTGAACTCGTGTACC---AAACGGGCGTGGTGGTAGCGGGTA-GGATT-AAAACCTCCCGT	
V. herbacoursi	TCGAATCCTGAAAAGCAGACCACT-GTGAACTCGTGTACC---CATGGTTCGGCAGGTGGGAGCGGGTT-GGAT--AATACCTCTCGT	
V. major	TCGAATCCTGAAAAGCAGACCACT-GTGAACTCGTGTACC---AAACGGGCGTGGTGGGAGCGGGTT-GGATT-AAAACCTCCC-C	
V. multiflora	TCGAATCCTGAAAAGCAGACCACT-GTGAACTCGTGTACC---AAACGGGCGTGGTGGGAGCGGGTT-GGATT-AAAACCTCCCGT	
V. procumbens	TCGAATCCTGAAAAGCAGACCACT-GTGAACTCGTGTACC---AAACGGGCGTGGTGGGAGCGGGTT-GGATTA AAAACCTCCCGT	
M. pinatubensis	TCGAATCCTGAAAAGCAGACGACC-GCGAACTTGTGTTAAT---GCCGGGCGTCGG--GGAACAGGG-GAGACT--AAAGCTCCC-C	
W. coccinea	TCGAATCCTGCGAGACGGACGCCGCGAACAGCTTAAACC---GCCGGGCGTCGG--GGAACAGGG-GAGACTC--AACCTCCC-C	

S. hierniana	TGCTCAC--CGCACCCACCGC-GTGCTTGACAGTGGACAATAACTCAACCCCGCGCGGAAAGCGCCAAAGCAAACCTAAAATTGGAT	
H. minutiflora 1	TCCCAG-CGCCGGCGCCCCCGC-GCGCTCGTCGCGCGGACACTAACTCAACCCCGCGCGGAAAGCGCCAAAGGAAAACCTGAAATTGGAT	
H. minutiflora 2	TCCCAG-CGCCGGCGCCCCCGC-GCGCTCGTCGCGCGGACACTAACTCAACCCCGCGCGGAAAGCGCCAAAGGAAAACCTGAAATTGGAT	
S. becquetii	TGCTCAC--CGGCGCTACCGC-GCGCTCGACGTGCGGACAATAACTTAAACCCCGCGCGGAAAGCGCCAAAGGAAAACCTAAAATTGGAT	
S. medusula	TGCTCAC--CGGCGCTACCGC-GTGCTCGACGTGCGGACAATAACTCAACCCCGCGCGGAAAGCGCCAAAGGAAAACCTAAAATTGGAT	
S. mildbraedii	TGCTCAC--CGGCGCTACCGC-GTGCTCGACGTGCGGACAATAACTCAACCCCGCGCGGAAAGCGCCAAAGGAAAACCTAAAATTGGAT	
S. nobilis	TGCTCAC--CGGCGCTACCGC-GTGCTCGACACACGACACAATAACTCAACCCCGCGCGGAAAGCGCCAAAGGAAAACCTAAAATTGGAT	
S. aspera	TGCTCAC--CGGCGCTACCGC-GTGCTCGACACGCGGACAATAACTCAACCCCGCGCGGAAAGCGCCAAAGGAAAACCTAAAATTGGAT	
S. caminata	TGCTCAC--CGGCGCTACCGC-GTGCTCGACACGCGGACAATAACTCAACCCCGCGCGGAAAGCGCCAAAGGAAAACCTAAAATTGGAT	
S. mexicana	TGCTCAC--CGGCGCTACCGC-GTGCTCGACACGCGGACAATAACTCAACCCCGCGCGGAAAGCGCCAAAGGAAAACCTAAAATTGGAT	
S. venosa	TGCTCAC--CGGCGCTACCGC-GTGCTCGACACGCGGACAATAACTCAACCCCGCGCGGAAAGCGCCAAAGGAAAACCTAAAATTGGAT	
S. xanthotricha	TGCTCAC--CGGCGCTACCGC-GTGCTCGACGCGCGGACAATAACTCAACCCCGCGCGGAAAGCGCCAAAGGAAAACCTAAAATTGGAT	
S. hirsutum	TGCTCAC--CGGCGCTACCGC-GTGCTCGACACGCGGACAATAACTCAACCCCGCGCGGAAAGCGCCAAAGGAAAACCTAAAATTGGAT	
S. elliptica	TGCTCAC--CGGCGCTACCGC-GTGCTCGACACGCGGACAATAACTCAACCCCGCGCGGAAAGCGCCAAAGGAAAACCTAAAATTGGAT	
T. capsulifera	-----C-----GGCGCCACCGC-GTGCTCGTCGCGTGGACATAACTCAACCCCGCGCGGAAAGCGCCAAAGGATAACTAAAATTGGAT	
V. angustifolia	TGTCACAC--CGGCGTCCATCAT-GCACCCATTGGGTGCACCATAACTAAAACCTCCGGCGCGGAAAGCGCCAAAGGAAAACAAAATTGGAT	
V. belingana	TGTCACAC--CAGCGTCCATCAT-GCACCCATTGGGTGCACCATAACTAAAACCTCCGGCGCGGAAAGCGCCAAAGGAAAACAAAATTGGAT	
V. herbacoursi	TGTCACAC--CAGTGTCCATCGT-GCATCTGTTTGGTGCACAATAACTAAAACCTCCGGCGCGGAAAGCGCCAAAGGAAAACAAAATTGGAT	
V. major	GTTGTACACCCGGTCCATCAT-GCACCCATTGGGTGCACCATAACTAAAACCTCCGGCGCGGAAAGCGCCAAAGGAAAACAAAATTGGAT	
V. multiflora	TGTCACAC--CAGCGTCCATCGT-GCACCTTTTGGTGCACAAAATAACTAAAACCTCCGGCGCGGAAAGCGCCAAAGGAAAACAAAATTGGAT	
V. procumbens	TGTCACAC--CGGCGTCCATCAT-GCACCCATTGGGTGCACCATAACTAAAACCTCCGGCGCGGAAAGCGCCAAAGGAAAACAAAATTGGAT	
M. pinatubensis	TAACTC-C-CGGCGCTCCCC---GCGCAC--CGCGCGGACAACAATAACTCAACCCCGCGCGGAAAGCGCCAAAGGAAAACCTAAAA-GGAT	
W. coccinea	TCCCTC-C-CGACGCCCCCCCGCGCGCACGTGCGCGGACGACAATAACTCAACCCCGCGCGGAAAGCGCCAAAGGAAAACCTAAAAG-TGAC	

**S5.8 gene**

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S. hierniana	AGCCTGC---CTCC-----CCGTTTCG-GG-GGGGTGCTGTGGCTTCTGTTG-TAACCAAAACGACTCTCGACAACGGATATC	
H. minutiflora 1	GGCCCGC---CTCC-----CCGTTTCG-GG-GGGGTGCCGCGCGGTCTGTCG-TAACCAAAACGACTCTCGGCAACGGATATC	
H. minutiflora 2	GGCCCGC---CTCC-----CCGTTTCG-GG-GGGGTGCCGCGCGGTCTGTCG-TAACCAAAACGACTCTCGGCAACGGATATC	
S. becquetii	AGCCCGC---CTCC-----CCGTTTCG-GG-GGGGTGCTATGGCTTCTATTG-TAACCAAAACGACTCTCGACAACGGATATC	
S. medusula	AGCCCGC---CTCC-----CCGTTTGT-GG-GGGGCGCTATGGCTTCTGTTG-TAACCAAAACGACTCTCGACAACGGATATC	
S. mildbraedii	AGCCCGC---CTCC-----CCGTTTGT-GG-GGGGCGCTATGGCTTCTGTTG-TAACCAAAACGACTCTCGACAACGGATATC	
S. nobilis	AGCCTGC---CTCC-----CCATTTCG-GG-GGGGTACTGTGGCTTCTGTTG-TAACCAAAACGACTCTCGACAACGGATATC	
S. aspera	AGCCTGC---CTCC-----CCGTTTCG-GG-GGGGTGATATGGCTTCTGTTG-TAACCAAAACGACTCTCGACAACGGATATC	
S. caminata	AGCCTGC---CTCC-----CCGTTTCG-GG-GGGGTGCTGTGGCTTCTGTTG-TAACCAAAACGACTCTCGACAACGGATATC	
S. mexicana	AGCCTGC---CTCC-----CCGTTTCG-GG-GGGGTGATGTGGCTTCTGTTG-TAACCAAAACGACTCTCGACAACGGATATC	
S. venosa	AGCCTGC---CTCC-----CCGTTTCG-GG-GGGGTGATGTGGCTTCTGTTG-TAACCAAAACGACTCTCGACAACGGATATC	
S. xanthotricha	AGCCTGC---CTCC-----CCGTTTCG-GG-GGGGTGCTGTGGCTTCTATTG-TAACCAAAACGACTCTCGACAACGGATATC	
S. hirsutum	AGCCTGC---CTCC-----CCGTTTCG-GG-GGGGTGCTGTGGCTTCTGTTG-TAACCAAAACGACTCTCGACAACGGATATC	
S. elliptica	AGCCCGC---CTTC-----CCGTTTCG-GG-GAGTACTGTGGCTTCTATCG-TAACCAAAACGACTCTCGACAACGGATATC	
T. capsulifera	TGCCCGT---CTCC-----CCGTTTTCG-GG-GGGTACTGTGGCTTCTGTCG-TAATCTAAACGACTCTCGGCAACGGATATC	
V. angustifolia	TGCTCGTTA-CCTTT-----CGTCCG-GT-GGGGTATCGTGGATCTGTCG-TAATCTAAACGACTCTCGGCAACGGATATC	
V. belingana	TGCCCGTACCTTT-----CGTTCG-GG-GGGGTATGTGGATCTGTCG-TAATCTAAACGACTCTCGGCAACGGATATC	
V. herbacoursi	TGCCCGTACCTTT-----CGTTCG-GG-GGGGTATCGTGGATCTGTCG-TAATCTAAACGACTCTCGGCAACGGATATC	
V. major	TGCCCGTACCTTT-----CGTTCG-GG-GGGGTATCGTGGATCTGTCG-TAATCTAAACGACTCTCGGCAACGGATATC	
V. multiflora	TGCCCGTACCTTT-----CGTTCG-GG-GGGGTATCGTGGATCTGTCG-TAATCTAAACGACTCTCGGCAACGGATATC	
V. procumbens	TGCCCGTACCTTT-----CGTTCG-GT-GGGGTATCGTGGATCTGTCG-TAATCTAAACGACTCTCGGCAACGGATATC	

M. pinatubensis TGCCGC---CTCC-----CCGTGCGC-GG-GGTGTGTTGTGGCATCTGTCTG-TAACCAAACGACTCTCGGCAACGGATATC  
W. coccinea GGCCCGTCCCCCGCCGCCCGTTCGCGGAGCGCAGGCGGGGAGCCGCGGCTGTCTGCTTAACCTAAACGACTCTCGGCAACGGATATC

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S. hierniana TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
H. minutiflora 1 TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
H. minutiflora 2 TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
S. becquetii TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
S. medusula TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
S. mildbraedii TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
S. nobilis TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
S. aspera TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
S. caminata TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
S. mexicana TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
S. venosa TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
S. xanthotricha TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
S. hirsutum TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
S. elliptica TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
T. capsulifera TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
V. angustifolia TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
V. belingana TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
V. herbacoursi TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
V. major TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
V. multiflora TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
V. procumbens TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
M. pinatubensis TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG  
W. coccinea TCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAG

ITS2



S. hierniana TTGCGCCGAAGCCATCAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCAATTTGACGGG--TAGCGGAT  
H. minutiflora 1 TTGCGCCGAAGCCATTAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCCCATC----GCGGGG--CGGCGGAA  
H. minutiflora 2 TTGCGCCGAAGCCATTAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCCCATC----GCGGGG--CGGCGGAA  
S. becquetii TTGCGCCGAAGCCATCAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCAATTCGCGGGGTAGCGGAT  
S. medusula TTGCGCCGAAGCCATCAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCAATTCGCGGGGTAGCGGAT  
S. mildbraedii TTGCGCCGAAGCCATCAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCAATTCGCGGGGTAGCGGAT  
S. nobilis TTGCGCCGAAGCCATCAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCAATTCGCGGGG--TAGCGGAT  
S. aspera TTGCGCCGAAGCCATCAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCC--GTTCAATTCATGGGG--TAGCGGAT  
S. caminata TTGCGCCGAAGCCATCAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCAATTCGCGGGG--TAGCGGAT  
S. mexicana TTGCGCCGAAGCCATCAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCC--GTTCAATTCATGGGG--TAGCGGAT  
S. venosa TTGCGCCGAAGCCATCAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCC--GTTCAATTCATGGGG--TAGCGGAT  
S. xanthotricha TTGCGCCGAAGCCATCAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCC--GTTCAATTCGAGGG--TAGCGGAT  
S. hirsutum TTGCGCCGAAGCCATCAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCAATTCGCGGGG--TAGCGGAT  
S. elliptica TTGCGCCGAAGCCATCAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCTTGTGCCACCCCTTGTCTATT--CGGGG--GAAGCGGAA  
T. capsulifera TTGCGCCAAAGCCATTAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATAGCGTCGCCATCCCA---ATTGAGGGG--TGGCGGAT  
V. angustifolia TTGCGCCAAAGCCATTAGGCCGAGGGCACGCTGCCTGGGCGTCACACATTGCGTTGCCACCCCACTA---CGGGG--TGGCAGAG  
V. belingana TTGCGCCGAAGCCATTAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCCCACTA---CGGGG--CGGCGAT  
V. herbacoursi TTGCGCCGAAGCCATTAGGCCGAGGGCACGCTGCCTGGGCGTCACACATTGCGTTGCCACCCCACTA---GGGG--TGGCGGAT  
V. major TTGCGCCGAAGCCATTAGGCCGAGGGCACGCTGCCTGGGCGTCACACATTGCGTTGCCACCCCACTA---CGGGGTGGCGGAT  
V. multiflora TTGCGCCGAAGCCATTAGGCCGAGGGCACGCTGCCTGGGCGTCACACATTGCGTTGCCACCCCACTA---GGGG--TGGCGGAT  
V. procumbens TTGCGCCGAAGCCATTAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCCCACTA---TFTT--GCGGGG--CGGCGGAT  
M. pinatubensis TTGCGCCGAAGCCATTAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCCCACTA---TFTT--GCGGGG--CGGCGGAT  
W. coccinea TTGCGCCGAAGCTGTAGGCCGAGGGCACGCTGCCTGGGCGTCACGCATCGCGTCGCCACCCCACTA---ATC--GCGGGG--GCGCGGAT

S. hierniana AATGGCCTCCCGTACCACCA--GGCGGGCTGGCCATAATGCGAGTCTCGGTGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAAC  
H. minutiflora 1 AATGGCCTCCCGTACCACCA--GGCGGGCTGGCCATAATGCGAGTCTCGGTGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAAC  
H. minutiflora 2 AATGGCCTCCCGTACCACCA--GGCGGGCTGGCCATAATGCGAGTCTCGGTGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAAC  
S. becquetii AATGGCCTCCCGTACCACCA--GGTGGCTGGCCATAATGCGAGTCTCGGCGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAAC  
S. medusula AATGGCCTCCCGTACCACCA--GGTGGCTGGCCATAATGCGAGTCTCGGCGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAAC  
S. mildbraedii AATGGCCTCCCGTACCACCA--GGTGGCTGGCCATAATGCGAGTCTCGGCGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAAC  
S. nobilis AATGGCCTCCCGTACCACCA--GGCGGGCTGGCCATAATGCGAGTCTCGGCGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAAC  
S. aspera AATGGCCTCCCGTACCACCA--GGCGGGCTGGCCATAATGCGAGTCTCGGCGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAAC  
S. caminata AATGGCCTCCCGTACCACCA--GGCGGGCTGGCCATAATGCGAGTCTCGGCGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAAC  
S. mexicana AATGGCCTCCCGTACCACCA--GGCGGGCTGGCCATAATGCGAGTCTCGGCGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAAC  
S. venosa AATGGCCTCCCGTACCACCA--GGCGGGCTGGCCATAATGCGAGTCTCGGCGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAAC  
S. xanthotricha AATGGCCTCCCGTACCACCA--GGCGGGCTGGCCATAATGCGAGTCTCGGCGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAAC  
S. hirsutum AATGGCCTCCCGTACCACCA--GGCGGGCTGGCCATAATGCGAGTCTCGGCGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAAC  
S. elliptica AATGGCCTCCCGTACCACCA--GGTGGCTGGCCATAATGCGAGTCTCGGCGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAAC  
T. capsulifera AATGGCCTCCCGTACCACCA--GGAGGGCTGGCCATAATGCGAGTCTCGGTGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAAC  
V. angustifolia AATGGCCTCCCGTACCACCA--GGAGGGCTGGCCATAATGCGAGTCTCGGTGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAAC  
V. belingana AATGGCCTCCCGTACCACCA--GGAGGGCTGGCCATAATGCGAGTCTCGGTGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAAC  
V. herbacoursi AATGGCCTCCCGTACCACCA--GGAGGGCTGGCCATAATGCGAGTCTCGGTGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAAC  
V. major AATGGCCTCCCGTACCACCA--GGAGGGCTGGCCATAATGCGAGTCTCGGTGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAAC  
V. multiflora AATGGCCTCCCGTACCACCA--GGAGGGCTGGCCATAATGCGAGTCTCGGTGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAAC  
V. procumbens AATGGCCTCCCGTACCACCA--GGAGGGCTGGCCATAATGCGAGTCTCGGTGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAAC  
M. pinatubensis ACTGGCCTCCCGTACCACCA--GGAGGGCTGGCCATAATGCGAGTCTCGGTGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAAC  
W. coccinea ACTGGCCTCCCGTACCACCA--GGAGGGCTGGCCATAATGCGAGTCTCGGTGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAAC



