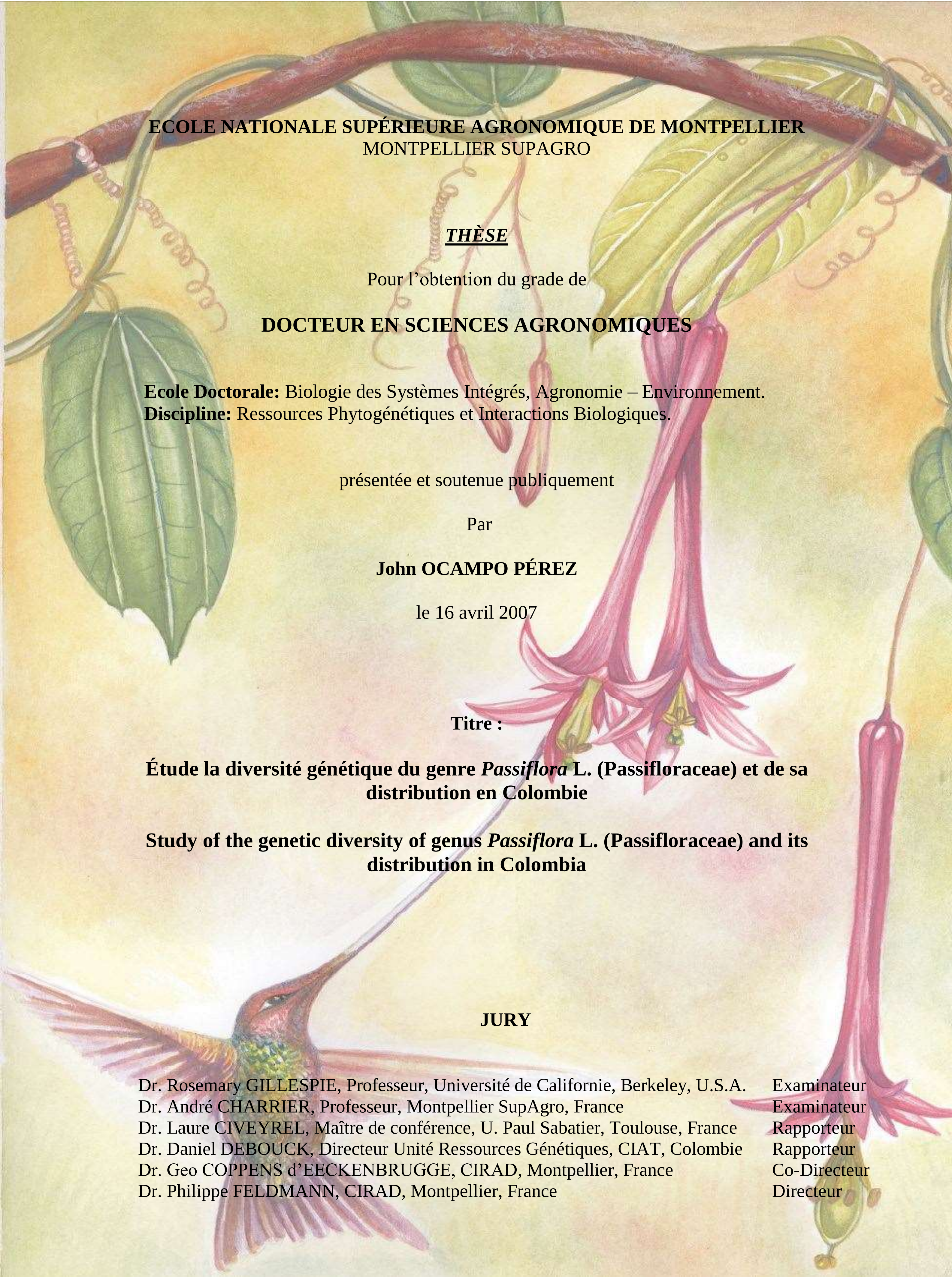

ECOLE NATIONALE SUPÉRIEURE AGRONOMIQUE DE MONTPELLIER
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THÈSE

Pour l'obtention du grade de

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Étude la diversité génétique du genre *Passiflora* L. (Passifloraceae) et de sa distribution en Colombie

Study of the genetic diversity of genus *Passiflora* L. (Passifloraceae) and its distribution in Colombia

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DEDICATED TO MY FAMILY

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SUMMARY

Given its economic importance, the characterization of genus *Passiflora* is seen as a priority for Andean countries and specific strategies are needed to optimize its use and conservation. The objective of this thesis was to study the distribution and organization of Passifloraceae in Colombia, with a triple aim of exploring the diversity of available genetic resources, evaluating the risk of their erosion and their potential as an indicator group for the conservation of biodiversity, particularly in the coffee growing zone.