S. hierniana TCGAGTCCT-GTCGTGTTGGCAAACCCACCGTTAACT-----CCCTT-GACCCTACA-GCATGCACCCTGGTG---CAAGCCTCGACCG  
H. minutiflora 1 TCGAGTCCT-GTCGTGCCGGCGAATCCCCCGTTGTCTCGGACTCCCACGACCCACG-GCGCGCGTACGGCG---CRAGCCTCGACCG  
H. minutiflora 2 TCGAGTCCTGTCTGTGCCGGCAATCCCCCGTTGTCTCGGACTCCCACGACCCACG-GCGCGCGTACGGCG---CGAGCY-CGACCG  
S. becquetii TCGAGTCCT-GTCGTGTTGGCAAACCCGCGTTAACT-----CCCTT-GACCCTACA-GCATGCACCCTGGTG---CAAGCCTCGACCG  
S. medusula TCGAGTCCT-GTCGTGTTGGCAAACCCGCGTTAACT-----CCCTT-GACCCTGCA-GCATGCACCCTGGTG---CAAGCCTCGACCG  
S. mildbraedii TCGAGTGCT-GTCGTGTTGGCAAACCCGTCGTTAACT-----CCCTT-GACCCTGCA-GCATGCACCCTGGTG---CAAGCCTCGACCG  
S. nobilis TCGAGTCCT-GTTGTGTTGGCAAATCCCGCGTTAACT-----CCCTT-GGCCCTATA-GCATGCACCCTGGTG---CAAGCCTCGACCG  
S. aspera TCGAGTCCT-GTTGTGTTGGCAAACCTCGCCGTTAACT-----CCTTTTACCCTACA-GCATGCACCCTGGTG---CAAGCCTCGACCG  
S. caminata TCGAGTCCT-GTCGTGTTGGCAAACCCGCGTTAACT-----CCCTT-GACCCTACA-GCATGCACCCTGGTG---CAAGCCTCGACCG  
S. mexicana TCGAGTCCT-GTTGTGTTGGCAAACCCGCGTTAACT-----CCTTTTACCCTACA-GCATGCACCCTGGTG---CAAGCCTCGACCG  
S. venosa TCGAGTCCT-GTTGTGTTGGCAAACCTCGCCGTTAACT-----CCCTT--ACCCTACA-GCATGCACCCTGGTG---CAAGCCTCGACCG  
S. xanthotricha TCGAGTCCT-GTCGTGTTGGCAAACCCGCGTTAACT-----CCCTT-GACCCTACA-GCATGCACCCTGGTG---CAAGCCTCGACCG  
S. hirsutum TCGAGTCCT-GTTGTGTTGGCAAACCCGCGTTAACT-----CCCTC-GACCCTACA-GCATGCACCCTGGTG---CAAGCCTCGACCG  
S. elliptica TCGAGTCCT-GTCGTGTTGGCAAACCCGTCGTTAACT-----CCTTTGACCCTACA-GCATGCACCCTGGTG---CAAGCCTCGACCG  
T. capsulifera TCGAGTCCT-GTCGTGCCGATGAGTCCCATATCT-GGACTCCTATGACCCTGCA-GCATGCCTTTGACG---TAAGCCTCGACTG  
V. angustifolia TCGAGTGCT-GTCGTGTTGACGAATCTCC-CGTTA-TT-GGACTCTGTTGACCCTATA-GCGCAGCTCTTGACG---TGAGCATCAAT-G  
V. belingana TCGAGTGCT-GTCGTGTTGACGAATCTCC-CGTTA-CTTGGACTCTGTTGACCCTATA-GCGCAGCTCTTGACG---TGAGCATCAATTG  
V. herbacoursi TCGAGTGCT-GTCGTGTTGACGAATCTCC-CGTTA-TTGGACTTTGCTGACCCTATA-GCGCAGCTCTTGACG---TGAGCATCAATTG  
V. major TCGAGTGCT-GTCGTGTTGACGAATCTCC-CGTTA-CTTGGACTCTGTTGACCCTATA-GCGCAGCTCTTGACG---TGAGCATCAATTG  
V. multiflora TCGAGTGCT-GTCGTGTTGACGAATCTCC-CGTTA-CTTGGACTTAGTTGACCCTATT-GCGCAGCTCTTGACG---TGAGCATCAATTG  
V. procumbens TCGAGTGCT-GTCGTGTTGACGAATCTCC-CGTTA--TTGGACTCTGTTGACCCTATA-GCGCAGCTCTTGACG---TGAGCATCAAT-G  
M. pinatubensis TCGATTCT-GTCGTGTCATTGGCCCTCGTCGTT-TCTCGGCTCCTT-GACCCTTCTTGCTTGCATCTCGATG---CGAGCCTCGACCG  
W. coccinea TCGATTCT-GTCGTGCCCGCACCCCCCGCGTT-TCTCGG-CTCCCC-GACCCTTCA-GCTCGCTCTTGACGGCGTAGGCCCTCGACCG

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S. hierniana CGACCC-A  
H. minutiflora 1 CGACCC-A  
H. minutiflora 2 CGACCC--  
S. becquetii CGACCC-A  
S. medusula CGACCC-A  
S. mildbraedii CGACCC-A  
S. nobilis CGACCC-A  
S. aspera CGACCC-A  
S. caminata CGACCC-A  
S. mexicana CGACCC--  
S. venosa CGACCC-A  
S. xanthotricha CGACCC-A  
S. hirsutum CGACC--A  
S. elliptica CGACCC-A  
T. capsulifera CGACCC-A  
V. angustifolia CGACCC-A  
V. belingana CGACCC-A  
V. herbacoursi CGACCC-A  
V. major CGACCC-A  
V. multiflora CGACCC-A  
V. procumbens CGACCCCA  
M. pinatubensis CGACCCCA  
W. coccinea CGACCA--

**rpoC1 Matrix (484 bp)**

**exon1**



S. hierniana AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC 90  
H. minutiflora 1 AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
H. minutiflora 2 AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
S. becquetii AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
S. medusula AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
S. mildbraedii AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
S. nobilis AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
S. aspera AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
S. caminata AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
S. mexicana AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
S. venosa AGACTCTGCTTGGCAA--CGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
S. xanthotricha AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
S. hirsutum AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCSTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
S. elliptica AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
T. capsulifera AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
V. angustifolia AGACTCTGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
V. belingana GGRMCTGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
V. herbacoursi GGRMCTGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
V. major GGRMCTGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
V. multiflora AGACTCTGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
V. procumbens AGACTCTGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
M. pinatubensis GGRMCTGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC  
W. coccinea -ARMCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCCTTCACTTTCATTACATCGATGTGGATTGCCTC



S. medusula ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 S. mildbreadii ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 S. nobilis ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 S. aspera ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 S. caminata ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 S. mexicana ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 S. venosa ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 S. xanthotricha ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 S. hirsutum ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCYWWWCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 S. elliptica ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 T. capsulifera ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 V. angustifolia ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 V. belingana ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 V. herbacoursi ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 V. major ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 V. multiflora ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 V. procumbens ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 M. pinatubensis ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
 W. coccinea ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC

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S. hierniana TTTTGTCTCCAGCTATTGGG-ATCCCATTTCCGT  
 H. minutiflora 1 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 H. minutiflora 2 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 S. becquetii TTTTGTCTCCAGCTATTGGG-ATCCCATTTCCGT  
 S. medusula TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 S. mildbreadii TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 S. nobilis TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 S. aspera TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 S. caminata TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 S. mexicana TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 S. venosa TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 S. xanthotricha TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 S. hirsutum TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 S. elliptica TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 T. capsulifera TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 V. angustifolia TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 V. belingana TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 V. herbacoursi TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 V. major TTTTGTCTCCAGCTATTGGG-ATCCCATTTCCGK  
 V. multiflora TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 V. procumbens TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 M. pinatubensis TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
 W. coccinea TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG

**trnT-F Matrix (1810 bp)**

**trnT-L spacer**



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S. hierniana TAGTTAGTAACTAGTATTTCTTATCCATTCATAATCGATATAAAATACAGAAAGGAATAAAATAGAATTTTAAATAAATTATTGAATATTA  
 H. minutiflora 1 -----  
 H. minutiflora 2 -----  
 S. becquetii TAGTTAGTAACTAGTATTTCTTATCCATTCATAATCGATATAAAATACAGAAAGGGATAAAATAGAATTTGAAATAAATTATTGAATATTA  
 S. medusula TAGTTAGTAACTAGTATTTCTTATCCATTCATAATCGATATAAAATACAGAAAGGAATAAAATAGAATTTTAAATAAATTATTGAATATTA  
 S. mildbraedii TAGTTAGTAACTAGTATTTCTTATCCATTCATAATCGATATAAAATACAGAAAGGAATAAAATAGAATTTTAAATAAATTATTGAATATTA  
 S. nobilis TAGTTAGTAACTAGTATTTCTTATCCATTCATAATCGATATAAAATACAGAAAGGAATAAAATAGAATTTTAAATAAATTATTGAATATTA  
 S. aspera TAGTTAGTAACTAGTATTTCTTATCCATTCATAATCGATATAAAATACAGAAAGGAATAAAATAGAATTTTAAATAAATTATTGAATATTA  
 S. caminata TAGTTAGTAACTAGTATTTCTTATCCATTCATAATCGATATAAAATACAGAAAGGAATAAAATAGAATTTTAAATAAATTATTGAATATTA  
 S. mexicana -----AGTATTTCTTATCCATTCATAATCGATATAAAATACAGAAAGGAATAAAATAGAATTTTAAATAAATTATTGAATATTA  
 S. venosa TAGTTAGTAACTAGTATTTCTTATCCATTCATAATCGATATAAAATACAGAAAGGAATAAAATAGAATTTTAAATAAATTATTGAATATTA  
 S. xanthotricha TAGTTAGTAACTAGTATTTCTTATCCATTCATAATCGATATAAAATACAGAAAGGAATAAAATAGAATTTTAAATAAATTATTGAATATTA  
 S. hirsutum TAGTTAGTAACTAGTATTTCTTATCCATTCATAATCGATATAAAATACAGAAAGGAATAAAATAGAATTTTAAATAAATTATTGAATATTA  
 S. elliptica TAGTTAGTAACTAGTATTTCTTATCCATTCATAATCGATATAAAATACAGAAAGGAATAAAATAGAATTTTAAATAAATTATTGAATATTA  
 T. capsulifera -----TCATAATCAATATAAAATATAGAAAGGAATAAAATCGAATTTTAAATAAATTATTGAATATTA  
 V. angustifolia -----  
 V. belingana -----TTATCCATTCAGAATTC-TATAAAATAGAGAAAGGAATAAAATAGAATTTTAAATAAATTATTGAATATTA  
 V. herbacoursi -----  
 V. major -----TTATCCATTCAGAATTC-TATAAAATAGAGAAAGGAATAAAATAGAATTTGAAATAAATTATTGAATATTA  
 V. multiflora -----TCATCCATTCAGAATTC-TATAAAATAGAGAAAGGAATAAAATAGAATTTTAAATAAATTATTGAATATTA  
 V. procumbens -----TTATCCATTCAGAATTC-TATAAAATAGAGAAAGGAATAAAATAGAATTTGAAATAAATTATTGAATATTA  
 M. pinatubensis TAGTTAGTAACTATTATTTCTTATCTATTCATAATCGATATGGAATATAGAAAGGAATAAAATAGAATTTTAAATAAATTATTGAATATTC  
 W. coccinea TAGTTAGTAACTATTATTTCTTATCTATTCATAATCGATATGGAATATAGAAAGGAATAAAATAGAATTTTAAATAAATTATTGAATATTA

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S. hierniana TAGAAGAC-----AAGGACTAATATAGCGATATAGAATTTTCGATTTATTATCACTAATAGAATTTAGA--ATTCAAATA----  
 H. minutiflora 1 -----  
 H. minutiflora 2 -----  
 S. becquetii TAGAAGAC-----AAGGACTAATATAGCGATATAGAATTTTCGATTTATTATCACTAATAGAATTTAGA--ATTCAAATA----

S. medusula TAGAAGAC-----AAGGACTAATATAGCGATATAGAATTTTCGATTATTATCTACTAATAGAATTTAGA--ATTCAAATA----  
 S. mildbraedii TAGAAGAC-----AAGGACTAATATAGCGATATAGAATTTTCGATTATTATCTACTAATAGAATTTAGA--ATTCAAATA----  
 S. nobilis TAGAAGAC-----AAGGACTAATATAGCGATATAGAATTTTCGATTATTATCTACTAATAGAATTTAGA--ATTCAAATATTAT  
 S. aspera TAGAAGACA-----AAGGACTAATATAGCGATATAGAATTTTCGATTATTATCTACTAATAGAATTTAGA--ATTCAAATA----  
 S. caminata TAGAAGAC-----AAGGACTAATATAGCGATATAGAATTTTCGATTATTATCTACTAATAGAATTTAGA--ATTCAAATA----  
 S. mexicana TAGAAGAC-----AAGGACTAATATAGCGATATAGAATTTTCGATTATTAGTTATCTACTAATAGAATTTAGA--ATTCAAATA----  
 S. venosa TAGAAGAC-----AAGGACTAATATAGCGATATAGAATTTTCGATTATTATCTACTAATAGAATTTAGA--ATTCAAATA----  
 S. xanthotricha TAGAAGAC-----AAGGACTAATATAGCGATATAGAATTTTCGATTATTATCTACTAATAGAATTTAGA--ATTCAAATA----  
 S. hirsutum TAGAAGAC-----AAGGACTAATATAGCGATATAGAATTTTCGATTATTATCTACTAATAGAATTTAGA--ATTCAAATAT---  
 S. elliptica TAGAAGAC-----AAGGACTAATATAGCGATATAGAATTTTCGATTATTATCTACTAATAGAATTTAGA--ATTCAAATA----  
 T. capsulifera TAGAAGAC-----AAGGACTAATATAGCGATATAGAATTTTCGATTATTATCTACTAATCTATTATCTACTAATAGAATTTCGA  
 V. angustifolia -----  
 V. belingana TAGAAGACTTATAGAAGGCAAGGCCTAAAATAGCGATATAGAATTTTCGATTATTATCTACTAATATATTATTTAT--CACTAATAGAAT  
 V. herbacoursi -----  
 V. major TAGAAGACTTATAGAAGGCAAGGCCTAAAATAGCGATATAGAATTTTCGATTATTATCTACTAATATATTATTTAT--CACTAATAGAAT  
 V. multiflora TAGAAGACTTATAGAAGGCAAGGCCTAAAATAGCGATATAGAATTTTCGATTATTATCTACTAATATATTATTTAT--CACTAATAAAAT  
 V. procumbens TAGAAGACTTATAGAAGGCAAGGCCTAAAATAGCGATATAGAATTTTCGATTATTATCTACTAATATATTATTTAT--CACTAATAGAAT  
 M. pinatubensis TAGAACAC-----AACAAATTAATATAGCGATATAGAATTTTCGATTATTATCTACTAATATAATT-----CGAATA----  
 W. coccinea TAGAATAC-----AACGATTAATATAACGATATAGAATTTTCGATTATTATCTACTAATATAATT-----CGAATA----

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S. hierniana -----TTATTAATTCGAATTATCATTTAATATT--CGATTAGATAGTAAATAGTTTGTAGT  
 H. minutiflora 1 -----  
 H. minutiflora 2 -----  
 S. becquetii -----TTATTAATTCGAATTATCATTTAATATT--CGATTAGATAGTAAATAGTTTGTAGT  
 S. medusula -----TTATTAATTCGAATTATCATTTAATATT--CGATTAGATAGTAAATAGTTTGTAGT  
 S. mildbraedii -----TTATTAATTCGAATTATCATTTAATATT--CGATTAGATAGTAAATAGTTTGTAGT  
 S. nobilis TAAATTCGAATTATCATTTAATATTTCGACAAATATTATTAATTCGAATTATCATTTAATATT--CGATTAGATAGTAAATAGTTTGTAGT  
 S. aspera -----TTATTAATTCGAATTATCATTTAATATT--CGATTAGATAGTAAATAGTTTGTAGT  
 S. caminata -----TTATTAATTCGAATTATCATTTAATATT--CGATTAGATAGTAAATAGTTTGTAGT  
 S. mexicana -----TTATTAATTCGAATTATCATTTAATATT--CGATTAGATAGTAAATAGTTTGTAGT  
 S. venosa -----TTATTAATTCGAATTATCATTTAATATT--CGATTAGATAGTAAATAGTTTGTAGT  
 S. xanthotricha -----TTATTAATTCGAATTATCATTTAATATT--CGATTAGATAGTAAATAGTTTGTAGT  
 S. hirsutum -----TTATTAATTCGAATTATCATTTAATATT--CGATTAGATAGTAAATAGTTTGTAGT  
 S. elliptica -----TTATTAATTCGAATTATCATTTAATATT--CGATTAGATAGTAAATAGTTTGTAGT  
 T. capsulifera ATTCAAATA-----TTATTAATTCGAATTATCATTTAATATT--CGATTAGATAGTAAATAGTTTGTAGT  
 V. angustifolia -----  
 V. belingana TTATTTATCTACTAATAGAATTTAGAATTCGAATATTATTAACCTCGAATTATCATTTACTAGT--CGATTAGATAGTAAATAGTTTGTAGT  
 V. herbacoursi -----  
 V. major TTAGAATTCGAATA-----TTATTAACCTCGAATTATCATTTACTAGT--CGATTAGATAGTAAATAGTTTGTAGT  
 V. multiflora TTAGAATTCGAATA-----TTATTAACCTCGAATTATCATTTACTAGT--CGATTAGATAGTAAATAGTTTGTAGT  
 V. procumbens TTAGAATTCGAATA-----TTATTAACCTCGAATTATCATTTACTAGT--CGATTAGATAGTAAATAGTTTGTAGT  
 M. pinatubensis -----TTATTAATTCGAATTATCATTTAGTATT--AGATTAAATAGGAAATAATTTTAGCT  
 W. coccinea -----TTATTAATTCGAATTATCATTTAGTATT--AGATTAGATAGTAAATAGTTTGTAGT

360

S. hierniana AGTTAAATTAGTTAAATTTTTCATTTTGAATTCAAA--TGACATTTGAAATT---TTTTTACACTTATAGT-----ATAT----  
 H. minutiflora 1 -----  
 H. minutiflora 2 -----  
 S. becquetii AGTTAAATTAGTTAAATTTTGCATTTTGAATTCAAA--TGACATTTGAAATT---TTTTTACACTTTTACACTT-----ATAGTATA  
 S. medusula AGTTAAATTAGTTAAATTTTTCATTTTGAATTCAAA--TGACATTTGAAATT---TTTTTACACTTATAGT-----ATAT----  
 S. mildbraedii AGTTAAATTAGTTAAATTTTTCATTTTGAATTCAAA--TGACATTTGAAATT---TTTTTACACTTATAGT-----ATAT----  
 S. nobilis AGTTAAATTAGTTAAATTTTTCATTTTGAATTCAAA--TGACATTTGAAATT---TTTTTACACTTATAGT-----ATAT----  
 S. aspera AGTTAAATTAGTTAAATTTTTCATTTTGAATTCAAA--TGACATTTGAAATT---TTTTTACACTTATAGT-----ATAT----  
 S. caminata AGTTAAATTAGTTAAATTTTTCATTTTGAATTCAAA--TGACATTTGAAATT---TTTTTACACTTATAGT-----ATAT----  
 S. mexicana AGTTAAATTAGTTAAATTTTTCATTTTGAATTCAAA--ATGACATTTGAAATT---TTTTTACACTTATAGT-----ATAT----  
 S. venosa AGTTAAATTAGTTAAATTTTTCATTTTGAATTCAAA--TGACATTTGAAATT---TTTTTACACTTATAGT-----ATAT----  
 S. xanthotricha AGTTAAATTAGTTAAATTTTTCATTTTGAATTCAAA--TGACATTTGAAATT---TTTTTACACTTATAGT-----ATAT----  
 S. hirsutum AGTTAAATTAGTTAAATTTTTCATTTTGAATTCAAA--TGACATTTGAAATT---TTTTTACACTTATAGT-----ATAT----  
 S. elliptica AGTTAAATTAGTTAAATTTTTCATTTTGAATTCAAA--TGACATTTGAAATT---TTTTTACACTTTTTCACACTT---ATAGTATA  
 T. capsulifera AATTAATTTAGTTAAATTTTTCATTTTGAATTCAAA--TGACATTTGAAATT---TTTTTCCACTTTTCTTACACTAATCTTATAG--TA  
 V. angustifolia -----  
 V. belingana AATTAATTTAGTTCCATTTTTCATTTTGAATTCAAA--TGACATTTGAAATT---TTTTTACACTTATAGT-----ATAT----  
 V. herbacoursi -----TTTTTGAATTCAAA--TGATATTTGAAATT---TTTTTACACTTATAGT-----ATAT----  
 V. major AATTAATTTAGTTCCATTTTTCATTTTGAATTCAAA--TAACATTTGAAATT---TTTTTACACTTATAGT-----ATAT----  
 V. multiflora AATTAATTTAGTTAAATTTTGCATTTTGAATTCAAA--TGATATTTGAAATT---TTTTTACACTTATAGT-----ATAGTATA  
 V. procumbens AATTAATTTAGTTCCATTTTTCATTTTGAATTCAAA--TGACATTTGAAATT---TTTTTACACTTATAGT-----ATAT----  
 M. pinatubensis AGTTAAATTAGTTCAATTTTTCATTTTGAATTCAAA--TGACATTTGAAATT---TTTTTACACTTTTTCACACTT---ATAT--ATT  
 W. coccinea AGTTAAATTAGTTCAATTTTTCACACTTTTGAATTC--AA--ATGACATTTGAAATTCTTTTTCACACTTC-----TATTATA

450

S. hierniana -ATATTTTT-ATACTATTTGATTTCTATATCATAATCATATATTTCTAATTAATTTAGGA-----ATGATTAGTTCTAACTAATG  
 H. minutiflora 1 -----  
 H. minutiflora 2 -----  
 S. becquetii TATATTTTT-ATACTATTTGATTTCTATATCATAATCATATATTTCTAATTAATTTAGGA-----ATGATTAGTTCTAACTAATG  
 S. medusula -ATATTTTT-ATACTATTTGATTTCTATATCATAATCATATATTTCTAATTAATTTAGGA-----ATGATTAGTTCTAACTAATG  
 S. mildbraedii -ATATTTTT-ATACTATTTGATTTCTATATCATAATCATATATTTCTAATTAATTTAGGA-----ATGATTAGTTCTAACTAATG  
 S. nobilis -ATATTTTT-ATACTATTTGATTTCTATATCATAATCATATATTTCTAATTAATTTAGGA-----ATGATTAGTTCTAACTAATG  
 S. aspera -ATATTTTT-ATACTATTTGATTTCTATATCATAATCATATATTTCTAATTAATTTAGGA-----ATGATTAGTTCTAACTAATG

S. caminata -ATATTTTT-ATACTATTTGATCTATATCATAATCATATATTTCTAATTAATAGGA-----ATGATTAGTTCTAACTAATG  
 S. mexicana -ATATTTTT-ATACTATTTGATCTATATCATAATCATATATTTCTAATTAATAGGA-----ATGATTAGTTCTAACTAATG  
 S. venosa -ATATTTTT-ATACTATTTGATCTATATCATAATCATATATTTCTAATTAATAGGA-----ATGATTAGTTCTAACTAATG  
 S. xanthotricha -ATATTTTT-ATACTATTTGATCTATATCATAATCATATATTTCTAATTAATAGGA-----ATGATTAGTTCTAACTAATG  
 S. hirsutum -ATATTTTT-ATACTATTTGATCTATATCATAATCATATATTTCTAATTAATAGGATTAATAGGAATGATTAGTTCTAACTAATG  
 S. elliptica TATATTTTT-ATACTATTTGATCTATATCATAATCATATATTTCTAATTAATAGGA-----ATGATTAGTTCTAACTAATG  
 T. capsulifera TATATTTTT-ATACTATTTGATCTATATCATAATCATATATATCT-----AATTAGGA-----ATGATTAGTTCTAACTAATG  
 V. angustifolia -----TTAGTTCTAACTAATA  
 V. belingana -ATATTTTT-ATACTATTTGATCTATATCATAATCATATATTTTG-----AATTAGGA-----ATGATTAGTTCTAACTAATA  
 V. herbacoursi -ATATTTTT-ATACTATTTGATCTATATCATAATCATATATTTTG-----AATTAGGA-----ATGATTAGTTCTAACTAATA  
 V. major -ATATTTTT-ATACTATTTGATCTATATCATAATCATATATTTTG-----AATTAGGA-----ATGATTAGTTCTAACTAATA  
 V. multiflora TATATTTTT-ATACTATTTGATCTATATCATAATCATATATTTTG-----AATTAGGA-----ATGATTAGTTCTAACTAATA  
 V. procumbens -ATATTTTT-ATACTATTTGATCTATATCATAATCATATATTTTG-----AATTAGGAC-----TGATTAGTTCTAACTAATA  
 M. pinatubensis TCATTATTTTGAATTATTTGATCTATATCATAATCATATATTTCT-----AATTAGGA-----ATAATTAGTTCTAACTAATG  
 W. coccinea TATATT---TATATTACTTGATCTATATCATAATCATATATTTCT-----AATTAGGA-----ATGATTAGTTCTAACTAATG

540

S. hierniana AGACATTCTCCGCTTTCATTCATAAAG-----ATGTAATGTAATAGTAAAGGCGGAAATTTAGACGACAAAAAAGAATCGACCGTT  
 H. minutiflora 1 -----  
 H. minutiflora 2 -----  
 S. becquetii AGACATTCTCCGCTTTCATTCATAAAG-----ATGTAATGTAATAGTAAAGGCGGAAATTTAGACGACAAAAAAGAATCGACCGTT  
 S. medusula AGACATTCTCCGCTTTCATTCATAAAG-----ATGTAATGTAATAGTAAAGGCGGAAATTTAGACGACAAAAAAGAATCGACCGTT  
 S. mildbraedii AGACATTCTCCGCTTTCATTCATAAAG-----ATGTAATGTAATAGTAAAGGCGGAAATTTAGACGACAAAAAAGAATCGACCGTT  
 S. nobilis AGACATTCTCCGCTTTCATTCATAAAG-----ATGTAATGTAATAGTAAAGGCGGAAATTTAGACGACAAAAAAGAATCGACCGTT  
 S. aspera AGACATTCTCCGCTTTCATTCATAAAG-----ATGTAATGTAATAGTAAAGGCGGAAATTTAGACGACAAAAAAGAATCGACCGTT  
 S. caminata AGACATTCTCCGCTTTCATTCATAAAG-----ATGTAATGTAATAGTAAAGGCGGAAATTTAGACGACAAAAAAGAATCGACCGTT  
 S. mexicana AGACATTCTCCGCTTTCATTCATAAAG-----ATGTAATGTAATAGTAAAGGCGGAAATTTAGACGACAAAAAAGAATCGACCGTT  
 S. venosa AGACATTCTCCGCTTTCATTCATAAAG-----ATGTAATGTAATAGTAAAGGCGGAAATTTAGACGACAAAAAAGAATCGACCGTT  
 S. xanthotricha AGACATTCTCCGCTTTCATTCATAAAG-----ATGTAATGTAATAGTAAAGGCGGAAATTTAGACGACAAAAAAGAATCGACCGTT  
 S. hirsutum AGACATTCTCCGCTTTCATTCATAAAG-----ATGTAATGTAATAGTAAAGGCGGAAATTTAGACGACAAAAAAGAATCGACCGTT  
 S. elliptica AGACATTCTCCGCTTTCATTCATAAAG-----ATGTAATGTAATAGTAAAGGCGGAAATTTAGACGACAAAAAAGAATCGACCGTT  
 T. capsulifera AGACATTCTCCGCTTTCATTCATAAAG-----ATGTAATGTAATAGTAAAGGCGGAAATTTAGACGACAAAAAAGAATCGACCGTT  
 V. angustifolia AGACATTCTCCGCTTTCAGTCATAAAGCATATAGATGTAATGTAATAGTAAAGGCGGAAATTAAGACGACAAAAAAGAATCGACCGTT  
 V. belingana AGACATTCTCCGCTTTCAGTCATAAAGCATATAAGATGTAATGTAATAGTAAAGGCGGAAATTAAGACGACAAAAAAGAATCGACCGTT  
 V. herbacoursi AGACATTCTCCGCTTTCAGTCATAAAGCATATAAGGTGTAATGTAATAGTAAAGGCGGAAATTAAGACGACAAAAAAGAATCGACCGTT  
 V. major AGACATTCTCCGCTTTCAGTCATAAAGCATATAAGGTGTAATGTAATAGTAAAGGCGGAAATTAAGACGACAAAAAAGAATCGACCGTT  
 V. multiflora AGACATTCTCCGCTTTCATTCATAAAGCATATAAGGTGTAATGTAATAGTAAAGGCGGAAATTAAGACGACAAAAAAGAATCGACCGTT  
 V. procumbens AGACATTCTCCGCTTTCAGTCATAAAGCATATAAGATGTAATGTAATAGTAAAGGCGGAAATTAAGACGACAAAAAAGAATCGACCGTT  
 M. pinatubensis AGACATTCTCCGCTTTCATTCATAAAG-----ATATGATGTAATAGTAAAGGCGGAAATTAAGACGACAAAAAATA-GAATCGACCGTT  
 W. coccinea AGACATTCTCCGCTTTCATTCATAAAG-----ATGTAATATAAATAGTAAAGGCGGAAATTAAGATGACAAAAAAGAATCGACCGTT

630

S. hierniana CAAGTATTCAAAATTGTATCGGAAAGCTGACAGGGAGATATATATCTAAGATATATATCCCTCTATATTGAATTGCGGATACGGAAAT  
 H. minutiflora 1 -----  
 H. minutiflora 2 -----  
 S. becquetii CAAGTATTCAAAATTGTATCGGAAAGCTGACAGGGAGATATATATCTAAGATATATATCCCTCTATATTGAATTGCGGATACGGAAAT  
 S. medusula CAAGTATTCAAAATTGTATCGGAAAGCTGACAGGGAGATATATATCTAAGATATATATCCCTCTATATTGAATTGCGGATACGGAAAT  
 S. mildbraedii CAAGTATTCAAAATTGTATCGGAAAGCTGACAGGGAGATATATATCTAAGATATATATCCCTCTATATTGAATTGCGGATACGGAAAT  
 S. nobilis CAAGTATTCAAAATTGTATCGGAAAGCTGACAGGGAGATATATATCTAAGATATATATCCCTCTATATTGAATTGCGGATACGGAAAT  
 S. aspera CAAGTATTCAAAATTGTATCGGAAAGCTGACAGGGAGATATATATCTAAGATATATATCCCTCTATATTGAATTGCGGATACGGAAAT  
 S. caminata CAAGTATTCAAAATTGTATCGGAAAGCTGACAGGGAGATATATATCTAAGATATATATCCCTCTATATTGAATTGCGGATACGGAAAT  
 S. mexicana CAAGTATTCAAAATTGTATCGGAAAGCTGACAGGGAGATATATATCTAAGATATATATCCCTCTATATTGAATTGCGGATACGGAAAT  
 S. venosa CAAGTATTCAAAATTGTATCGGAAAGCTGACAGGGAGATATATATCTAAGATATATATCCCTCTATATTGAATTGCGGATACGGAAAT  
 S. xanthotricha CAAGTATTCAAAATTGTATCGGAAAGCTGACAGGGAGATATATATCTAAGATATATATCCCTCTATATTGAATTGCGGATACGGAAAT  
 S. hirsutum CAAGTATTCAAAATTGTATCGGAAAGCTGACAGGGAGATATATATCTAAGATATATATCCCTCTATATTGAATTGCGGATACGGAAAT  
 S. elliptica CAAGTATTCAAAATTGTATCGGAAAGCTGACAGGGAGATATATATCTAAGATATATATCCCTCTATATTGAATTGCGGATACGGAAAT  
 T. capsulifera CAAGTATTCAAAATTGCATCGGAAAGCTAACAGGGAGATATATATCTAAGATATATATCCATCTATATTGAATTGCGGATACGGAAAT  
 V. angustifolia CAAGTATTCAAAATTGCATCGGAAAGCTAACAGGGAGATATATATCTAAGATATATATCCATCTATATTGAATTGCGGATACGGAAAT  
 V. belingana CAAGTATTCAAAATTGCATCGGAAAGCTAACAGGGAGATATATATCTAAGATATATATCCATCTATATTGAATTGCGGATACGGAAAT  
 V. herbacoursi CAAGTATTCAAAATTGCATCGGAAAGCTAACAGGGAGATATATATCTAAGATATATATCCATCTATATTGAATTGCGGATACGGAAAT  
 V. major CAAGTATTCAAAATTGCATCGGAAAGCTAACAGGGAGATATATATCTAAGATATATATCCATCTATATTGAATTGCGGATACGGAAAT  
 V. multiflora CAAGTATTCAAAATTGCATCGGAAAGCTAACAGGGAGATATATATCTAAGATATATATCCATCTATATTGAATTGCGGATACGGAAAT  
 V. procumbens CAAGTATTCAAAATTGCATCGGAAAGCTAACAGGGAGATATATATCTAAGATATATATCCATCTATATTGAATTGCGGATACGGAAAT  
 M. pinatubensis CAAGTATTCAAAATTGCATCGGAAAGCTGAAAGGGAGATATATATATAAAGATATATATCCCTCTATATTGAATTGCGGATACGGAAAT  
 W. coccinea CAAGTATTCAAAATTGCATCGGAAAGCTGACAGGGAGATATATATCT-T-AGATATATATTCATCTATATTGAATTGCGGATACGAGAAAT

720

S. hierniana GATAAAATCATATTGGATTGGACCAAATAGAAAT-AGGGGTCTCCTCTATAGAAGATAA-GTAAGAAAT-CAAAGAAAAGAAAACAGTTT  
 H. minutiflora 1 -----  
 H. minutiflora 2 -----  
 S. becquetii GATAAAATCATATTGGATTGGACCAAATAGAAAT-AGGGGTCTCCTCTATAGAAGATAA-GTAAGAAAT-CAAAGAAAAGAAAACCGTTT  
 S. medusula GATAAAATCATATTGGATTGGACCAAATAGAAAT-AGGGGTCTCCTCTATAGAAGATAA-GTAAGAAAT-CAAAGAAAAGAAAACAGTTT  
 S. mildbraedii GATAAAATCATATTGGATTGGACCAAATAGAAAT-AGGGGTCTCCTCTATAGAAGATAA-GTAAGAAAT-CAAAGAAAAGAAAACAGTTT  
 S. nobilis GATAAAATCATATTGGATTGGACCAAATAGAAAT-AGGGGTCTCCTCTATAGAAGATAA-GTAAGAAAT-CAAAGAAAAGAAAACAGTTT  
 S. aspera GATAAAATCATATTGGATTGGACCAAATAGAAAT-AGGGGTCTCCTCTATAGAAGATAA-GTAAGAAAG-CAAAGAAAACA---G---TTT  
 S. caminata GATAAAATCATATTGGATTGGACCAAATAGAAAT-AGGGGTCTCCTCTATAGAAGATAA-GTAAGAAAT-CAAAGAAAACA---G---TTT  
 S. mexicana GATAAAATCATATTGGATTGGACCAAATAGAAAT-AGGGGTCTCCTCTATAGAAGATAA-GTAGGAAAT-CAAAGAAAACA---G---TTT  
 S. venosa GATAAAATCATATTGGATTGGACCAAATAGAAAT-AGGGGTCTCCTCTATAGAAGATAA-GTAGGAAAT-CAAAGAAAACA---G---TTT  
 S. xanthotricha GATAAAATCATATTGGATTGGACCAAATAGAAAT-AGGGGTCTCCTCTATAGAAGATAA-GTAAGAAAT-CAAAGAAAAGAAAACAGTTT

S. hirsutum GATAAAATCATATTGGATTGGACCAAAATAGAAAT-AGGGGTCTCCTCTATAGAAGATAA-GTAAGAAAT-CAAAGAAAAGAAAACAGTTT  
 S. elliptica GATAAAATCATATTGGATTGGACCAAAATAGAAAT-AGGGGTCTCCTCTATAGAAGATAA-GTAAGAAAT-CAAAGAAAAGAAAACAGTTT  
 T. capsulifera GATAAAATCATATTGGATTGGACCAAAATAGG-----GGTCTCCTC--TAGAAGATAA-GTAAGAAAT-GAAAGAAAAGAAAACAGTTT  
 V. angustifolia GATAAAATCATATTGGATTGGACCAAGATAGG-----GGTCTCCTCTATAGAGGATAA-GTAAGAAAG-CAAAGAAAAGAAAACCGTTT  
 V. belingana GATAAAATCATATTGGATTGGACCAAGATAGG-----GGTCTCCTCTATAGAGGATAA-GTAAGAAAG-CAAAGAAAAGAAAACCGTTT  
 V. herbacoursi GATAAAATCATATTGGATTGGACCAAGATAGG-----GGTCTCCTCTATAGAGGATAA-GTAAGAAAG-CAAAGAAAAGAAAACCGTTT  
 V. major GATAAAATCATATTGGATTGGACCAAGATAGG-----GGTCTCCTCTATAGAGGATAA-GTAAGAAAG-CAAAGAAAAGAAAACCGTTT  
 V. multiflora GATAAAATCATATTGGATTGGACCAAGATAGG-----GGTCTCCTCTATAGAGGATAA-GTAAGAAAG-CAAAGAAAAGAAAACCGTTT  
 V. procumbens GATAAAATCATATTGGATTGGACCAAGATAGG-----GGTCTCCTCTATAGAGGATAA-GTAAGAAAG-CAAAGAAAAGAAAACCGTTT  
 M. pinatubensis GATAAAATCATATTGGATTGGACCAAAATAGG-----GGTCTCCT--ATAGAAGATAG-GTAAGAAAT-CAAAGAAAACAAAAGACTTT  
 W. coccinea GATAAAATCATATTGGAGTGGACCAAAATAGG-----GGTCTCCT--ATAGTAGATAG-GTAAGAAAT-----CAAAAAAACACTTT