Colombian Passifloraceae were listed, gathering and georeferencing 3,930 records, for a total of 167 species. Forty-two produce an edible fruit, and nine are commercially cultivated. Most of the 58 endemic species, including 37 narrow endemics, are Andean species of subgenera *Tacsonia* and *Decaloba*. Applying the UICN criteria, 70% of the species appear threatened and three extinct. When compared with other regions, the Andes of Colombia and Ecuador constitute the center of *Passiflora* diversity, whose elevational distribution shows a small peak below 500 m, and two higher ones at 1000-2,000 and 2,500-3,000 m. This pattern corresponds to divergent adaptive trends among infrageneric divisions, subgenus *Tacsonia* contributing markedly to the highest peak.

The climatic data associated with our 3,930 records allowed modeling and summing the distribution of 80 species, so predicting the distribution of species richness. Nine areas with very high richness, but no particular endemism, were identified in the Andean region, three of which correspond to collection gaps as they do not appear on the map of observed diversity. Their striking correspondence with coffee growing zone ecotopes imposes a strategy integrating agricultural and environmental management at the landscape level for preserving this threatened richness as well as a region of particular importance for the country. Both aspects may be combined if Passifloraceae can be used as an indicator of biodiversity in this region, which seems justified by their diversity and characteristics, including multiple ecological interactions with many organisms.

Morphological variation was studied in 124 accessions from 60 *Passiflora* species and eight subgenera with 127 descriptors. Twenty-four quantitative traits showing

high variation among subgenera were selected. The three principal components of variation are associated with (i) flower length; (ii) flower width and bract shape; and (iii) peduncle branching, stem width and leaf length. The projection of accessions in the resulting tridimensional space consistently separates subgenera. A similar selection of 32 qualitative traits, and four categorized quantitative traits, allowed classifying our sample consistently. Most discriminating characters include size of stems and leaves, presence of tendrils, number and distribution of extrafloral nectaries, dimensions and general shape of bracts, width and length of flowers and corona complexity. Our results support seven of the eight Killip's subgenera of our sample, but no infrasubgeneric classifications. However, the new classification of subgenus *Decaloba* by Feuillet & MacDougal was partly supported. They converge on many points with previous phylogenetic results obtained with DNA sequences, although the latter group subgenera *Tacsonia* and *Distephana* with subgenus *Passiflora*.

The chloroplast and mitochondrial DNA diversity of 213 genotypes belonging to 151 *Passiflora* species and 15 subgenera recognized by Killip was studied by PCR-RFLP, identifying 280 haplotypes for cpDNA and 372 for mtDNA. The principal co-ordinate analysis on cpDNA data allowed visualizing a strong separation of subgenera *Apodogyne*, *Decaloba*, *Murucuja*, *Pseudomurucuja* and *Psilanthus* (constituting the "*Decaloba* group"), while the neighbor-joining cluster analysis showed three well-supported clusters within *Passiflora*, corresponding to the three major divisions of the taxonomy proposed by Feuillet & MacDougal. The first one, named the "*Passiflora* group", includes subgenera *Calopathanthus*, *Deidamioides*, *Distephana*, *Dysosmia*, *Dysosmioides*, *Manicata*, *Passiflora*, *Tacsonia*, and *Tacsonioides*, with a very loose substructure and considerable intraspecific variation. The second one includes subgenus *Astrophea*, and the third is the '*Decaloba* group'. The outgroup species, take an undefined position among the *Passiflora* clusters. The phenogram from mtDNA data separates four moderately supported clusters. As for cpDNA, a first one corresponds to the '*Decaloba* group'. The other are different, as subgenera *Astrophea* and *Tryphostemmatoides* appear integrated within the '*Passiflora* group', while subgenus *Tacsonia* forms a uniform distinct cluster, close to another one comprising species of *Passiflora* series *Kermesinae*, *Simplicifoliae*, *Lobatae*, and *Menispermifoliae*. The

analyses of cpDNA and mtDNA give different pictures of the *Passiflora* diversity, in the position of the outgroup, the relative position of four subgenera, and the relationships between species, which we attribute to different rates of evolution and modes of transmission of the chloroplastic and mitochondrial genomes, combined with reticulate evolution in the genus.

***Keywords*:** *Passiflora* L., Colombia, Andes, coffee growing zone, distribution, biodiversity, endemism, morphological descriptors, PCR-RFLP, chloroplast, mitochondria.

RÉSUMÉ

De par son importance économique, la caractérisation du genre *Passiflora* est considérée prioritaire par les pays andins, impliquant des stratégies spécifiques pour optimiser son utilisation et sa conservation. L'objectif de cette thèse est d'étudier la distribution et l'organisation des Passifloraceae en Colombie, dans le triple but d'explorer la diversité des ressources génétiques disponibles, d'évaluer le risque de leur érosion ainsi que leur potentiel comme groupe indicateur pour la conservation de la biodiversité, en particulier dans la région caféière.