810

S. hierniana TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 H. minutiflora 1 -----  
 H. minutiflora 2 -----  
 S. becquetii TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 S. medusula TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 S. mildbraedii TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACAAGATGAAATCCTAAT  
 S. nobilis TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 S. aspera TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 S. caminata TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 S. mexicana TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 S. venosa TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 S. xanthotricha TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 S. hirsutum TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 S. elliptica TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 T. capsulifera TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 V. angustifolia TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 V. belingana TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 V. herbacoursi TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 V. major TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 V. multiflora TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 V. procumbens TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 M. pinatubensis TTTCGAGATAGGAATCGGTATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT  
 W. coccinea TTTCGAGATAGGAATCAATATCTAATGAATTCACAATTTTCAGTATAAATGAAAG-AAAAAAGAACCACGATCACA-ATGAAATCCTAAT

trnL gene



900

S. hierniana CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 H. minutiflora 1 -----  
 H. minutiflora 2 -----  
 S. becquetii CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 S. medusula CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 S. mildbraedii CTCAAAACAAAAN-----NNNNNNNN--NNNNNNCGAAATCGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 S. nobilis CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 S. aspera CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 S. caminata CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 S. mexicana CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 S. venosa CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 S. xanthotricha CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 S. hirsutum CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 S. elliptica CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 T. capsulifera CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 V. angustifolia CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 V. belingana CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 V. herbacoursi CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 V. major CTCAAAACAAAAGAAAAGGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 V. multiflora CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 V. procumbens CTCAAAACAAAAGAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 M. pinatubensis CTCAAAACAAA-----GGAAGGGG--ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA  
 W. coccinea CTCAAAACAAA-----GGAAGGGGG-ATATGGCGAAATTTGGTAGACGCTACGGACTTAATTGG-ATTGGGCCTTGGTATGGAAA

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S. hierniana CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCCTGGAATTAATAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCCAAA  
 H. minutiflora 1 CCCACTAAGTGATAACTTTCAA- TTCAGAGAAACCCCTGGAATTAATAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCCAAA  
 H. minutiflora 2 CCCCTAAGTGATAACTTTCAAATTCAGAGAAACCCCTGGAATTAATAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCCAAA  
 S. becquetii CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCCTGGAATTAATAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCCAAA  
 S. medusula CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCCTGGAATTAATAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCCAAA  
 S. mildbraedii CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCCTGGAATTAATAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCCAAA  
 S. nobilis CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCCTGGAATTAATAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCCAAA  
 S. aspera CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCCTGGAATTAATAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCCAAA  
 S. caminata CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCCTGGAATTAATAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCCAAA  
 S. mexicana CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCCTGGAATTAATAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCCAAA  
 S. venosa CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCCTGGAATTAATAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCCAAA  
 S. xanthotricha CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCCTGGAATTAATAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCCAAA  
 S. hirsutum CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCCTGGAATTAATAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCCAAA  
 S. elliptica CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCCTGGAATTAATAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCCAAA  
 T. capsulifera CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCCTGGAATTAATAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCCAAA  
 V. angustifolia CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCCTGGAATTAATAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCCAAA

V. belingana CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCTGGAATTAATAAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCAA  
 V. herbacoursi CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCTGGAATTAATAAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCAA  
 V. major CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCTGGAATTAATAAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCAA  
 V. multiflora CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCTGGAATTAATAAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCAA  
 V. procumbens CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCTGGAATTAATAAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCAA  
 M. pinatubensis CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCTGGAATTAATAAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCAA  
 W. coccinea CCCACTAAGTGATAACTTTCAAATTCAGAGAAACCCTGGAATTAATAAAAAAGGGGCAATCCTGAGCCAAATCCTGTTTTCCGAAACCAA

1080

S. hierniana GGTTC---AAAGTGTGAAA---GGGATAGGTGCAGAGAC-----  
 H. minutiflora 1 GGTTC-----AAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAATACAATGGAGTTGACTGCGTTAGT  
 H. minutiflora 2 GGTTC-----AAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAATACAATGGAGTTGACTGCGTTAGT  
 S. becquetii GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGCGTTAGT  
 S. medusula GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGCGTTAGT  
 S. mildbraedii GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGCGTTAGT  
 S. nobilis GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGCGTTAGT  
 S. aspera GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGAGTTAGT  
 S. caminata GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGAGTTAGT  
 S. mexicana GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGAGTTAGT  
 S. venosa GGTTCAG---AAAGTGAAAA-----  
 S. xanthotricha GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGCGTTAGT  
 S. hirsutum GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGCGTTAGT  
 S. elliptica GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGCGTTAGT  
 T. capsulifera GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGCGTTAGT  
 V. angustifolia GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGCGTTAGT  
 V. belingana GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGCGTTAGT  
 V. herbacoursi GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGCGTTAGT  
 V. major GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGCGTTAGT  
 V. multiflora GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGCGTTAGT  
 V. procumbens GGTTCAG---AAAGTGAAAA---GGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGACTGCGTTAGT  
 M. pinatubensis GGTTCGAAACAAAGTGAAAAAAGGGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGGCTGCGTTAGT  
 W. coccinea GGTTC---AGAAAGTGAAAAA---GGATAGGTGCAGAGACTCAACGGAAGCTGTTCTAACAAAT-----GGAGTTGGCTGCGTTAGT

1170

S. hierniana -----  
 H. minutiflora 1 AGAAAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGTGAAGGATAAAACAAACGTATGTACAGACGTATTGAATACTATAT  
 H. minutiflora 2 AGAAAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGTGAAGGATAAAACAAACGTATGTACAGACGTATTGAATACTATAT  
 S. becquetii AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGTGAAGGATAAAACG---TATGTACATACGTATTGAATACTATAT  
 S. medusula AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGTGAAGGATAAAACG---TATGTACATACGTATTGAATACTATAT  
 S. mildbraedii AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGTGAAGGATAAAACG---TATGTACATACGTATTGAATACTATAT  
 S. nobilis AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGTGAAGGATAAAACG---TATGTACATACGTATTGAATACTATAT  
 S. aspera AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGTGAAGGATAAAACG---TATGTACATACGTATTGAATACTATAT  
 S. caminata AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGTGAAGGATAAAACG---TATGTACATACGTATTGAATACTATAT  
 S. mexicana AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGTGAAGGATAAAACG---TATGTACATACGTATTGAATACTATAT  
 S. venosa -----  
 S. xanthotricha AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGTGAAGGATAAAACG---TATGTACATACGTATTGAATACTATAT  
 S. hirsutum AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGTGAAGGATAAAACG---TATGTACATACGTATTGAATACTATAT  
 S. elliptica AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGTGAAGGATAAAACG---TATGTACATACGTATTGAATACTATAT  
 T. capsulifera AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGTGAAGGATAAAACG---TATGTACATACGTATTGAATACTATAT  
 V. angustifolia AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGGGAAGGATAAAACG---TATGTACATACGTAGTGAATACTCTAT  
 V. belingana AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGGGAAGGATAAAACG---TATGTACATACGTAGTGAATACTCTAT  
 V. herbacoursi AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGGGAAGGATAAAACG---TATGTACATACGTAGTGAATACTCTAT  
 V. major AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGGGAAGGATAAAACG---TATGTACATACGTAGTGAATACTCTAT  
 V. multiflora AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGTGAAGGATAAAACG---TATGTACATACGTAGTGAATACTCTAT  
 V. procumbens AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGGGAAGGATAAAACG---TATGTACATACGTAGTGAATACTCTAT  
 M. pinatubensis AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GATAAAGTGAAGGATAAAACG---TATGTACATACGTAGTGAATACTCTAT  
 W. coccinea AGAGAAATCTTTCCATCGAAAAATTCAGAAAAG-----GGATAAAGTGAAGGATAAAAC---GTATATACATACGTATTGAATACTATAT

1260

S. hierniana -----  
 H. minutiflora 1 CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTA----TATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 H. minutiflora 2 CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTA----TATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 S. becquetii CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTA----TATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 S. medusula CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTA----TATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 S. mildbraedii CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTA----TATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 S. nobilis CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTA----TATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 S. aspera CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTTT-ATATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 S. caminata CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTTT-ATATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 S. mexicana CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTTT-ATATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 S. venosa -----  
 S. xanthotricha CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTA----TATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 S. hirsutum CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTTTTTTATATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 S. elliptica CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTA----TATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 T. capsulifera CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTTT-ATATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 V. angustifolia CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTA----TATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 V. belingana CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTA----TATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 V. herbacoursi CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTA----TATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 V. major CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTA----TATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
 V. multiflora CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTA----TATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA

V. procumbens CAAATGATTAATGACGACTCGACTGAATCTGTATTTTTTTA-----TATGAAAAACGGAAGAATTGGTGTGACTAGATTCCACATTGAAGA  
M. pinatubensis CAAATGATTAATGACCCTCGGCTGAATCTGTATTTTTTTT----ATATGAAAAACGGAAGAATTGGTGTGAAATAGATTCCACATTGAAGA  
W. coccinea CAAATGATTAATGACAACCCGGCTGAATCTGTATTTTTTTTTT--ATATGAAAAACGGAAGAATTGGTGTGAAATAGATTCCACATTGAAGA

1350

S. hierniana -----  
H. minutiflora 1 AAGAATCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
H. minutiflora 2 AAGAATCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
S. becquetii AAGAATCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
S. medusula AAGAGTCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
S. mildbraedii AAGAATCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
S. nobilis AAGA-TCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
S. aspera AAGAATCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
S. caminata AAGAATCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
S. mexicana AAGAATCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGAATCTTTTCAAGAA-----  
S. venosa -----  
S. xanthotricha AAGAATCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
S. hirsutum AAGAATCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
S. elliptica AAGAATCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
T. capsulifera AAGAATCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
V. angustifolia A-GAATCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
V. belingana A-GAGTCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
V. herbacoursi A-GAATCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
V. major A-GAATCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
V. multiflora A-GAATCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
V. procumbens A-GAATCGAATATTTATTGATCAAATGATTCCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGACGA-----  
M. pinatubensis AAAAAATCGAACATTCATTGATCAAATGATTCCTCAGAGTCTGATAGATCGTTTCAAGAACGGATTAATCGGACGA-----  
W. coccinea AAGAATCGTATATTCATTGATCAAATGATTAACCTCATAGTCTGATAGATCTTTTCAAGAACGGATTAATCGGTCGA-----

1440

S. hierniana -----  
H. minutiflora 1 -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
H. minutiflora 2 -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
S. becquetii -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
S. medusula -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
S. mildbraedii -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
S. nobilis -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
S. aspera -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
S. caminata -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
S. mexicana CGGATTAATCGGACGAGAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
S. venosa -----  
S. xanthotricha -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
S. hirsutum -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
S. elliptica -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
T. capsulifera -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
V. angustifolia -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
V. belingana -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
V. herbacoursi -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
V. major -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
V. multiflora -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
V. procumbens -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
M. pinatubensis -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAATTTATAGTAAGAGGAAAAATCCGTCG  
W. coccinea -----GAATAAAGATAGAGTCCCGTTCTACATGTCAATGTCGGCAACAATGAAACTTATAGTAAGAGGAAAAATCCGTCG

**trnL-F**



1530

S. hierniana -----  
H. minutiflora 1 ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCAACTATTTATCCTATCTCTTCTCGTTAGC  
H. minutiflora 2 ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCAACTATTTATCCTATCTCTTCTCGTTAGC  
S. becquetii ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCAACTATTTATCCTATCTCTTCTCGTTAGC  
S. medusula ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCAACTATTTATCCTATCTCTTCTCGTTAGC  
S. mildbraedii ACTTTAAGAATCG-----AAGCCTATTTGACTTCCCAACTATTTATCCTATCTCTTCTCGTTAGC  
S. nobilis ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCAACTATTTATCCTATCTCTTCTCGTTAGC  
S. aspera ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCAACTATTTATCCTATCTCTTCTCGTTAGC  
S. caminata ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCAACTATTTATCCTATCTCTTCTCGTTAGC  
S. mexicana ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCAACTATTTATCCTATCTCTTCTCGTTAGC  
S. venosa -----  
S. xanthotricha ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCAACTATTTATCCTATCTCTTCTCGTTAGC  
S. hirsutum ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCAACTATTTATCCTATCTCTTCTCGTTAGC  
S. elliptica ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCAACTATTTATCCTATCTCTTCTCGTTAGC  
T. capsulifera ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCAACTATTTATCCTATCTCTTCTCGTTAGC  
V. angustifolia ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCTCAACTATTTATCCTATCTCTTCTCGTTAGC  
V. belingana ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCTCAACTATTTATCCTATCTCTTCTCGTTAGC  
V. herbacoursi ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCTCAACTATTTATCCTATCTCTTCTCGTTAGC  
V. major ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCTCAACTATTTATCCTATCTCTTCTCGTTAGC  
V. multiflora ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCTCAACTATTTATCCTATCTCTTCTCGTTAGC  
V. procumbens ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCTCAACTATTTATCCTATCTCTTCTCGTTAGC  
M. pinatubensis ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCCTATTTGACTTCCCAA--TATTTATCCTATCTCTTCTAGTTAGC  
W. coccinea ACTTTAAAAATCGTGAGGGTTCAAGTCCCTCTATCCCCAAAAAGCATATTTGACTTCCCAACTATTTATCCTATCTCTTCTCGTTAGC



1620

S. hierniana -----  
H. minutiflora 1 GGTTCAAAATCCCTTATTCATTCACTCTATTCTCTTAGAAATCGATCGGGACGGAATGCCCTTTTCTT-----ATCACAAAGTC-----TA  
H. minutiflora 2 GGTTCAAAATCCCTTATTCATTCACTCTATTCTCTTAGAAATCGATCGGGACGGAATGCCCTTTTCTT-----ATCACAAAGTC-----TA  
S. becquetii GGTTCAAAATCCCTTATTCATTCACTCTATTCTCTTAGAAATCGATCGGGACGGAATGCCCTTTTCTT-----ATCACAAAGTC-----TA  
S. medusula GGTTCAAAATCCCTTATTCATTCACTCTATTCTCTTAGAAATCGATCGGGACGGAATGCCCTTTTCTT-----ATCACAAAGTC-----TA  
S. mildbraedii GGTTCAAAATCCCTTATTCATTCACTCTATTCTCTTAGAAATCGATCGGGACGGAATGCCCTTTTCTT-----ATCACAAAGTC-----TA  
S. nobilis GGTTCAAAATCCCTTATTCATTCACTCTATTCTCTTAGAAATCGATCGGGACGGAATGCCCTTTTCTT-----ATCACAAAGTC-----A  
S. aspera GGTTCAAAATCCCTTATTCATTCACTCTATTCTCTTAGAAATCGATCGGGACGGAATGCCCTTTTCTT-----ATCACAAAGTC-----TA  
S. caminata GGTTCAAAATCCCTTATTCATTCACTCTATTCTCTTAGAAATCGATCGGGACGGAATGCCCTTTTCTT-----ATCACAAAGTC-----TA  
S. mexicana GGTTCAAAATCCCTTATTCATTCACTCTATTCTCTTAGAAATCGATCGGGACGGAATGCCCTTTTCTT-----ATCACAAAGTC-----TA  
S. venosa -----  
S. xanthotricha GGTTCAAAATCCCTTATTCATTCACTCTATTCTCTTAGAAATCGATCGGGACGGAATGCCCTTTTCTT-----ATCACAAAGTC-----TA  
S. hirsutum GGTTCAAAATCCCTTATTCATTCACTCTATTCTCTTAGAAATCGATCGGGACGGAATGCCCTTTTCTT-----ATCACAAAGTC-----TA  
S. elliptica GGTTCAAAATCCCTTATTCATTCACTCTATTCTCTTAGAAATCGATCGGGACGGAATGCCCTTTTCTT-----ATCACAAAGTC-----TA  
T. capsulifera GGTTCAAAATCCCTTATTCATTCACTCTATTCTCTTAGAAATCGATCGGGACGGAATGCCCTTTTCTT-----ATCACAAAGTC-----TA  
V. angustifolia GGTTGAAAATCCCTTATTCATTCACTTTATTCTCTTAGAAATCGATCGGGACGGAACGCCCTTTTCTT-----ATCACAAAGTC-----TA  
V. belingana GGTTGAAAATCCCTTATTCATTCACTTTTCTCTTAGAAATCGATCGGGACGGAACGCCCTTTTCTT-----ATCACAAAGTC-----TA  
V. herbacoursi GGTTGAAAATCCCTTATTCATTCACTTTATTCTCTTAGAAATCGATCGGGACGGAACGCCCTTTTCTT-----ATCACAAAGTC-----TA  
V. major GGTTGAAAATCCCTTATTCATTCACTTTATTCTCTTAGAAATCGATCGGGACGGAACGCCCTTTTCTT-----ATCACAAAGTC-----A  
V. multiflora AGTTCAAAATCCCTTATTTATTCACTTTATTCTCTTAGAAATCGATCGGGACGGAACGCCCTTTTCTT-----ATCACAAAGTC-----TA  
V. procumbens GGTTGAAAATCCCTTATTCATTCACTTTATTCTCTTAGAAATCGATCGGGACGGAACGCCCTTTTCTT-----ATCACAAAGTC-----TA  
M. pinatubensis GGTTCAAAATCCCTTATTCATTCACTCTATTCTCTTAGAAAGAGATCTGGACGGAATGATCTTTTCTT-----ATCACAAAGTCAGTCTT  
W. coccinea GGTTCAAAATACCTTATTCATTCACTCTATTCTCTTAGAAATCGATCTGGACGGAATGCCCTTTTCTT-----ATCACAAAGTC-----TT

1710

S. hierniana -----  
H. minutiflora 1 TCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
H. minutiflora 2 TCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
S. becquetii GCGTTCATATGATATACATACAAAATCCCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
S. medusula GCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
S. mildbraedii GCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
S. nobilis GCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
S. aspera GCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
S. caminata GCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
S. mexicana GCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
S. venosa -----  
S. xanthotricha GCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
S. hirsutum GCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
S. elliptica GCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
T. capsulifera GCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
V. angustifolia GCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
V. belingana GCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
V. herbacoursi GCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
V. major GCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
V. multiflora GCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTAAATCGATAGAATACTACTCATACTGA  
V. procumbens GCGTTCATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATAGAATACTACTCATACTGA  
M. pinatubensis GTGTTATATGATATACATACAAAATTGAACATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA  
W. coccinea GTGTTATATGATATACATAGAACTGAACATCTTTGAGCAAGAAATCCCATTTGAATGATTTACAATCGATATAAATACTACTCATACTGA

1800

S. hierniana -----  
H. minutiflora 1 A-----GTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
H. minutiflora 2 A-----GTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
S. becquetii AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
S. medusula AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
S. mildbraedii AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
S. nobilis AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
S. aspera AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
S. caminata AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
S. mexicana AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
S. venosa -----  
S. xanthotricha A-CTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
S. hirsutum AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
S. elliptica AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
T. capsulifera AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
V. angustifolia AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATACAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
V. belingana AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
V. herbacoursi AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
V. major AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATACAGTACCTAGATAAAAAC-----CCCTTTCTTCTTTTAATTGACACAG  
V. multiflora AACTTCCAAAGTACTCTTTTTTAGATCCAAGAAATCCAGAAA-TAGAAAAAATTC-GAACCCCTTTCTTCTTTTAATTGACAAA-  
V. procumbens AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTCGGAACCCCTTTCTTCTTTTAATTGACACAG  
M. pinatubensis AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGATAAAAACCTTAGAATTCCTTTCTTCTTTTAATTGACATAG  
W. coccinea AACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCACTACCTAGATAAAAACCTTGAATCCACTTTCTTCTTTTAATTGACATAG

1810

S. hierniana -----  
H. minutiflora 1 ACCTCATTTT  
H. minutiflora 2 ACCTCATTTT

S. becquetii ACCCCATTTT  
 S. medusula ACCCCATTTT  
 S. mildbraedii ACCCCATTTT  
 S. nobilis ACCC-ATTT-  
 S. aspera ACCCCATTTT  
 S. caminata ACCCCATTTT  
 S. mexicana ACCCCATTTT  
 S. venosa -----  
 S. xanthotricha ACCCCATTTT  
 S. hirsutum ACCCCATTTT  
 S. elliptica ACCCCATTTT  
 T. capsulifera ACCCCATTTT  
 V. angustifolia ACCCCATTTT  
 V. belingana ACCCCATTTT  
 V. herbacoursi ACCCCATTTT  
 V. major ACCCCATTTT  
 V. multiflora --CCCATTTT  
 V. procumbens ACCCCATTTT  
 M. pinatubensis ACCCCATTTT  
 W. coccinea ACC-CATTTT

**Appendix 3. Aligned ETS, ITS, *rpoC1*, and *trnT-F* data matrices used in the combined ETS-ITS-*rpoC1-trnT-F* analysis (Chapter 6.2).**

**ETS Matrix (455 bp)**

90

H. minutiflora 2 ----CAGG-ATCAAACCAGGTAGCATTCTCACAGACACCAATGCCACTTAAGGACGGAAGACCGACACCTCAAAGCAACAATGGCAGTC  
 S. becquetii -----  
 S. xanthotricha -----  
 S. elliptica -----  
 T. capsulifera -----  
 V. angustifolia 1 -----CAGGTAGCATTCTCACAGACACCAATGCAACTCAAGGACGGAAGACCGACAC-TCGAAGAAGCAATGGCAGTC  
 V. belingana 1 --TTGCAGG-ATCAAAC-AGGTAGCATTCTCACAGACACCAACGCCACTCAAGGACGGAAGACCGACAC-TCGAAGAAGCGATGGAAGTC  
 V. belingana 2 -----CGCCACTCAAGGACGGAAGACCGACAC-TCGAAGAAGCGATGGAAGTC  
 V. belingana 3 -----GGACGGAAGACCGACAC-TCGAAGAAGCGATGGAAGTC  
 V. herbacoursi 1 --TGCAGG-ATCAAACCAGGTAGCATTCTCACAGACACCAATGCCACTTAAGGACGGAAGACCGACACCTCAAAGCAACAATGGCAGTC  
 V. herbacoursi 2 --TGCAGG-ATCAAACCAGGTAGCATTCTCACAGACACCAATGCCACTTAAGGACGGAAGACCGACAC-TCGAAGAAGCGATGGAAGTC  
 V. major 1 GGTGCAGG-ATCAA-C-AGGTAGCATTCTCACAGACACCAACGCCACTCAAGGACGGAAGACCGACAC-TCGAAGAAGCGATGGAAGTC  
 V. major 2 --TGCAGGTATCA-ACCAGGTAGCATTCTCACAGACACCAACGCCACTCAAGGACGGAAGACCGACAC-TCGAAGAAGCGATGGAAGTC  
 V. multiflora 1 -----CAGGTAGCATTCTCACAGACACCAATGCCACTGAAGGACGGAAGACCGACACCTCAAAGCAGCAATGGCAGTC  
 V. multiflora 2 -----CAGGTAGCATTCTCACAGACACCAATGCCACTGAAGGACGGAAGACCGACACCTCAAAGCAGCAATGGCAGTC  
 V. multiflora 3 -----CAGGTAGCATTCTCACAGACACCAATGCCACTGAAGGACGGAAGACCGACACCTCAAAGTAGCAATGGCAGTC  
 V. multiflora 4 -----CCAGGTAGCATTCTCACAGACACCAATGCCACTGAAGGACGGAAGACCGACACCTCAAAGCAGCAATGGCAGTC  
 V. procumbens 2 -----TTC-TC-C-G--ACCCATGC-ACTCATGGACGGAAGACCGACAC-TCGAAGAAGCAATGGCAGTC  
 V. procumbens 3 -----CAGGTAGCATTCTCACAGACACCAATGCCACTCAAGGACGGAAGACCGACAC-TCGAAGAAGCAATGGCAGTC  
 Virectaria sp. 1 -----CAGGTAGCATTCTCACAGACACCAATGCCACTCAAGGACGGAAGACCGACAC-TCGAAGAAGCAATGGCAGTC  
 Virectaria sp. 2 -GTGCAGT-ATCA-ACCAGGTAGCATTCTCACAGACACCAATGCCACTCAAGGACGGAAGACCGACAC-TCGAAGAAGCAATGGCAGTC

180

H. minutiflora 2 GTTCGGTAAAGAGTGATCAACACTCAGTTAAGCTAAACAGAGGTAGGCAACCTCATAGCCCC-ACAATATTCCACATCCCGGAGGACAAG  
 S. becquetii -----  
 S. xanthotricha -----  
 S. elliptica -----  
 T. capsulifera -----  
 V. angustifolia 1 GTTCGGTAAAGAGTGATCAACACTCGTTTCAGCCAAAGAGAGGTAGGCAACCTCATAGCCCC-ACAATATTCCGATCCCGGAGGACAAG  
 V. belingana 1 GTTCGGTAAAGAGTGATCAACACTCATTTTCGGCCAAAGAGAGGTAGGCAACCTCATAGCCCCACAATATTCCGATCCCGGAGGACAAG  
 V. belingana 2 GTTCGGTAAAGAGTGATCAACACTCATTTTCGGCCAAAGAGAGGTAGGCAACCTCATAGCCCCACAATATTCCGATCCCGGAGGACAAG  
 V. belingana 3 GTTCGGTAAAGAGTGATCAACACTCATTTTCGGCCAAAGAGAGGTARGCAACCTCATAGCCCCACAATATTCCGATCCCGGAGGACAAG  
 V. herbacoursi 1 GTTCGGTAAAGAGTGATCAACACTCAGTTAAGCTAAACAGAGGTAGGCAACCTCATAGCCCC-ACAATATTCCACATCCCGGAGGACAAG  
 V. herbacoursi 2 GTTCGGTAAAGAGTGATCAACACTCAGTTAAGCTAAACAGAGGTAGGCAACCTCATAGCCCC-ACAATATTCCACATCCCGGAGGACAAG  
 V. major 1 GTTCGGTAAAGAGTGATCAACACTCATATCGGCCAAAAGAGGTACGCAACCTCATAGCCCC-ACAATATTCCGATCCCGGAGGACAAG  
 V. major 2 GTTCGGTAAAGAGTGATCAACACTCATATCGGCCAAAAGAGGTACGCAACCTCATAGCCCC-ACAATATTCCGATCCCGGAGGACAAG  
 V. multiflora 1 GTTCGGTAAAGAGTGATCAACACTCGATTTCGGCTAAACAGAGGT-CGCAACCTCATAGCCCC-ACAATATTCCACATCCCGGAGGACAAG  
 V. multiflora 2 GTTCGGTAAAGAGTGATCAACACTCGATTTCGGCTAAACAGAGGT-CGCAACCTCATAGCCCC-ACAATATTCCACATCCCGGAGGACAAG  
 V. multiflora 3 GTTCGGTAAAGAGTGATCAACACTCGATTTCGGCTAAACAGAGGT-CGCAACCTCATAGCCCC-ACAATATTCCACATCCCGGAGGACAAG  
 V. multiflora 4 GTTCGGTAAAGAGTGATCAACACTCGATTTCGGCTAAACAGAGGT-CGCAACCTCATAGCCCC-ACAATATTCCACATCCCGGAGGACAAG  
 V. procumbens 2 GTTCGGTAAAGAGTGATCAACACTCGTTTCAGCCAAAGAGAGGTAGGCAACCTCATAGCCCC-ACAATATTCCGATCCCGGAGGACAAG  
 V. procumbens 3 GTTCGGTAAAGAGTGATCAACACTCGTTTCAGCCAAAGAGAGGTAGGCAACCTCATAGCCCC-ACAATATTCCGATCCCGGAGGACAAG  
 Virectaria sp. 1 GTTCGGTAAAGAGTGATCAACACTCGTTTCAGCCAAAGAGAGGTACGCAACCTCATAGCCCC-ACAATATTCCGATCCCGGAGGACAAG  
 Virectaria sp. 2 GTTCGGTAAAGAGTGATCAACACTCGTTTCAGCCAAAGAGAGGTAGGCAACCTCATAGCCCC-ACAATATTCCGATCCCGGAGGACAAG

270

H. minutiflora 2 CAACAATTTATGTGCCAAGTCCACAACACTCAACGTGAGCGGAATTGGAACACAATGCCACTTCAAGGTTCTACCGGCGACATTCTCA  
 S. becquetii -----  
 S. xanthotricha -----  
 S. elliptica -----

T. capsulifera -----  
V. angustifolia 1 CAACCGTTTATGTGCCAAGTCCACAACACTCAATGTGTGCGGAAGAGGAACACAAAGGCCACTTCAAGGTTCTACCAGCGCTATTCTCG  
V. belingana 1 CAACCGTTTCATGTGCCAAGTCCACAACACTCAATGTGAGCGGAAGAGGAACACAAAGGCCACTTCAAGGTTCTACCAGCGCAATTTCTCG  
V. belingana 2 CAACCGTTTCATGTGCCAAGTCCACAACACTCAATGTGAGCGGAAGAGGAACACAAAGGCCACTTCAAGGTTCTACCAGCGCAATTTCTCG  
V. belingana 3 CAACCGTTTCATGTGCCAAGTCCACAACACTCAATGTGAGCGGAAGAGGAACACAAAGGCCACTTCAAGGTTCTACCAGCGCAATTTCTCG  
V. herbacoursi 1 CAACAATTTATGTGCCAAGTCCACAACACTCAACGTGAGCGGAATTTGGAACACAAATGCCACTTCAAGGTTCTACCAGCGCAATTTCTCG  
V. herbacoursi 2 CAACAATTTATGTGCCAAGTCCACAACACTCAACGTGAGCGGAATTTGGAACACAAATGCCACTTCAAGGTTCTACCAGCGCAATTTCTCG  
V. major 1 CAACCGTTTATGTGCCAAGTCCACAACACTCAACGTGAGCGGAAGAGGAACACAAAGGCCACTTCAAGGTTCAACCAGCGCCATTCTCG  
V. major 2 CAACCGTTTATGTGCCAAGTCCACAACACTCAACGTGAGCGGAAGAGGAACACAAAGGCCACTTCAAGGTTCAACCAGCGCCATTCTCG  
V. multiflora 1 CAACCGTTTATGTGCCAAGTCCACAACACTTAACTGAGCAGAAATTTGGAACACAAAGGCCACTTCAAGGTTCTACCAGCGCAATTTCTCG  
V. multiflora 2 CAACCGTTTATGTGCCAAGTCCACAACACTTAACTGAGCAGAAATTTGGAACACAAAGGCCACTTCAAGGTTCTACCAGCGCAATTTCTCG  
V. multiflora 3 CAACCGTTTATGTGCCAAGTCCACAACACTTAACTGAGCAGAAATTTGGAACACAAAGGCCACTTCAAGGTTCTACCAGCGCAATTTCTCG  
V. multiflora 4 CAACCGTTTATGTGCCAAGTCCACAACACTTAACTGAGCAGAAATTTGGAACACAAAGGCCACTTCAAGGTTCTACCAGCGCAATTTCTCG  
V. procumbens 2 CAACCGTTTATGTGCCAAGTCCACAACACTCAATGTGTGCGGAAGAGGAACACAAAGGCCACTTCAAGGTTCTACCAGCGCTATTCTCG  
V. procumbens 3 CAACCGTTTATGTGCCAAGTCCACAACACTCAATGTGTGCGGAAGAGGAACACAAAGGCCACTTCAAGGTTCTACCAGCGCTATTCTCG  
Virectaria sp. 1 CAACCGTTTATGTGCCAAGTCCACAACACTCAATGTGTGCGGAAGAGGAACACAAAGGCCACTTCAAGGTTCTACCAGCGCTATTCTCG  
Virectaria sp. 2 CAACCGTTTATGTGCCAAGTCCACAACACTCAATGTGTGCGGAAGAGGAACACAAAGGCCACTTCAAGGTTCTACCAGCGCTATTCTCG

360

H. minutiflora 2 TAAGAGGGA-CAACGCAGCGAACACACATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAACACAAGAAACCCGAAGAAGGCCAA  
S. becquetii -----  
S. xanthotricha -----  
S. elliptica -----  
T. capsulifera -----  
V. angustifolia 1 AATGAGGGAACAACGCAGCGAACGAACATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAACACAAGAAACCCAAAGACGGCCAA  
V. belingana 1 AATGAGGGAACAACGCAGCGAACGAACATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAACACAAGAAACCCAAAGACGGCCAA  
V. belingana 2 AATGAGGGAACAACGCAGCGAACGAACATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAACACAAGAAACCCAAAGACGGCCAA  
V. belingana 3 AATGAGGGAACAACGCAGCGAACGAACATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAACACAAGAAACCCAAAGACGGCCAA  
V. herbacoursi 1 TAAGAGGGA-CAACGCAGCGAACACACATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAACACAAGAAACCCGAAGAAGGCCAA  
V. herbacoursi 2 TAAGAGGGA-CAACGCAGCGAACACACATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAACACAAGAAACCCGAAGAAGGCCAA  
V. major 1 AATGAGGGAACAACGCAGCGAACGAACATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAACACAAGAAACCCAAAGACGGCCAA  
V. major 2 AATGAGGGAACAACGCAGCGAACGAACATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAACACAAGAAACCCAAAGACGGCCAA  
V. multiflora 1 TATGAGG-AACAACGCAGCGAACACTCATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAGCACAAGAAACCCAAATAAGGCCAA  
V. multiflora 2 TATGAGG-AACAACGCAGCGAACACTCATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAGCACAAGAAACCCAAATAAGGCCAA  
V. multiflora 3 TATGAGG-AACAACGCAGCGAACGCTAATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAGCACAAGAAACCCAAAGACGGCCAA  
V. multiflora 4 TATGAGG-AACAACGCAGCGAACACTCATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAGCACAAGAAACCCAAATAAGGCCAA  
V. procumbens 2 AATGAGGGAACAACGCAGCGAACGAACATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAACACAAGAAACCCAAAGACGGCCAA  
V. procumbens 3 AATGAGGGAACAACGCAGCGAACGAACATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAACACAAGAAACCCAAAGACGGCCAA  
Virectaria sp. 1 AATGAGGGAACAACGCAGCGAACGAACATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAACACAAGAAACCCAAAGACGGCCAA  
Virectaria sp. 2 AATGAGGGAACAACGCAGCGAACGAACATGTTTTGAAACATGAAAATTCCTTCATGTAGGTATACAACACAAGAAACCCAAAGACGGCCAA

450

H. minutiflora 2 GGCAAACGTTGCTCTTAGACCAATAAATGCAAAGGCTTATCGGGTAGGATGTCGCTG----CCCAAGCAGGGATCCAACCAACCC-ATA  
S. becquetii -----  
S. xanthotricha -----  
S. elliptica -----  
T. capsulifera -----  
V. angustifolia 1 GGCAAACGTTGCTCTTAGACCAATAAATGCAAAGGCTTATCGGGTAGGATGTCGCTG----CCCAAGCAGGGATCCA-----  
V. belingana 1 GGCAAACGTTGCTCTTAGACCAATAAATGCAAAGGCTTATCGGGTAGGATGTCGCTG----CACAAGCAGGGATCCAACCAACCC-ATA  
V. belingana 2 GGCAAACGTTGCTCTTAGACCAATAAATGCAAAGGCTTATCGGGTAGGATGTCGCTG----CACA-----  
V. belingana 3 GGCAAACGTTGCTCTTAGACCAATAAATGCAAAGGCTTATCGGGTAGGATG-----  
V. herbacoursi 1 GGCAAACGTTGCTCTTAGACCAATAAATGCAAAGGCTTATCGGGTAGGATGTCGCTG----CCCAAGCAGGGATCCA-CAACCCCCATA  
V. herbacoursi 2 GGCAAACGTTGCTCTTAGACCAATAAATGCAAAGGCTTATCGGGTAGGATGTCGCTG----CCCAAGCAGGGATCCA-CAACCCCCATA  
V. major 1 GGCAATCGTTGCTCTTAGACCAATAAATGCAAAGGCTTATCGGGTAGGATGTCGCTG----CACAAGCAGGGATCCAACAACCCCCATA  
V. major 2 GGCAATCGTTGCTCTTAGACCAATAAATGCAAAGGCTTATCGGGTAGGATGTCGCTGCGCTGCGCTGCACAAGCAGGGATCCAACCAACCC-ATA  
V. multiflora 1 GGCAAACGTTGCTCTTAGACCAATAAATGCAAAGGCTTATCGGGTAGGATGTCGCTG----CCCAAGCAGGGATCCA-----  
V. multiflora 2 GGCAAACGTTGCTCTTAGACCAATAAATGCAAAGGCTTATCGGGTAGGATGTCGCTG----CCCA--AGGGATCA-----  
V. multiflora 3 GGCAACCATTTGCTCTTAGACCAATAAATGCAAAGGCTTATCAGGTAGGATGTCGCTG----CCCAAGCAGGGATCCA-----  
V. multiflora 4 GGCAAACGTTGCTCTTAGACCAATAAATGCAAAGGCTTATCGGGTAGGATGTCGCTG----CCCAAGCAGGGATCCAAC-----  
V. procumbens 2 GGCAAACGTTGCTCTTAGACCAATAAATGCAAAGGCTTATCGGGTAGGATGTCGCTG----CCCAAGCAGGGATCCAACAACCC-ATA  
V. procumbens 3 GGCAAACGTTGCTCTTAGACCAATAAATGCAAAGGCTTATCGGGTAGGATGTCGCTG----CCCAAGCAG-----  
Virectaria sp. 1 GGCAAACGTTGCTCTTAGACCAATAAATGCAAAGGCTTATCGGGTAGGATGTCGCTG----CCCAAGCAGGGATCCAACCA-----  
Virectaria sp. 2 GGCAAACGTTGCTCTTAGACCAATAAATGCAAAGGCTTATCGGGTAGGATGTCGCTG----CCCAAGCAGGGATCCA-CAACCCCCATA