La liste des espèces colombiennes a été établie en rassemblant et localisant 3.930 registres, pour un total de 167 espèces, dont 42 produisent un fruit comestible et neuf sont cultivées commercialement. La plupart des 58 espèces endémiques, y compris 37 endémiques étroites, sont des espèces andines des sous-genres *Tacsonia* et *Decaloba*. En appliquant les critères de l'UICN, 70% des espèces semblent menacées et trois éteintes. Par comparaison avec d'autres régions, les Andes de la Colombie et de l'Equateur constituent le centre de diversité de *Passiflora*, dont la distribution altitudinale montre un petit pic en-deçà de 500 m, et deux plus élevés, vers 1.000-2.000 et 2.500-3.000 m. Ce patron reflète des tendances adaptatives divergentes entre divisions infragénériques, le sous-genre *Tacsonia* contribuant nettement au dernier pic.

Les données climatiques associées à nos 3.930 registres ont permis de modéliser la distribution de 80 espèces et de prédire la distribution de la richesse d'espèces. Neuf zones de richesse très élevée, mais sans niveau d'endémisme particulier, ont été identifiées dans la région andine. Trois d'entre elles n'ont pas été prospectées. La correspondance entre ces neuf zones et des ecotopes caféiers impose une stratégie intégrant la gestion agricole et environnementale au niveau du paysage pour préserver en même temps cette richesse biologique et une région d'importance particulière pour le pays. Les deux aspects peuvent être combinés si les Passifloraceae peuvent y être employées comme indicateurs de biodiversité, ce qui semble justifié par leur diversité et leurs caractéristiques, notamment leurs interactions écologiques avec de nombreux organismes.

La variation morphologique a été étudiée parmi 124 accessions de 60 espèces et huit sous-genres de *Passiflora*, avec 127 descripteurs. Vingt-quatre traits quantitatifs variant entre sous-genres ont été retenus. Les trois composants principaux de leur variation sont associés à (i) la longueur de fleur ; (ii) la largeur de fleur et la forme des bractées ; et (iii) la bifurcation du pédoncule, la largeur de tige et la longueur de feuille. La projection des accessions dans l'espace tridimensionnel correspondant sépare bien les sous-genres. Un tri semblable de 32 traits qualitatifs, et de quatre traits quantitatifs catégorisés, a permis de classer notre échantillon de façon cohérente. Les caractères distinctifs incluent la taille des tiges et des feuilles, la présence de vrilles, le nombre et la distribution des nectaires extrafloraux, les dimensions et la forme générale des bractées, la largeur et la longueur des fleurs et la complexité de la couronne. Nos résultats appuient sept des huit sous-genres de Killip inclus dans l'échantillon, mais aucune classification infrasubgénérique, sauf, pour partie, la nouvelle classification du sous-genre *Decaloba* par Feuillet & MacDougal. Ils convergent sur de nombreux points avec des études phylogénétiques à partir de séquences d'ADN, bien que celles-ci unissent les sous-genres *Tacsonia* et *Distephana* au sous-genre *Passiflora*.

L'analyse, par PCR-RFLP, de l'ADN chloroplastique et mitochondrial de 213 accessions de 151 espèces de *Passiflora* et 15 sous-genres a permis d'identifier 280 haplotypes pour le premier et 372 pour le second. L'analyse factorielle des données d'ADNcp sépare fortement les sous-genres *Apodogyne*, *Decaloba*, *Murucuja*, *Pseudomurucuja* et *Psilanthus* (constituant le "groupe *Decaloba*"), tandis que la classification par la méthode du neighbor-joining met en évidence trois groupes majeurs dans *Passiflora*, correspondant aux trois divisions principales de la taxonomie proposée par Feuillet & MacDougal. Le premier, appelé "groupe *Passiflora*", inclut les sous-genres *Calopathanthus*, *Deidamioides*, *Distephana*, *Dysosmia*, *Dysosmioides*, *Manicata*, *Passiflora*, *Tacsonia* et *Tacsonioides*, avec une sous-structure très lâche et une variation intraspécifique considérable. Le second inclut le sous-genre *Astrophea*, et le troisième est le "groupe *Decaloba*". Les espèces du groupe extérieur prennent une position indéfinie entre les groupes de *Passiflora*. Le phénogramme résultant de l'analyse de l'ADNmt sépare quatre groupes. Comme pour l'ADNcp, un premier correspond au "groupe

Decaloba". Les autres sont différents, car les sous-genres *Astrophea* et *Tryphostemmatoides* sont intégrés avec le ‘groupe *Passiflora*’, tandis que le sous-genre *Tacsonia* forme un groupe différencié et homogène, proche d’un groupe plus varié d’espèces des séries *Kermesinae, Simplicifoliae*, *Lobatae* et *Menispermifoliae* du sous-genre *Passiflora*. Les analyses des deux génomes, chloroplastique et mitochondrial, donnent donc des images divergentes de la diversité de *Passiflora*, par la position des groupes extérieurs, la position relative de quatre sous-genres, et les relations entre espèces. Ces divergences semblent liées à des différences dans les taux d'évolution et dans leur mode de transmission, en relation avec une évolution réticulée dans le genre.

Mots-clés: *Passiflora* L., Colombie, Andes, région caféière, distribution, biodiversité, endémisme, descripteurs morphologiques, PCR-RFLP, chloroplastes, mitochondries.

RESUMEN

Teniendo en cuenta su importancia económica, la caracterización del género *Passiflora* es considerada una prioridad por los países andinos y se necesitan estrategias específicas para optimizar su uso y conservación. El objetivo de esta tesis fue estudiar la distribución y organización de las Passifloraceae de Colombia, con un triple objetivo de analizar la diversidad de los recursos genéticos disponibles, evaluar el riesgo de su erosión así como su potencial como grupo indicador para la protección de la biodiversidad, particularmente en la zona cafetera.

Las especies colombianas fueron inventoriadas con base en 3.930 registros, para un total de 167 especies, de las cuales 42 producen fruto comestible y nueve son cultivadas comercialmente. La mayoría de las 58 especies endémicas, incluyendo 37 de distribución restringida, son principalmente andinas, de los subgéneros *Tacsonia* y *Decaloba*. Aplicando los criterios de la UICN, 70 % de las especies aparecen en peligro y tres son consideradas extintas. En comparación con otras regiones, los Andes de Colombia y Ecuador constituyen el centro de diversidad de *Passiflora*, cuya distribución altitudinal muestra un leve pico debajo de 500 m, y dos más marcados en los 1.000-2.000 y 2.500-3.000 m. Este patrón refleja tendencias adaptativas según divisiones infragenéricas, con particular contribución del subgénero *Tacsonia* al tercer pico.

Los datos climáticos relacionados con los 3.930 registros permitieron modelizar y sumar la distribución de 80 especies, y predecir la distribución de su diversidad. Nueve zonas ultra-diversas fueron identificadas en la región andina, tres de ellas subexploradas. Estas áreas no muestran un nivel de endemismo particular. La correspondencia entre ellas y los ecotopos cafeteros impone una estrategia de conservación que integre la gestión agrícola y el medio ambiente a escala del paisaje para preservar al mismo tiempo esta riqueza biológica y una región de especial importancia para el país. Ambos aspectos pueden ser combinados si se emplean las Passifloraceae como un grupo indicador de biodiversidad en esta región. Esto es justificado por su diversidad y características particulares, incluyendo sus múltiples interacciones con diferentes organismos.

La variación morfológica fue estudiada en 124 accesiones de 60 especies de *Passiflora*, y ocho subgéneros de Killip, usando 127 descriptores. Por su diferenciación entre subgéneros, 24 descriptores cuantitativos fueron seleccionados para un análisis de componentes principales. Los tres primeros componentes están relacionados con (i) longitud de la flor; (ii) ancho de la flor y forma de la bráctea; (iii) bifurcación del pedúnculo, diámetro del tallo y longitud de la hoja. La proyección de las accesiones en un espacio tridimensional muestra una clara separación entre subgéneros. Una selección de 32 caracteres cualitativos y cuatro cuantitativos categorizados ha permitido clasificar la muestra de manera coherente. Los caracteres discriminantes incluyen tamaño del tallo y la hoja, presencia de zarcillos, número y distribución de los nectarios extraflorales, dimensiones y forma general de la bráctea, ancho y longitud de flor y complejidad de la corona. Los resultados soportan siete de los ocho subgéneros de Killip representados en la muestra, pero ninguna clasificación infra-subgenérica, con la excepción parcial del subgénero *Decaloba sensu* Feuillet & MacDougal. El análisis converge en muchos puntos con los estudios filogenéticos realizados a partir de secuencias de ADN, aunque éstos agrupan los subgéneros *Tacsonia* y *Distephana* con el subgénero *Passiflora*.