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H. minutiflora 2 CAAGA  
S. becquetii -----  
S. xanthotricha -----  
S. elliptica -----  
T. capsulifera -----  
V. angustifolia 1 -----  
V. belingana 1 CA---  
V. belingana 2 -----  
V. belingana 3 -----  
V. herbacoursi 1 CA---  
V. herbacoursi 2 CA---  
V. major 1 CAA--  
V. major 2 CAAGA  
V. multiflora 1 -----

V. multiflora 2 -----  
 V. multiflora 3 -----  
 V. multiflora 4 -----  
 V. procumbens 2 CGAG-  
 V. procumbens 3 -----  
 Virectaria sp. 1 -----  
 Virectaria sp. 2 CAA--

**ITS Matrix (617 bp)**

**ITS1**



H. minutiflora 2 TCGAATCCTGCAAAGCAGACGACCGCGAACTCGTGACACC---GCACGGGTGCCGGTGGGAGCGGTTGGGAC--AAAACCTCCCG-TC  
 S. becquetii TCGAATCCTGCAAAGTAGACGACCGCGAACTTGTGTTATT---ATACGGCTGTCCGAGGAGCGGTTGGGAT--AATACCCTATCGTTG  
 S. xanthotricha TCGAATCCAGCAAAGTAGACGACCGCGAACTTGTGTTATT---ACACGGTTGTCCGAGGTGCGGGTTGGGAT--AATACCCTATCGTTG  
 S. elliptica TCGATTCTCGCAAAGCAGACGACCGCGAACTTGTGTGATT---ACACGGTTGCCGACAGGAACGGGTTGGGAT--AATACCCTATCGTTG  
 T. capsulifera TCGAATCCTGCAAAGCAGACGACCGCGAACTCGTATCATT---ACACGGGTGCCGGT-G-----CCTCAC----  
 V. angustifolia 1 TCGAATCCTGAAAAGCAGACGACCGCGAACTCGTGTGTTACC---AAACGGGCGTTGGTGGGAGCGGTT--GGATTA AAAACCTCCCGTTG  
 V. belingana 1 TCGAATCCTGAAAAGCAGACGACCGCGAACTCGTGTGTTACC---AAACGGGCGTTGGTGGGAGCGGTT--GGATTA AAAACCTCCCGTTG  
 V. belingana 2 TCGAATCCTGAAAAGCAGACGACCGCGAACTCGTGTGTTACC---AAACGGGCGTTGGTGGGAGCGGTT--GGATTA AAAACCTCCCGTTG  
 V. belingana 3 TCGAATCCTGAAAAGCAGACGACCGCGAACTCGTGTGTTACC---AAACGGGCGTTGGTGGGAGCGGTT--GGATTA AAAACCTCCCGTTG  
 V. herbacoursi 1 TCGAATCCTGAAAAGCAGACGACCGCGAACTCGTGTGTTACC---TCATGGTCCGAGGTGGGAGCGGTT--GGATTA AAAACCTCCCGTTG  
 V. herbacoursi 2 TCGAATCCTGAAAAGCAGACGACCGCGAACTCGTGTGTTACC---AAACGGGCGTTGGTGGGAGCGGTT--GGATTA AAAACCTCCCGTTG  
 V. major 1 TCGAATCCTGAAAAGCAGACGACCGCGAACTCGTGTGTTACC---AAACGGGCGTTGGTGGGAGCGGTT--GGATTA AAAACCTCCCGTTG  
 V. major 2 TCGAATCCTGAAAAGCAGACGACCGCGAACTCGTGTGTTACC---AAACGGGCGTTGGTGGGAGCGGTT--GGATTA AAAACCTCCCGTTG  
 V. multiflora 1 TCGAATCCTGAAAAGCAGACGACCGCGAACTCGTGTGTTACC---AAACGGGCGTTGGTGGGAGCGGTT--GGATTA AAAACCTCCCGTTG  
 V. multiflora 2 TCGAATCCTGAAAAGCAGACGACCGCGAACTCGTGTGTTACC---AAACGGGCGTTGGTGGGAGCGGTT--GGATTA AAAACCTCCCGTTG  
 V. multiflora 3 TCGAATCCTGAAAAGCAGACGACCGCGAACTCGTGTGTTACC---AAACGGGCGTTGGTGGGAGCGGTT--GGATTA AAAACCTCCCGTTG  
 V. multiflora 4 TCGAATCCTGAAAAGCAGACGACCGCGAACTCGTGTGTTACC---AAACGGGCGTTGGTGGGAGCGGTT--GGATTA AAAACCTCCCGTTG  
 V. procumbens 2 TCGAATCCTGAAAAGCAGACGACCGCGAACTCGTGTGTTACC---AAACGGGCGTTGGTGGGAGCGGTT--GGATTA AAAACCTCCCGTTG  
 V. procumbens 3 TCGAATCCTGAAAAGCAGACGACCGCGAACTCGTGTGTTACC---AAACGGGCGTTGGTGGGAGCGGTT--GGATTA AAAACCTCCCGTTG  
 Virectaria sp. 1 TCGAATCCTGAAAAGCAGACGACCGCGAACTCGTGTGTTACC---AAACGGGCGTTGGTGGGAGCGGTT--GGATTA AAAACCTCCCGTTG  
 Virectaria sp. 2 TCGAATCCTGAAAAGCAGACGACCGCGAACTCGTGTGTTACC---AAATGGGCGTTGGTGGGAGCGGTT--GGATTA AAAACCTCCCGTTG

90

H. minutiflora 2 CCAG-CGCGCGCGCCCCCGCGCGCTCGTGC GCGGACATAACTCAACCCCGCGCGGAAAGCGCCAAGGAAAACCTGAATTTGGATGGC  
 S. becquetii CCTC--ACCGGCGCTACCGCGCGCTCGAGTGGGACAATAACTTAACCCGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATAGC  
 S. xanthotricha CCTC--ACCGGCGCTACCGCGCGCTCGAGTGGGACAATAACTTAACCCGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATAGC  
 S. elliptica CCTC--ACCGGCGCTACCGCGCGCTCGAGTGGGACAATAACTTAACCCGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATAGC  
 T. capsulifera ---C-----GGCGCCACCGCGTGTCTGTCGCGTGCACATAACTCAACCCCGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC  
 V. angustifolia 1 TCAC--ACCGGCGTCCATCATGCACCCATTGGGTGCACCCATAACTAAACTCCGGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC  
 V. belingana 1 TCAC--ACCGGCGTCCATCATGCACCCATTGGGTGCACCCATAACTAAACTCCGGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC  
 V. belingana 2 TCAC--ACCGGCGTCCATCATGCACCCATTGGGTGCACCCATAACTAAACTCCGGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC  
 V. belingana 3 TCAC--ACCGGCGTCCATCATGCACCCATTGGGTGCACCCATAACTAAACTCCGGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC  
 V. herbacoursi 1 TCAC--ACCGGCGTCCATCATGCACCCATTGGGTGCACCCATAACTAAACTCCGGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC  
 V. herbacoursi 2 TCAC--ACCGGCGTCCATCATGCACCCATTGGGTGCACCCATAACTAAACTCCGGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC  
 V. major 1 TGTACACCGGCGTCCATCATGCACCCATTGGGTGCACCCATAACTAAACTCCGGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC  
 V. major 2 TGTACACCGGCGTCCATCATGCACCCATTGGGTGCACCCATAACTAAACTCCGGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC  
 V. multiflora 1 TCAC--ACCGGCGTCCATCATGCACCCATTGGGTGCACCCATAACTAAACTCCGGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC  
 V. multiflora 2 TCAC--ACCGGCGTCCATCATGCACCCATTGGGTGCACCCATAACTAAACTCCGGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC  
 V. multiflora 3 TCAC--ACCGGCGTCCATCATGCACCCATTGGGTGCACCCATAACTAAACTCCGGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC  
 V. multiflora 4 TCAC--ACCGGCGTCCATCATGCACCCATTGGGTGCACCCATAACTAAACTCCGGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC  
 V. procumbens 2 TCAC--ACCGGCGTCCATCATGCACCCATTGGGTGCACCCATAACTAAACTCCGGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC  
 V. procumbens 3 TCAC--ACCGGCGTCCATCATGCACCCATTGGGTGCACCCATAACTAAACTCCGGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC  
 Virectaria sp. 1 TCAC--ACCGGCGTCCATCATGCACCCATTGGGTGCACCCATAACTAAACTCCGGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC  
 Virectaria sp. 2 TCAC--ACCGGCGTCCATCATGCACCCATTGGGTGCACCCATAACTAAACTCCGGCGCGGAAAGCGCCAAGGAAAACCTAAAATTTGGATTGC

180

**S5.8 gene**



H. minutiflora 2 CCGC---CTCC--CCGTTCCGCGGGGGTGC CGCGCGTCTGTCGTAACCAAAACGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGAT  
 S. becquetii CCGC---CTCC--CCGTTCCGCGGGGGTGTATGGCTTCTATTGTAACCAAAACGACTCTCGCAACCGGATATCTCGGCTCTCGCATCGAT  
 S. xanthotricha CTGC---CTCC--CCGTTCCGCGGGGGTGTGTGGCTTCTATTGTAACCAAAACGACTCTCGCAACCGGATATCTCGGCTCTCGCATCGAT  
 S. elliptica CCGC---CTTC--CCGTTCCGCGGGGGTACTGTGGCTTCTATCGTAACCAAAACGACTCTCGCAACCGGATATCTCGGCTCTCGCATCGAT  
 T. capsulifera CCGT---CTCC--CCGTTTGC GGGGTTGCG--TGTGGCATCTGTCGTAATCTAAACGACTCTCGGCAACCGGATATCTCGGCTCTCGCATCGAT  
 V. angustifolia 1 TCGTTA--CCTTT--CGTCCGCGTGGGGTATCGTGGCATCTGTCGTAATCTAAACGACTCTCGGCAACCGGATATCTCGGCTCTCGCATCGAT  
 V. belingana 1 CCGCTACCTTT--CGTTCGCGGGGGTATTGTGGCATCTGTCGTAATCTAAACGACTCTCGGCAACCGGATATCTCGGCTCTCGCATCGAT  
 V. belingana 2 CCGCTACCTTT--CGTTCGCGGGGGTATTGTGGCATCTGTCGTAATCTAAACGACTCTCGGCAACCGGATATCTCGGCTCTCGCATCGAT  
 V. belingana 3 CCGCTACCTTT--CGTTCGCGGGGGTATTGTGGCATCTGTCGTAATCTAAACGACTCTCGGCAACCGGATATCTCGGCTCTCGCATCGAT  
 V. herbacoursi 1 CTGTTACCTTT--CGTTCGCGGGGGTATCGTGGCATCTGTCGTAATCTAAACGACTCTCGGCAACCGGATATCTCGGCTCTCGCATCGAT  
 V. herbacoursi 2 CTGTTACCTTT--CGTTCGCGGGGGTATCGTGGCATCTGTCGTAATCTAAACGACTCTCGGCAACCGGATATCTCGGCTCTCGCATCGAT  
 V. major 1 CCGCTACCTTT--CGTTCGCGGGGGTATCGTGGCATCTGTCGTAATCTAAACGACTCTCGGCAACCGGATATCTCGGCTCTCGCATCGAT  
 V. major 2 CCGCTACCTTT--CGTTCGCGGGGGTATCGTGGCATCTGTCGTAATCTAAACGACTCTCGGCAACCGGATATCTCGGCTCTCGCATCGAT  
 V. multiflora 1 CTGTTACCTT--CCGTTCCGCGGGGGTATCATGGCATCTGTCGTAATCTAAACGACTCTCGCAACCGGATATCTCGGCTCTCGCATCGAT  
 V. multiflora 2 CTGTTACCTT--CCGTTCCGCGGGGGTATCATGGCATCTGTCGTAATCTAAACGACTCTCGCAACCGGATATCTCGGCTCTCGCATCGAT  
 V. multiflora 3 CTGTTACCTT--CCGTTCCGCGGGGGTATCATGGCATCTGTCGTAATCTAAACGACTCTCGCAACCGGATATCTCGGCTCTCGCATCGAT  
 V. multiflora 4 CTGTTACCTT--CCGTTCCGCGGGGGTATCATGGCATCTGTCGTAATCTAAACGACTCTCGCAACCGGATATCTCGGCTCTCGCATCGAT  
 V. procumbens 2 TCGTTACCTTT--CGTTCGCGTGGGGTATCGTGGCATCTGTCGTAATCTAAACGACTCTCGGCAACCGGATATCTCGGCTCTCGCATCGAT  
 V. procumbens 3 TCGTTACCTTT--CGTTCGCGTGGGGTATCGTGGCATCTGTCGTAATCTAAACGACTCTCGGCAACCGGATATCTCGGCTCTCGCATCGAT  
 Virectaria sp. 1 CCGCTACCTTT--CGTTCGCGTGGGGTATCGTGGCATCTGTCGTAATCTAAACGACTCTCGGCAACCGGATATCTCGGCTCTCGCATCGAT  
 Virectaria sp. 2 CCGCTACCTTT--CGTTCGCGTGGGGTATTGTGGCATCTGTCGTAATCTAAACGACTCTCGGCAACCGGATATCTCGGCTCTCGCATCGAT

270

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H. minutiflora 2 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 S. becquetii GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATC  
 S. xanthotricha GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATC  
 S. elliptica GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATC  
 T. capsulifera GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 V. angustifolia 1 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 V. belingana 1 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 V. belingana 2 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 V. belingana 3 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 V. herbacoursi 1 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 V. herbacoursi 2 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 V. major 1 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 V. major 2 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 V. multiflora 1 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 V. multiflora 2 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 V. multiflora 3 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 V. multiflora 4 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 V. procumbens 2 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 V. procumbens 3 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 Virectaria sp. 1 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT  
 Virectaria sp. 2 GAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCCTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAAGCCATT

**ITS2**



450

H. minutiflora 2 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCATC----GCGGGG--CGGCGGAAAATGGCCTCCCGTTCCG  
 S. becquetii AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTACCA  
 S. xanthotricha AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTACCA  
 S. elliptica AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTACCA  
 T. capsulifera AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG  
 V. angustifolia 1 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG  
 V. belingana 1 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG  
 V. belingana 2 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG  
 V. belingana 3 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG  
 V. herbacoursi 1 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG  
 V. herbacoursi 2 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG  
 V. major 1 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG  
 V. major 2 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG  
 V. multiflora 1 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG  
 V. multiflora 2 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG  
 V. multiflora 3 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG  
 V. multiflora 4 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG  
 V. procumbens 2 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG  
 V. procumbens 3 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG  
 Virectaria sp. 1 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG  
 Virectaria sp. 2 AGGCCGAGGGCAGCTTGCCTGGGCGTCACGCATCGCGTCGCCACCCCGTTCATTCCGCGGGGTAGCGGATAATGGCCTCCCGTTCG

540

H. minutiflora 2 CGAGGCGGGCCGGCCAAACGCGAGTCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCTGTCTGCGC  
 S. becquetii CCAGGTGCGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 S. xanthotricha CCAGGCGGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 S. elliptica CCAGGTGCGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGTGACTTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 T. capsulifera TGAGGAGCGCCGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 V. angustifolia 1 CCAGGAGTGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 V. belingana 1 CCAGGAGTGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 V. belingana 2 CCAGGAGTGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 V. belingana 3 CCAGGAGTGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 V. herbacoursi 1 CTA-GAGTGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 V. herbacoursi 2 CTA-GAGTGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 V. major 1 CCAGGAGTGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 V. major 2 CCAGGAGTGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 V. multiflora 1 CGA-GAGTGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 V. multiflora 2 CGA-GAGTGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 V. multiflora 3 CGA-GAGTGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 V. multiflora 4 CGA-GAGTGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 V. procumbens 2 CCATGAGTGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 V. procumbens 3 CCATGAGTGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 Virectaria sp. 1 CCAGGAGTGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT  
 Virectaria sp. 2 CCAAGAGTGGCTGGCCTAAATGCGAGTCTCCTCGGCGAGGGACGTCACGACAAGTGGTGGTTGAATGCCTCAACTCGAGTCCCT-GTCGTGTT

H. minutiflora 2 GGCGAATCCCCCGTTGTCTCGGACTCCCACGACCCACG-GCGCGCTCAYGGCGGAGCY-CGACCGGACCC--  
 S. becquetii GGCAAAACCCCGCTTAACT-----CCCTT-GACCCTACA-GCATGCACCTCGGTGCAAGCTCGACCGGACCC-A  
 S. xanthotricha GGCAAAACCCCGCTTAACT-----CCCTT-GACCCTACA-GCATGCACCTCGGTGCAAGCTCGACCGGACCC-A  
 S. elliptica GGCAAAACCCCGCTTAACT-----CCTTTGACCCTACA-GCATGCACCTCGGTGCAAGCTCGACCGGACCC-A  
 T. capsulifera GATGAGTCCCCCATTTATCT-GGACTCCTATGACCCCTACA-GCATGCCTCTTGACCTAAGCTCGACTGCGACCC-A  
 V. angustifolia 1 GACGAATCTCC-CGTTA-TT-GGACTCTGTTGACCCCTATA-GCGCACGTCTTGACGTGAGCATCAAT-GCGACCC-A  
 V. belingana 1 GACGAATCTCC-CGTTA-CTTGACTCTGTTGACCCCTATA-GCGCACGTCTTGACGTGAGCATCAATGCGACCC-A  
 V. belingana 2 GACGAATCTCC-CGTTA-CTTGACTCTGTTGACCCCTATA-GCGCACGTCTTGACGTGAGCATCAATGCGACCC-A

V. belingana 3 GACGAATCTCC-CGTTA-CTTGGACTCTGTTGACCCATA-GCGCACGTCTTGACGTGAGCATCAATTGCGACCCCA  
 V. herbacoursi 1 GACGAAACTCC-CGTTAA-TTGGACTTTGCTGACCCATA-GCGCACGTCTTGACGTGAGCATCAATTGCGACCC-A  
 V. herbacoursi 2 GACGAAACTCC-CGTTAA-TTGGACTTTGCTGACCCATA-GCGCACGTCTTGAC-TGAGCATCAATTGCGACCCCA  
 V. major 1 GACGAATCTCC-CGTTA-CTTGGACTCTGCTGACCCATA-GCGCACGTCTTGACGTGAGCATCAATTGCGACCC-A  
 V. major 2 GACGAATCTCC-CGTTA-CTTGGACTCTGCTGACCCATA-GCGCACGTCTTGACGTGAGCATCAATTGCGACCC-  
 V. multiflora 1 GACGAAACTCC-CGTTA-CTTGGACTTAGTTGACCCATT-GCGCACGTCTTGACGTGAGCATCAATTGCGACCC-A  
 V. multiflora 2 GACGAAACTCC-CGTTA-CTTGGACTTAGTTGACCCATT-GCGCACGTCTTGACGTGAGCWTG-AWTGACCC-A  
 V. multiflora 3 GACGAAACTCC-CGTTA-CTTGGACTTAGTTGACCCATT-GCGCACGTCTT-ATGTGAGCATCAAT-GCGACC--A  
 V. multiflora 4 GATGAAACTCC-CGTTA-CTTGGACTTAGTTGACCCATT-GCGCACGTCTTGACGTGAGC-TCAATTGCGACCCCA  
 V. procumbens 2 GACGAATCTCC-CGTTA--TTGGACTCTGTTGACCCATA-GCGCACGTCTTGACGTGAGCATCAAT-GCGACCCCA  
 V. procumbens 3 GACGAATCTCC-CGTTA--TTGGACTCTGTTGACCCATA-GCGCACGTCTTGACGTGAGCATC-AT-GCGACCCCA  
 Virectaria sp. 1 GACGAATCTCC-CGTTA-CTTGGACTCTGTTGACCCATA-GCGCACGTCTTGACGTGAGCATCAATTGCGACCC-A  
 Virectaria sp. 2 GACGAATCTCC-CGTTA-CT-GGACTCTGTTGACCCATA-GCGCACGTCTTGACGTGAGCTACAATTGC-----

**rpoC1 Matrix (484 bp)  
 exon1**

▶ 90  
 H. minutiflora 2 AGACTCTGCTTGGCAAACGAGTTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 S. becquetii AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 S. xanthotricha AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 S. elliptica AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 T. capsulifera AGACTCTGCTTGGCAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 V. angustifolia 1 AGACTCTGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 V. belingana 1 GGRMTCGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 V. belingana 2 GGRMTCGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 V. herbacoursi 1 GGRMTCGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 V. herbacoursi 2 GGRMTCGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 V. major 1 GGRMTCGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 V. major 2 GGRMTCGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 V. multiflora 1 AGACTCTGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 V. multiflora 2 AGACTCTGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 V. multiflora 3 AGACTCTGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 V. multiflora 4 AGACTCTGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 V. procumbens 2 AGACTCTGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 V. procumbens 3 GGRMTCGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 Virectaria sp. 1 AGACTCTGCTTGGTAA- CGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC  
 Virectaria sp. 2 AGACTCTGCTTGGTAAACGAGTCGATTATTCAGGACGTTCCGTTATTGTTGTGGGTCTTCACTTTCATTACATCGATGTGGATTGCCTC

180  
 H. minutiflora 2 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 S. becquetii SAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 S. xanthotricha GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 S. elliptica GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 T. capsulifera GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 V. angustifolia 1 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 V. belingana 1 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 V. belingana 2 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 V. belingana 3 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 V. herbacoursi 1 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 V. herbacoursi 2 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 V. major 1 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 V. major 2 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 V. multiflora 1 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 V. multiflora 2 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 V. multiflora 3 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 V. multiflora 4 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 V. procumbens 2 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 V. procumbens 3 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 Virectaria sp. 1 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA  
 Virectaria sp. 2 GAGAAATAGCAATAGAACCTTTCCAGACATTTGTAATTCGTTGGTCTAATTAGACAACATCTTGCTTCGAACATAGGAGTTGCTAAGAATA

270  
 H. minutiflora 2 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGACATCCCATTGCTGAATAGAGCACCCTCTGC  
 S. becquetii AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGGACATCCCATTGCTGAATAGAGCACCCTCTGC  
 S. xanthotricha AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGGACATCCCATTGCTGAATAGAGCACCCTCTGC  
 S. elliptica AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGGACATCCCATTGCTGAATAGAGCACCCTCTGC  
 T. capsulifera AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGGACATCCCATTGCTGAATAGAGCACCCTCTGC  
 V. angustifolia 1 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGGACATCCCATTGCTGAATAGAGCACCCTCTGC  
 V. belingana 1 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGGACATCCCATTGCTGAATAGAGCACCCTCTGC  
 V. belingana 2 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGGACATCCCATTGCTGAATAGAGCACCCTCTGC  
 V. belingana 3 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGGACATCCCATTGCTGAATAGAGCACCCTCTGC  
 V. herbacoursi 1 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGTGGACATCCCATTGCTGAATAGAGCACCCTCTGC  
 V. herbacoursi 2 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGTGGACATCCCATTGCTGAATAGAGCACCCTCTGC  
 V. major 1 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGGACATCCCATTGCTGAATAGAGCACCCTCTGC  
 V. major 2 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGGACATCCCATTGCTGAATAGAGCACCCTCTGC  
 V. multiflora 1 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGGACATCCCATTGCTGAATAGAGCACCCTCTGC  
 V. multiflora 2 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGGACATCCCATTGCTGAATAGAGCACCCTCTGC

*V. multiflora* 3 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGACATCCCCTATTGCTGAATAGAGCACCCACTCTGC  
*V. multiflora* 4 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGACATCCCCTATTGCTGAATAGAGCACCCACTCTGC  
*V. procumbens* 2 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGACATCCCCTATTGCTGAATAGAGCACCCACTCTGC  
*V. procumbens* 3 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGACATCCCCTATTGCTGAATAGAGCACCCACTCTGC  
*Virectaria* sp. 1 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGACATCCCCTATTGCTGAATAGAGCACCCACTCTGC  
*Virectaria* sp. 2 AAATTCGGGAAAAAGAACCCATTGTATGGGAAATACTTCAGGAAGTTATGCGGGGACATCCCCTATTGCTGAATAGAGCACCCACTCTGC

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*H. minutiflora* 2 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*S. becquetii* ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*S. xanthotricha* ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*S. elliptica* ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*T. capsulifera* ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*V. angustifolia* 1 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*V. belingana* 1 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*V. belingana* 2 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*V. belingana* 3 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*V. herbacoursi* 1 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*V. herbacoursi* 2 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*V. major* 1 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*V. major* 2 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*V. multiflora* 1 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*V. multiflora* 2 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*V. multiflora* 3 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*V. multiflora* 4 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*V. procumbens* 2 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*V. procumbens* 3 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*Virectaria* sp. 1 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG  
*Virectaria* sp. 2 ATAGATTGGGCATACAGGCATTCCAGCCCGTTTTAGTGAAGGGCGTGCTATTTGTTTACATCCATTAGTTTGTAAAGGGATTCAATGCAG

**intron**



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*H. minutiflora* 2 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*S. becquetii* ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*S. xanthotricha* ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*S. elliptica* ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*T. capsulifera* ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*V. angustifolia* 1 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*V. belingana* 1 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*V. belingana* 2 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*V. belingana* 3 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*V. herbacoursi* 1 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*V. herbacoursi* 2 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*V. major* 1 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*V. major* 2 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*V. multiflora* 1 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*V. multiflora* 2 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*V. multiflora* 3 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*V. multiflora* 4 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*V. procumbens* 2 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*V. procumbens* 3 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*Virectaria* sp. 1 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC  
*Virectaria* sp. 2 ATTTTGATGGGGATCAAATGGCTGTTTCATGTACCTTTATCTTTGGAAGCCCAAGCGGAGGCCCGTTACTTATGTTTTCTCATATGAATC

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*H. minutiflora* 2 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*S. becquetii* TTTTGTCTCCAGCTATTGGG-ATCCCATTTCCTG  
*S. xanthotricha* TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*S. elliptica* TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*T. capsulifera* TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*V. angustifolia* 1 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*V. belingana* 1 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*V. belingana* 2 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*V. belingana* 3 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*V. herbacoursi* 1 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*V. herbacoursi* 2 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*V. major* 1 TTTTGTCTCCAGCTATTGGG-ATCCCATTTCCTG  
*V. major* 2 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*V. multiflora* 1 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*V. multiflora* 2 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*V. multiflora* 3 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*V. multiflora* 4 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*V. procumbens* 2 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*V. procumbens* 3 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*Virectaria* sp. 1 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG  
*Virectaria* sp. 2 TTTTGTCTCCAGCTATTGGGGATCCCATTTCCTG

**trnT-F Matrix (1760 bp)**  
**trnT-L spacer**

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H. minutiflora 2 -----  
 S. becquetii TAGTTAGTAACTAGTATTTCTT-ATCCATTTCATAATCGATATAAATACAGAAAGGGATAAAATAGAATTTGAAATAAATTTATGAATATT  
 S. xanthotricha TAGTTAGTAACTAGTATTTCTT-ATCCATTTCATAATCGATATAAATACAGAAAGGAATAAAATAGAATTTTAAATAAATTTATGAATATT  
 S. elliptica TAGTTAGTAACTAGTATTTCTT-ATCCATTTCATAATCGATATAAATACAGAAAGGAATAAAATAGAATTTTAAATAAATTTAGTGAATATT  
 T. capsulifera -----TCATAATCAATATAAATATAGAAAGGAATAAAATCGAATTTTAAATAAATTTATGAATATT  
 V. angustifolia 1 -----  
 V. belingana 1 -----TT-ATCCATTTCAGAATTC-TATAAATAGAGAAAGGAATAAAATAGAATTTTAAATAAATTTTGAATATT  
 V. belingana 2 -----TT-ATCCATTTCAGAATTC-TATAAATAGAGAAAGGAATAAAATAGAATTTTAAATAAATTTTGAATATT  
 V. belingana 3 -----TT-ATCCATTTCAGAATTC-TATAAATAGAGAAAGGAATAAAATAGAATTTTAAATAAATTTTGAATATT  
 V. herbacoursi 1 -----  
 V. herbacoursi 2 -----  
 V. major 1 -----TT-ATCCATTTCAGAATTC-TATAAATAGAGAAAGGAATAAAATAGAATTTGAAATAAATTTTGAATATT  
 V. major 2 -----  
 V. multiflora 1 -----TCATCCATTTCAGAATTC-TATAAATAGAGAAAGGAATAAAATAGAATTTTAAATAAATTTTGAATATT  
 V. multiflora 2 -----AACTAGTATTTCTTATCCATTTCATCCATTTCAGAATTC-TATAAATAGAGAAAGGAATAAAATAGAATTTTAAATAAATTTTGAATATT  
 V. multiflora 3 -----TCATCCATTTCAGAATTC-TATAAATAGAGAAAGGAATAAAATAGAATTTTAAATAAATTTTGAATATT  
 V. multiflora 4 -----TCATCCATTTCAGAATTC-TATAAATAGAGAAAGGAATAAAATAGAATTTTAAATAAATTTTGAATATT  
 V. procumbens 2 -----TT-ATCCATTTCAGAATTC-TATAAATAGAGAAAGGAATAAAATAGAATTTGAAATAAATTTTGAATATT  
 V. procumbens 3 -----TT-ATCCATTTCAGAATTC-TATAAATAGAGAAAGGAATAAAATAGAATTTGAAATAAATTTTGAATATT  
 Virectaria sp. 1 -----TCAGAATTC-TATAAATAGAGAAAGGAATAAAATAGAATTTGAAATAAATTTTGAATATT  
 Virectaria sp. 2 -----

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H. minutiflora 2 -----  
 S. becquetii ATAGAAGAC-----AAGGACTAATATAGCGATATAGAATTTTCGATTTATTTATCACTAATAGAATTTAGAAT--TCAAATA---  
 S. xanthotricha ATAGAAGAC-----AAGGACTAATATAGCGATATAGAATTTTCGATTTATTTATCACTAATAGAATTTAGAAT--TCAAATA---  
 S. elliptica ATAGAAGAC-----AAGGACTAATATAGCGATATAGAATTTTCGATTTATTTATCACTAATAGAATTTAGAAT--TCAAATA---  
 T. capsulifera ATAGAAGAC-----AAGGACTAATATAGCGATATAGAATTTTCGATTTATTTATCACTAATAGAATTTAGAATTTTCG  
 V. angustifolia 1 -----  
 V. belingana 1 ATAGAAGACTTATAGAAGGCAAGGCCTAAAATAGCGATATAGAATTTTCGATTTATTTATCACTAATATATTTATTTAT-CACTAATAGAA  
 V. belingana 2 ATAGAAGACTTATAGAAGGCAAGGCCTAAAATAGCGATATAGAATTTTCGATTTATTTATCACTAATAGATTTATTTAT-CACTAATAGAA  
 V. belingana 3 ATAGAAGACTTATAGAAGGCAAGGCCTAAAATAGCGATATAGAATTTTCGATTTATTTATCACTAATATATTTATTTAT-CACTAATAGAA  
 V. herbacoursi 1 -----  
 V. herbacoursi 2 -----  
 V. major 1 ATAGAAGACTTATAGAAGGCAAGGCCTAAAATAGCGATATAGAATTTTCGATTTATTTATCACTAATATATTTATTTAT-CACTAATAGAA  
 V. major 2 -----  
 V. multiflora 1 ATAGAAGACTTATAGAAGGCAAGGCCTAAAATAGCGATATAGAATTTTCGATTTATTTATCACTAATATATTTATTTAT-CACTAATAAAA  
 V. multiflora 2 ATAGAAGACTTATAGAAGGCAAGGCCTAAAATAGCGATATAGAATTTTCGATTTATTTATCACTAATATATTTATTTAT-CACTAATAAAA  
 V. multiflora 3 ATAGAAGACTTATAGAAGGCAAGGCCTAAAATAGCGATATAGAATTTTCGATTTATTTATCACTAATATATTTATTTAT-CACTAATAAAA  
 V. multiflora 4 ATAGAAGACTTATAGAAGGCAAGGCCTAAAATAGCGATATAGAATTTTCGATTTATTTATCACTAATATATTTATTTAT-CACTAATAAAA  
 V. procumbens 2 ATAGAAGACTTATAGAAGGCAAGGCCTAAAATAGCGATATAGAATTTTCGATTTATTTATCACTAATATATTTATTTAT-CACTAATAGAA  
 V. procumbens 3 ATAGAAGACTTATAGAAGGCAAGGCCTAAAATAGCGATATAGAATTTTCGATTTATTTATCACTAATATATTTATTTAT-CACTAATAGAA  
 Virectaria sp. 1 ATAGAAGACTTATAGAAGGCAAGGCCTAAAATAGCGATATAGAATTTTCGATTTATTTATCACTAATAATTTATTTATC--ACTAATAGAA  
 Virectaria sp. 2 -----

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H. minutiflora 2 -----  
 S. becquetii -----TTATTAATTCGAATTATCATTTAATATTCGATTAGATAGTAAATAGTTTGGAT  
 S. xanthotricha -----TTATTAATTCGAATTATCATTTAATATTCGATTAGATAGTAAATAGTTTGGAT  
 S. elliptica -----TTATTAATTCGAATTATCATTTAATATTCGATTAGATAGTAAATAGTTTGGAT  
 T. capsulifera AATTCAA-----ATATTATTAATTCGAATTATCATTTAATATTCGATTAGATAGTAAATAGTTTGGAT  
 V. angustifolia 1 -----  
 V. belingana 1 TTTATTTATCACTAATAGAATTTAGAATTCGAATATTATTAACCTCGAATTATCATTTACTAGTCGATTAGATAGTAAATAGTTTGGAT  
 V. belingana 2 TTTAGAATTC-----GAATATTATTAACCTCGAATTATCATTTACTAGTCGATTAGATAGTAAATAGTTTGGAT  
 V. belingana 3 TTTAGAATTC-----GAATATTATTAACCTCGAATTATCATTTACTAGTCGATTAGATAGTAAATAGTTTGGAT  
 V. herbacoursi 1 -----  
 V. herbacoursi 2 -----  
 V. major 1 TTTAGAATTC-----GAATATTATTAACCTCGAATTATCATTTACTAGTCGATTAGATAGTAAATAGTTTGGAT  
 V. major 2 -----  
 V. multiflora 1 TTTAGAATTC-----GAATATTAGTAACTTCGAATTATCATTTACTAGTCGATTAGATAGTAAATAGTTTGGAT  
 V. multiflora 2 TTTAGAATTC-----GAATATTAGTAACTTCGAATTATCATTTACTAGTCGATTAGATAGTAAATAGTTTGGAT  
 V. multiflora 3 TTTAGAATTC-----GAATATTAGTAACTTCGAATTATCATTTACTAGTCGATTAGATAGTAAATAGTTTGGAT  
 V. multiflora 4 TTTAGAATTC-----GAATATTAGTAACTTCGAATTATCATTTACTAGTCGATTAGATAGTAAATAGTTTGGAT  
 V. procumbens 2 TTTAGAATTC-----GAATATTATTAACCTCGAATTATCATTTACTAGTCGATTAGATAGTAAATAGTTTGGAT  
 V. procumbens 3 TTTAGAATTC-----GAATATTATTAACCTCGAATTATCATTTACTAGTCGATTAGATAGTAAATAGTTTGGAT  
 Virectaria sp. 1 TTTAGAATTC-----GAATATTATTAACCTCGAATTATCATTTACTAGTCGATTAGATAGTAAATAGTTTGGAT  
 Virectaria sp. 2 -----

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H. minutiflora 2 -----  
 S. becquetii AGTTAAATTAGTTAAATTTTGCATTTTGAATTCAAATGACATTTGAAATT--TTTTTACACTTTTAC-----ACTTATAGTATATAT  
 S. xanthotricha AGTTAAATTAGTTAAATTTTTCATTTTGAATTCAAATGACATTTGAAATT--TTTTTACACTTATAGT-----ATAT-----AT  
 S. elliptica AGTTAAATTAGTTAAATTTTTCATTTTGAATTCAAATGACATTTGAAATT--TTTTTACACTTTTACACTTTTACACTAATCTTATAG--TATAT  
 T. capsulifera AATTAATTAGTTAAATTTTTCATTTTGAATTCAAATGACATTTGAAATTTTCCACTTTTCTTTACACTAATCTTATAG--TATAT  
 V. angustifolia 1 -----  
 V. belingana 1 AATTAATTAGTTCCATTTTTCATTTTGAATTCAAATGACATTTGAAATT--TTTTTACACTTATAGT-----ATAT-----AT  
 V. belingana 2 AATTAATTAGTTCCATTTTTCATTTTGAATTCAAATGACATTTGAAATT--TTTTTACACTTATAGT-----ATAT-----AT  
 V. belingana 3 AATTAATTAGTTCCATTTTTCATTTTGAATTCAAATGACATTTGCAATT--TTTTTACACTTATAGT-----ATAT-----AT