Los genomas cloroplástico y mitocondrial de 213 representantes de 151 especies y 15 subgéneros de *Passiflora* fueron estudiados por PCR - RFLP, identificando 280 haplotipos para ADNcp y 372 para ADNmt. El análisis factorial de los datos de ADNcp permitió visualizar una fuerte separación de los subgéneros *Apodogyne*, *Decaloba*, *Murucuja*, *Pseudomurucuja* y *Psilanthus* (constituyendo el "grupo *Decaloba*"), mientras que la clasificación por el método de *neighbor joining* pone en evidencia tres grupos bien soportados dentro de *Passiflora*, correspondiendo a tres divisiones principales de la clasificación propuesta por Feuillet & MacDougal. El primero, llamado "grupo *Passiflora*", incluye los subgéneros *Calopathanthus*, *Deidamioides*, *Distephana*, *Dysosmia*, *Dysosmioides*, *Manicata*, *Passiflora*, *Tacsonia*, y *Tacsonioides*, con una débil subestructura y una diferenciación intra-específica considerable. El segundo incluye el subgénero *Astrophea*, y el tercero el "grupo *Decaloba*". Las especies del grupo externo toman una posición indeterminada entre los grupos de *Passiflora*. El fenograma del análisis de ADNmt separa cuatro grupos parcialmente soportados, uno de ellos correspondiendo al mismo "grupo *Decaloba*" del ADNcp. Los subgéneros *Astrophea* y *Tryphostemmatoides* aparecen integrados dentro del "grupo *Passiflora*", mientras que el subgénero *Tacsonia* constituye un grupo distinto y homogéneo, cerca de otro grupo que incluye especies de las series *Kermesinae*, *Simplicifoliae*, *Lobatae*, y *Menispermifoliae* del subgénero *Passiflora*. Así, los análisis de los dos genomas, cloroplástico y mitocondrial, muestran imágenes divergentes de la diversidad de *Passiflora*, esencialmente por la posición del grupo externo, la posición relativa de los cuatro subgéneros, y las relaciones entre especies. Estas divergencias parecen ligadas a las diferencias en las tasas de evolución y el modo de transmisión de los genomas, así como a una evolución reticulada en el género.

Palabras clave: *Passiflora* L., Colombia, Andes, zona cafetera, distribución, biodiversidad, endemismo, descriptores morfológicos, PCR-RFLP, cloroplasto, mitocondria.

OBJECTIVES

General objectives

To study the distribution and organization of the diversity of the Passifloraceae of Colombia, with a triple aim of exploring the diversity of available genetic resources, evaluating the risk of their erosion and their potential as an indicator group for the conservation of biodiversity, particularly in the Colombian coffee growing zone.

Specific objectives

- To map the distribution and the diversity of the Passifloraceae species of Colombia using a Geographic Information System (GIS).

- To characterize the morphologic and molecular diversity at inter- and intra-specific levels.

- To evaluate the potential of *Passiflora* as an indicator group to evaluate the risks of biodiversity erosion and take them into account in the development of strategies for *in situ* genetic resources management and the conservation of the corresponding natural habitats.

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ANNEXES

Front cover: *Passiflora trinervia* (Juss.) pollinated by a sword-billed hummingbird (*Ensifera ensifera* Boissoneau) in the Colombian Andes (drawing by Jesus Salcedo).

Photographs by:

John Ocampo
Passiflora alata Curtis, *P. antioquiensis* Karst., *P. arborea* Spreng., *P. bogotensis* Benth, *P. caerulea* L., *P. capsularis* L., *P. coriacea* Juss., *P. edulis* f. *edulis* Sims, *P. edulis* f. *flavicarpa* Degener, *P. emarginata* Humb. & Bonpl., *P. erytrophylla* Mast., *P. flexipes* Triana & Planch., *P. foetida*, L., *P. lanata* (Juss.) Poir., *P. linearistipula* Escobar, *P. magdalenae* Triana & Planch., *P. maliformis* L., *P. manicata* (Juss) Pers., *P. parritae* (Mast.) Bailey, *P. popenovii* Killip, *P. quadrangularis* L., *P. rubra* L., *P. sphaerocarpa* Triana & Planch., *P. tarminiana* Coppens & Barney, *P. tenerifensis* Escobar, *P. trinervia* (Juss.) Poir., *P. tripartita* var. *mollissima* Holm-Nielsen & Jørgensen, *P. vitifolia* Kunth.

Alvinxon Castro
Passiflora arbelaezii Uribe

Geo Coppens d'Eeckenbrugge
Passiflora ligularis Juss.

Gustavo Morales
Passiflora longipes Juss.

CHAPTER I

General introduction

I.1. Introduction

I.1.1. History

Some plants have received attention from man because they are important to him as sources of food, shelter, medicine, or even narcotics. But the first time passion flowers caught the attention of Europeans, it was for another reason, for the Spaniards who first encountered these plants in the New World in the 16th century, saw in them the elements of the passion of Christ, and a sign that the New World would successfully be converted to Christianity (Uribe 1955a). This religious symbolism gave these plants their common name of *Flos Passionis*, or “passion flowers”. The Spanish Jesuit Juan Romero presented the first drawing to Pope Paul V (Camollo Borgense) in 1608. A few years later, many similar drawings were made available to a wider audience in Italy and Germany (Kugler & King, 2004). The botanical features in these drawings were transformed to support the religious interpretation very explicitly (Figure 1).