V. herbacoursi 1 -----TTTTGAATTCAAATGATATTTGAAATT--TTTTTACACTTATAGT-----ATAT-----AT  
 V. herbacoursi 2 -----  
 V. major 1 AATTAATAGTTCATTTTTTCATTTTTGAATTCAAATAACATTTGAAATT--TTTTTACACTTATAGT-----ATAT-----AT  
 V. major 2 -----  
 V. multiflora 1 AATTAATAGTAAATTTTGCATTTTTGAATGCAAATGATATTTGAAATT--TTTTTACACTTATACT-----TATAGTATATAT  
 V. multiflora 2 AATTAATAGTAAATTTTGCATTTTTGAATGCAAATGATATTTGAAATT--TTTTTACACTTATACT-----TATAGTATATAT  
 V. multiflora 3 AATTAATAGTAAATTTTGCATTTTTGAATGCAAATGATATTTGAAATT--TTTTTACACTTATACT-----TATAGTATATAT  
 V. multiflora 4 AATTAATAGTAAATTTTGCATTTTTGAATGCAAATGATATTTGAAATT--TTTTTACACTTATACT-----TATAGTATATAT  
 V. procumbens 2 AATTAATAGTTCATTTTTTCATTTTTGAATTCAAATGACATTTGCAATT--TTTTTACACTTATAGT-----ATAT-----AT  
 V. procumbens 3 AATTAATAGTTCATTTTTTCATTTTTGAATTCAAATGACATTTGCAATT--TTTTTACACTTATAGT-----ATAT-----AT  
 Virectaria sp. 1 AATTAATAGTTCATTTTTTCATTTTTGAATTCAAATGACATTTGCAATT--TTTTTACACTTATAGT-----ATAT-----AT  
 Virectaria sp. 2 -----

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H. minutiflora 2 -----  
 S. becquetii ATTTTTTATACTATTTGATTCTATATCATAATCATATATTTCTAATTAATAGGAATGATTAGTTCTAACTAATGAGACATTCTCCGCTT  
 S. xanthotricha ATTTTTTATACTATTTGATTCTATATCATAATCATATATTTCTAATTAATAGGAATGATTAGTTCTAACTAATGAGACATTCTCCGCTT  
 S. elliptica ATTTTTTATACTATTTGATTCTATATCATAATCATATATTTCTAATTAATAGGAATGATTAGTTCTAACTAATGAGACATTCTCCGCTT  
 T. capsulifera ATTTTTTATACTATTTGATTCTATATCATAATCATATATATCT----AATTAGGAATGATTAGTTCTAACTAATGAGACATTCTCCGCTT  
 V. angustifolia 1 -----TTAGTTCTAACTAATAAGACATTCTCCGCTT  
 V. belingana 1 ATTTTTTATACTATTTGATTCTATATCATAATCATATATTTTG----AATTAGGAATGATTAGTTCTAACTAATAAGACATTCTCCGCTT  
 V. belingana 2 ATTTTTTATACTATTTGATTCTATATCATAATCATATATTTTG----AATTAGGAATGATTAGTTCTAACTAATAAGACATTCTCCGCTT  
 V. belingana 3 ATTTTTTATACTATTTGATTCTATATCATAATCATATATTTTG----AATTAGGAATGATTAGTTCTAACTAATAAGACATTCTCCGCTT  
 V. herbacoursi 1 ATTTTTTATACTATTTGATTCTATATCATAATCATATATTTTG----AATTAGGAATGATTAGTTCTAACTAATAAGACATTCTCCGCTT  
 V. herbacoursi 2 -----  
 V. major 1 ATTTTTTATACTATTTGATTCTATATCATAATCATATATTTTG----AATTAGGAATGATTAGTTCTAACTAATAAGACATTCTCCGCTT  
 V. major 2 -----  
 V. multiflora 1 ATTTTTTATACTATTTGATTCTATATCATAATCATATATTTTG----AATTAGGAATGATTAGTTCTAACTAATAAGACATTCTCCGCTT  
 V. multiflora 2 ATTTTTTATACTATTTGATTCTATATCATAATCATATATTTTG----AATTAGGAATGATTAGTTCTAACTAATAAGACATTCTCCGCTT  
 V. multiflora 3 ATTTTTTATACTATTTGATTCTATATCATAATCATATATTTTG----AATTAGGAATGATTAGTTCTAACTAATAAGACATTCTCCGCTT  
 V. multiflora 4 ATTTTTTATACTATTTGATTCTATATCATAATCATATATTTTG----AATTAGGAATGATTAGTTCTAACTAATAAGACATTCTCCGCTT  
 V. procumbens 2 ATTTTTTATACTATTTGATTCTATATCATAATCATATATTTTG----AATTAGGACTGATTAGTTCTAACTAATAAGACATTCTCCGCTT  
 V. procumbens 3 ATTTTTTATACTATTTGATTCTATATCATAATCATATATTTTG----AATTAGGACTGATTAGTTCTAACTAATAAGACATTCTCCGCTT  
 Virectaria sp. 1 ATTTTTTATACTATTTGATTCTATATCATAATCATATATTTTG----AATTAGGACTGATTAGTTCTAACTAATAAGACATTCTCCGCTT  
 Virectaria sp. 2 -----

540

H. minutiflora 2 -----  
 S. becquetii TCATTCATAAAG-----ATGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 S. xanthotricha TCATTCATAAAG-----ATGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 S. elliptica TCATTCATAAAG-----ATGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 T. capsulifera TCATTCATAAAGCATAAATATGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 V. angustifolia 1 TCAGTCATAAAGCATAAAGATGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 V. belingana 1 TCAGTCATAAAGCATAAAGATGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 V. belingana 2 TCAGTCATAAAGCATAAAGATGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 V. belingana 3 TCAGTCATAAAGCATAAAGATGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 V. herbacoursi 1 TCATTCATAAAGCATAAAGGTGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 V. herbacoursi 2 -----  
 V. major 1 TCAGTCATAAAGCATAAAGATGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 V. major 2 -----  
 V. multiflora 1 TCATTCATAAAGCATAAAGGTGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 V. multiflora 2 TCATTCATAAAGCATAAAGGTGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 V. multiflora 3 TCATTCATAAAGCATAAAGGTGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 V. multiflora 4 TCATTCATAAAGCATAAAGGTGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 V. procumbens 2 TCAGTCATAAAGCATAAAGATGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 V. procumbens 3 TCAGTCATAAAGCATAAAGATGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 Virectaria sp. 1 TCAGTCATAAAGCATAAAGATGTAATGTAAGTAGTAAAGCGGAAATTTAGACGACAAAAAA--GAATCGACCGTTCAAGTATT--CAAAA  
 Virectaria sp. 2 -----

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H. minutiflora 2 -----  
 S. becquetii TTGTATCGGAAAGCTGACAGGGAGATATATATATC--TAAGATATATATCCCTCTATATTGAATTTGCCGATACGGAAA--TGATAAAAT--C  
 S. xanthotricha TTGTATCGGAAAGCTGACAGGGAGATATATATATC--TAAGATATATATCCCTCTATATTGAATTTGCCGATACGGAAA--TGATAAAAT--C  
 S. elliptica TTGTATCGGAAAGCTGACAGGGAGATATATATATC--TAAGATATATATCCCTCTATATTGAATTTGCCGATACGGAAA--TGATAAAAT--C  
 T. capsulifera TTGCATCGGAAAGATAACAGGGAGATATATATATATC--TAAGATATATATCCCTCTATATTGAATTTGCCGATACGGAAA--TGATAAAAT--C  
 V. angustifolia 1 TTGCATCGGAAAGCTAACAGGGAGATATATATATATC--TAAGATATATATCCCTCTATATTGAATTTGCCGATACGGAAA--TGATAAAAT--C  
 V. belingana 1 TTGCATCGGAAAGCTAACAGGGAGATATATATATATC--TAAGATATATATCCCTCTATATTGAATTTGCCGATACGGAAA--TGATAAAAT--C  
 V. belingana 2 TTGCATCGGAAAGCTAACAGGGAGATATATATATATC--TAAGATATATATCCCTCTATATTGAATTTGCCGATACGGAAA--TGATAAAAT--C  
 V. belingana 3 TTGCATCGGAAAGCTAACAGGGAGATATATATATATC--TAAGATATATATCCCTCTATATTGAATTTGCCGATACGGAAA--TGATAAAAT--C  
 V. herbacoursi 1 TTGCATCGGAAAGCTAACAGGGAGATATATATATATC--TAAGATATATATCCCTCTATATTGAATTTGCCGATACGGAAA--TGATAAAAT--C  
 V. herbacoursi 2 -----  
 V. major 1 TTGCATCGGAAAGCTAACAGGGAGATATATATATATC--TAAGATATATATCCCTCTATATTGAATTTGCCGATACGGAAA--TGATAAAAT--C  
 V. major 2 -----  
 V. multiflora 1 TTGCATCGGAAAGCTAACAGGGAGATATATATATATC--TAAGATATATATCCCTCTATATTGAATTTGCCGATACGGAAA--TGATAAAAT--C  
 V. multiflora 2 TTGCATCGGAAAGCTAACAGGGAGATATATATATATC--TAAGATATATATCCCTCTATATTGAATTTGCCGATACGGAAA--TGATAAAAT--C  
 V. multiflora 3 TTGCATCGGAAAGCTAACAGGGAGATATATATATATC--TAAGATATATATCCCTCTATATTGAATTTGCCGATACGGAAA--TGATAAAAT--C  
 V. multiflora 4 TTGCATCGGAAAGCTAACAGGGAGATATATATATATC--TAAGATATATATCCCTCTATATTGAATTTGCCGATACGGAAA--TGATAAAAT--C  
 V. procumbens 2 TTGCATCGGAAAGCTAACAGGGAGATATATATATATC--TAAGATATATATCCCTCTATATTGAATTTGCCGATACGGAAA--TGATAAAAT--C  
 V. procumbens 3 TTGCATCGGAAAGCTAACAGGGAGATATATATATATC--TAAGATATATATCCCTCTATATTGAATTTGCCGATACGGAAA--TGATAAAAT--C







S. elliptica CGGGACGGAAATGCCCTTTTCTT-----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCC  
T. capsulifera CGGGACGGAAATGCCCTTTTCTT-----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATCCC  
V. angustifolia 1 CGGGACGGAAACGCCCTTTTCTT----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATTCC  
V. belingana 1 CGGGACGGAAACGCCCTTTTCTT-----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATTCC  
V. belingana 2 CGGGACGGAAACGCCCTTTTCTT----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATTCC  
V. belingana 3 CGGGACGGAAACGCCCTTTTCTT----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATTCC  
V. herbacoursi 1 --GGACGGAAACGCCCTTTTCTT-----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATTCC  
V. herbacoursi 2 --GGACGGAAACGCCCTTTTCTT-----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATTCC  
V. major 1 CGGGACGGAAACGCCCTTTTCTT----ATCACAAAGTCAAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATTCC  
V. major 2 CGGGACGGAAACGCCCTTTTCTT----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATTCC  
V. multiflora 1 CGGGACGGAAACGCCCTTTTCTT----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATTCC  
V. multiflora 2 CGGGACGGAAACGCCCTTTTCTT----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATTCC  
V. multiflora 3 CGGGACGGAAACGCCCTTTTCTT----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATTCC  
V. multiflora 4 CGGGACGGAAACGCCCTTTTCTT----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATTCC  
V. procumbens 2 CGGGACGGAAACGCCCTTTTCTT----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATTCC  
V. procumbens 3 CGGGACGGAAACGCCCTTTTCTT----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATTCC  
Virectaria sp. 1 CGGGACGGAAACGCCCTTTTCTT----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACCATCTTTGAGCAAGAAATTCC  
Virectaria sp. 2 CGGGACGGAAACGCCCTTTTCTT----ATCACAAAGTCTAGCGTTCTATATGATATACATACAAAATTACC-----

1710

H. minutiflora 2 CATTGGAATGATTTACAATCGATATAACTACTCATACTGAA-----GTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGAT  
S. becquetii CATTGGAATGATTTACAATCGATATAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGAT  
S. xanthotricha CATTGGA-TGATTTACAATCGATATAACTACTCATACTGAA-CTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGAT  
S. elliptica CATTGGAATGATTTACAATCGATATAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGAT  
T. capsulifera CATTGGAATGATTTACAATCGATATAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGAT  
V. angustifolia 1 CATTGGAATGATTTACAATCGATAGAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATACAGTACCTAGAT  
V. belingana 1 CATTGGAATGATTTACAATCGATATAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATACAGTACCTAGAT  
V. belingana 2 CATTGGAATGATTTACAATCGATATAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATACAGTACCTAGAT  
V. belingana 3 CATTGGAATGATTTACAATCGATATAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATACAGTACCTAGAT  
V. herbacoursi 1 CATTGGAATGATTTACAATCGATATAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGAT  
V. herbacoursi 2 CATTGGAATGATTTACAATCGATATAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGAT  
V. major 1 CATTGGAATGATTTACAATCGATATAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATACAGTACCTAGAT  
V. major 2 CATTGGAATGATTTACAATCGATATAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATACAGTACCTAGAT  
V. multiflora 1 CATTGGAATGATTTAAATCGATAGAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTTAGATCCAAGAAATCCAGAAA-TAGAA  
V. multiflora 2 CATTGGAATGATTTACAATCGATATAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGAT  
V. multiflora 3 CATTGGAATGATTTACAATCGATATAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATACAGTACCTAGAT  
V. multiflora 4 CATTGGAATGATTTAAATCGATAGAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTTAGATCCAAGAAATCCAGAAA-TAGAA  
V. procumbens 2 CATTGGAATGATTTACAATCGATAGAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATACAGTACCTAGAT  
V. procumbens 3 CATTGGAATGATTTACAATCGATAGAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATACAGTACCTAGAT  
Virectaria sp. 1 CATTGGAATGATTTACAATCGATATAACTACTCATACTGAAACTTCCAAAGTACTCTTTTTAAGATCCAAGAAATCCAGTACCTAGAT  
Virectaria sp. 2 -----

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H. minutiflora 2 AAAACTTCGGAACCCCTTTCTTCTTTTAAATTGACACAGACCCCATTTT  
S. becquetii AAAACTTCGGAACCCCTTTCTTCTTTTAAATTGACACAGACCCCATTTT  
S. xanthotricha AAAACTTCGGAACCCCTTTCTTCTTTTAAATTGACACAGACCCCATTTT  
S. elliptica AAAACTTCGGAACCCCTTTCTTCTTTTAAATTGACACAGACCCCATTTT  
T. capsulifera AAAACTTCGGAACCCCTTTCTTCTTTTAAATTGACACAGACCCCATTTT  
V. angustifolia 1 AAAACTTCGGAACCCCTTTCTTCTTTTAAATTGACACAGACCCCATTTT  
V. belingana 1 AAAACTTCGGAACCCCTTTCTTCTTTTAAATTGACACAGACCCCATTTT  
V. belingana 2 AAAACTTCGGAACCCCTTTCTTCTTTTAAATTGACACAGACCCCATTTT  
V. belingana 3 AAAACTTCGGAACCCCTTTCTTCTTTTAAATTGACACAGACCCCATTTT  
V. herbacoursi 1 AAAACTTCGGAACCCCTTTCTTCTTTTAAATTGACACAGACCCCATTTT  
V. herbacoursi 2 AAAACTTCGGAACCCCTTTCTTCTTTTAAATTGACACAGACCCCATTTT  
V. major 1 AAAAC-----CCCTTCTTCTTTTAAATTGACACAGACCCCATTTT  
V. major 2 AAAAC-----CCCTTCTTCTTTTAAATTGACACAGACCCCATTTT  
V. multiflora 1 AAAAATTC-GAACCCCTTTCTTCTTTTAAATTGACAAA---CCCATTTT  
V. multiflora 2 AAAACTTCGGAACCCCTTTCTTCTTTTAAATTGACACAGACCCCATTTT  
V. multiflora 3 AAAACTTCGGAACCCCTTTCTTCTTTTAAATTGACACAGACCCCATTTT  
V. multiflora 4 AAAAATTC-GAACCCCTTTCTTCTTTTAAATTGACAAA---CCCATTTT  
V. procumbens 2 AAAACTTCGGAACCCCTTTCTTCTTTTAAATTGACACAGACCCCATTTT  
V. procumbens 3 AAAACTTCGGAACCCCTTTCTTCTTTTAAATTGACACAGACCCCATTTT  
Virectaria sp. 1 AAAACTTCGGAACCCCTTTCTTCTTTTAAATTGACACAGACCCCATTTT  
Virectaria sp. 2 -----

## DARSTELLUNG DES EIGENANTEILS

### Kapitel 1: " **Sabiceae and Virectarieae (Rubiaceae): One or two tribes? – New tribal and generic limits of Sabiceae and biogeography of *Sabicea* s.l.**"

Fast alle DNA Proben wurden von mir an der Universität Bayreuth isoliert. Die ITS Sequenzen wurden von mir gewonnen, die *trnT-F* Sequenzen stammen von Sylvain G. Razafimandimbison (Universität Stockholm). Die Analyse der Daten wurde ausschließlich von mir durchgeführt. Die erste Version des Manuskriptes stammt aus meiner Feder, ebenso die Überarbeitung nach einer kritischen Durchsicht durch Sylvain G. Razafimandimbison, Sigrid Liede-Schumann und Birgitta Bremer.

### Kapitel 2: "**Phylogenetic relationships within Sabiceae s.l. (Ixoroideae, Rubiaceae) – phylogeography of *Virectaria* Bremek.**"

Fast alle DNA Proben wurden von mir an der Universität Bayreuth isoliert. Die zusätzlichen ITS Sequenzen ebenso wie die *rpoC1* Sequenzen wurden von mir, teilweise mit Unterstützung der Technischen Assistentin Frau Angelika Täuber, in Bayreuth gewonnen. Die zusätzlichen and *trnT-F* Sequenzen ebenso wie der ETS Datensatz stammen von Sylvain G. Razafimandimbison (Universität Stockholm). Die Analyse der Daten wurde ausschließlich von mir durchgeführt, ebenso habe ich die erste Version des Manuskriptes geschrieben, die von Sylvain G. Razafimandimbison, Sigrid Liede-Schumann und Birgitta Bremer editiert wurde.

### Kapitel 3 " **Taxonomic Revision of Neotropical *Sabicea* (Rubiaceae – Ixoroideae)"**

Die morphologischen Untersuchungen wurden alleine von mir durchgeführt, die Landkarten und Illustrationen ausschließlich von mir angefertigt. Die Abgrenzung einiger kritischer Taxa erfolgte in Diskussion mit Sigrid Liede-Schumann. Die SEM Aufnahmen wurden zusammen mit Ulrich Meve angefertigt. Die erste Version des Manuskriptes stammt aus meiner Feder, ebenso die Überarbeitung nach einer kritischen Durchsicht durch Sigrid Liede-Schumann und Ulrich Meve.

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## **ERKLÄRUNG**

Hiermit erkläre ich, Saleh Ahammad Khan, dass ich die vorliegende Arbeit selbständig verfasst und dabei keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.

Ferner erkläre ich, dass ich diese Arbeit weder einer anderen Prüfungsbehörde vorgelegt noch anderweitig mit oder ohne Erfolg versucht habe, eine Dissertation einzureichen oder mich der Doktorprüfung zu unterziehen.

Bayreuth, den 03 September 2007

Saleh Ahammad Khan