Figure 1. First drawings of *Passiflora* representing the passion of Christ: left, by Dominican monk Simone Parlasca's 1609; right, by Eugenio Petrelli in 1610 (http://www.flwildflowers.com/passiflora.html).

I.1.2. Taxonomy and general distribution

The family Passifloraceae is placed in the order Malpighiales (Judd et al., 2002), and divided in two tribes, *Paropsieae* and *Passifloreae*, with ca. 630 species distributed around the world. Of the 20 currently recognized genera, four are present in America (*Ancistrothyrsus*, *Dilkea*, *Mitostemma* and *Passiflora*). *Passiflora* is the largest one, comprising approximately 525 species, mostly distributed in the tropical regions of America, from the coastal zones up to 3,800 m in Andean páramos (Holm-Nielsen et al., 1988). Only 22 species grow in the Old World, in the tropical and sub-tropical regions of Southeast Asia and the Austral Pacific (Figure 2).

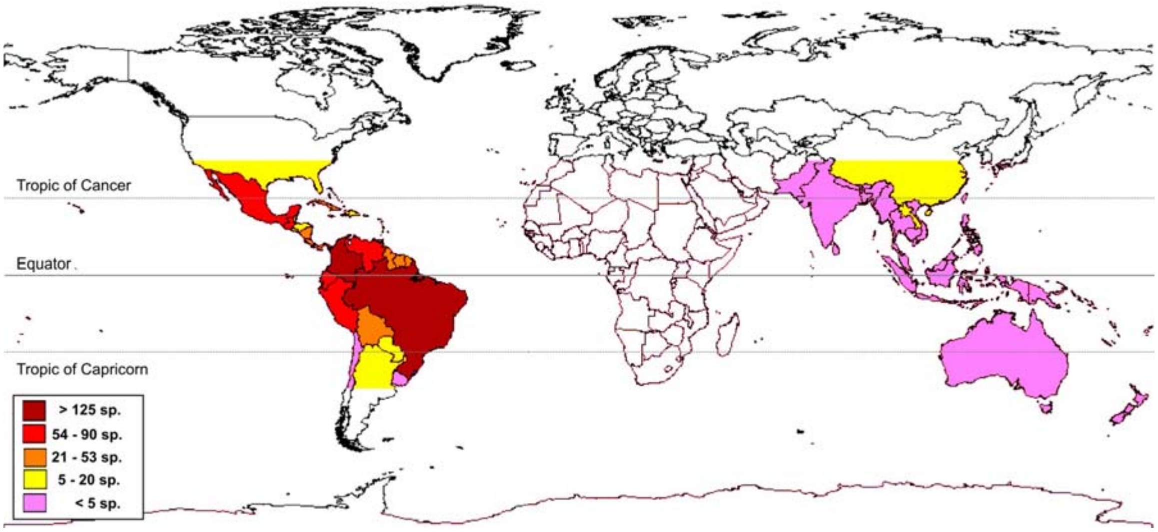


Figure 2. Distribution of genus *Passiflora* in the world (by John Ocampo).

According to Killip (1938), the genus *Passiflora* was created by Linnaeus in 1753, who described 24 species in his *Species Plantarum*, a number increased to 35 by Lamarck (1789). The first extensive monograph of the family was published by Cavanilles in 1790 with 43 species treated. He was followed by authors like Jussieu (1805), De Candolle (1822, 1828), Masters (1872, 1877), and Harms (1898, 1925), who described about 250 species divided into 21 sections (Killip, 1938). In his monograph of 1938, *The American Species of Passifloraceae*, Killip made the most extensive description of New World species, classifying 355 species into four and 22 subgenera, on the basis of floral morphology (Annex 1). In Colombia, the priest Uribe (1954, 1955a, 1955b, 1957, 1958, 1972) described several new species and Escobar (1986, 1987, 1988a, 1988b, 1989, 1990, 1990 inedited, 1994) revised subgenera *Distephana*, *Manicata* (syn. *Granadillastrum*), *Rathea* and *Tacsonia*, including *Tacsoniopsis* in the latter, and described one additional subgenus, *Porphyropathanthus*. She passed away in 1993, leaving an inedited document on her revision of subgenus *Astrophea*. In the last decade, MacDougal and Feuillet have published many papers including the description of about 15 new species, mainly of the subgenera *Decaloba* and *Astrophea* (MacDougal, 1992, 1994, 2006; Feuillet, 2002, 2004). Recently, Feuillet & MacDougal (2003; Annex 2) proposed a new infrageneric classification in *Passiflora.* According to their proposal, based on morphological characters, four subgenera would be recognized: *Astrophea* and *Deidamioides*, from South and Central America, *Decaloba*, from America, Southeast Asia and Australia, and *Passiflora,* exclusively from America (Ulmer & MacDougal, 2004). Additionally, they downgraded genus *Tetrastylis* as a section of subgenus *Deidamioides*.

I.1.3. Botany

The plants of genus *Passiflora* are mostly climbers with herbaceous or woody stems and axillary tendrils, or very rarely arbustive or arborescent. Their leaves are alternate, generally simple, entire, lobed or palmate. Stipules are generally present at the base of petioles; the tendrils are also axillary, arising from sterile pedicels. Passion flowers are bisexual or unisexual, regular. Figure 3 shows the different elements of the flowers of two species of subgenera *Passiflora* and *Tacsonia*. The large receptacle is often hollowed out like a cup or basin, and bears numerous filamentous or annular appendages between the corolla and stamens, which may be brightly colored and form a conspicuous corona of great diversity. The calyx is composed of 3–5 free or basely connate, imbricate sepals, and the corolla of 3–5 free or basely connate petals, which may be absent in rare cases. The 3–5 (10) stamens are inserted either at the bottom of the perianth, or at the base or top of the gynophore; their filaments are subulate or filiform, free or monoadelphous, sheathing the gynophore; the anthers are versatile, introrse, two-celled, with a longitudinal dehiscence. The ovary is superior, more or less stipitate, very rarely sessile, unilocular, consisting of 3–5 united carpels. The styles are equal in number to the placentae, cohering at the base, distinct at the top, spreading, simple or branched, or separate; stigma are clavate or peltate, sometimes bilobed; The ovules are numerous, anatropous, 1–2 seriate, attached to 3–5 parietal linear placentae by longer or shorter funicles, enlarged into a cupule at the umbilicus. The fruit is a 1-celled, indehiscent berry or a capsule with 3–5 semi-placentiferous valves. Seeds are numerous, with a funicle dilated into a pulpy cupuliform or saccate aril; their testa is crustaceous, foveolate, easily separable from the membranous endopleura, which bears a longitudinal raphe. The straight embryo occupies the axis of a fleshy dotted albumen; the cotyledons are foliaceous and flat, the radicle cylindric, near the hilum, centrifugal.

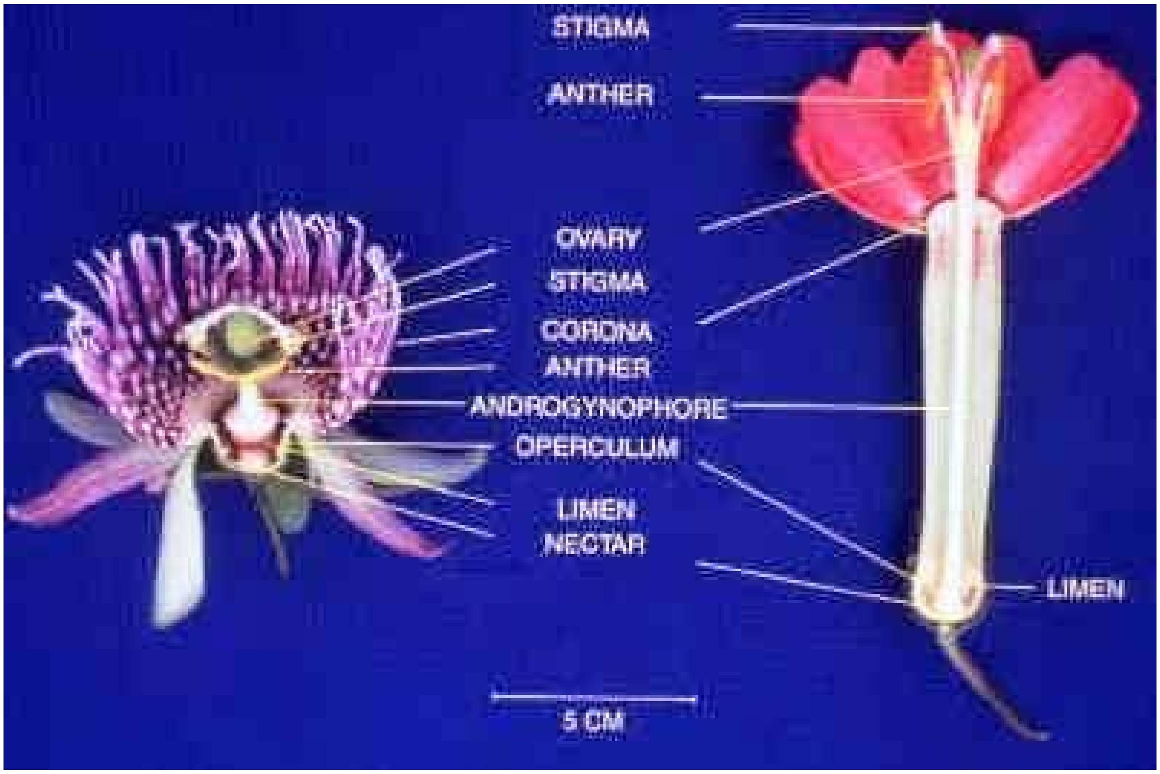


Figure 3. Floral elements in the subgenera *Passiflora* (left, *P. ligularis*) and *Tacsonia* (right, *P. tripartita* var. *mollissima*). Photograph by Geo Coppens d'Eeckenbrugge.

I.1.4. Biology of reproduction

The high variability of flower shape and colors in *Passiflora* corresponds to several pollination syndromes, showing adaptations to insects, birds and bats (Figure 4). The pollinator behavior may be influenced by morphological as well as chemical floral features (Varassin et al., 2001). Hypanthium length, corolla and corona color, stigma position, and concentrations of sugars or salt in their nectar rewards are fundamental for each pollinator type. Small bees and wasps are common pollinators of small-flowered species, particularly those of subgenera *Astrophea*, *Decaloba* and *Tryphostemmatoides*. Species with flowers of medium or large size are pollinated by large wasps (*Xylocopa* spp.) mainly in subgenus *Passiflora*. Insect pollination is generally associated with a well-developed corona, with concentric combination of white, yellow and/or purple colors. The width and depth of the flower, the resistance of the operculum closing the nectary chamber, and the distance between the corona and sexual organs are correlated with the size of the insect. Hummingbird pollination syndrome is the second most prevalent one. It is associated with dominant orange, pink or red colors and a tubular general morphology resulting from a tubular hypanthium and/or an erect corona prolonging the floral tube around the androgynophore. Such syndromes are dominant in particular groups. The highest specialization is presented by Andean species of subgenus *Tacsonia* and *P. trinervia* (subgenus *Psilanthus*), whose very long hypanthia are essentially adapted to the sword-billed hummingbird *Ensifera ensifera* Boissoneau (Buchert & Mogens, 2001). The same syndrome is displayed in the bright-red flowers of subgenera *Distephana* and *Murucuja*, pollinated by smaller hummingbird lowland species, such as *Phaethornis superciliosus* L. and *Trochilus polytmus* L. (Snow, 1982). Some species, for example *P. kermesina* and *P. coccinea,* are also visited and apparently pollinated by *Heliconius* butterflies (Benson et al., 1976). Bat-pollination has been described in several species from the Amazon, such as *P. mucronata* Lam. and *P. ovalis* Vell. *ex* Roemer, pollinated by the phyllostomid *Glossophaga soricina* Pallas, as well as in *P. penduliflora* Bert, whose most frequent visitor is the Greater Antillean long-tongued bat *Monophyllus redmani* Leach (Sazima & Sazima, 1978; Kay, 2001). The corresponding pollination syndrome is mainly constituted by nocturnal anthesis, white flowers, the release of an unpleasant odor and a particular arrangement of stigmas and styles.

In many species, rapid movements of the stigmas are observed. When the flower opens, the styles are erect; they then bend, bringing the stigma surface close to the stamens, enabling contact with the pollinator; the styles straighten up again before the flower closes. In some flowers, however, this process is incomplete or even absent, precluding natural pollination (Fouqué & Fouqué, 1980; Escobar, 1985; Ruggiero et al., 1976). The female fertility of these flowers is relatively low, some exhibiting incomplete development of the pistil, while male fertility remains unchanged. The proportion of these male functional flowers varies during flowering, being apparently dependent on the resources the plant has previously expended in fruit production (May & Spears, 1988). Most species open their flowers in the morning, until the end of the afternoon, favoring pollen transfer by diurnal pollinators. In bat-pollinated species anthesis logically takes place during the night. In *P. penduliflora*, it starts in the early evening and ends in the early morning, giving hummingbirds the possibility to contribute to pollination (Kay, 2001).

High variability in pollen morphology has been described in more than 200 *Passiflora* species (Erdtman, 1952; Presting, 1969; García et al., 2002; Barrios et al., 2005). Pollen grains are generally of medium size, prolate to oblate-spherical, reticulated, with luminae of irregular diameter.

Passiflora species are very generally allogamous. Cross-pollination is favored by the placement of the anthers below the stigma, large, heavy and sticky pollen grains (Nishida, 1958), and frequent physiological self-incompatibility (Bruckner et al., 1999). The genus *Passiflora* contains both self-compatible and self-incompatible species (Vasconcellos, 1991). Ho & Shii (1986) observed that the self-incompatibility reaction takes place in the stigma papillae. Their diallel crosses suggested that it is controlled sporophytically by a single multiallelic locus. Bruckner et al. (1995) first confirmed this result, however they later found evidence for a second site of rejection in the style (Rêgo et al., 1998, 2000), which appeared consistent with the action of a second locus acting at the gametophytic level (Suassuma et al., 2003). According to Escobar (1992), self-compatibility is the rule in subgenera *Tacsonia* and *Manicata*, whose species set seedy fruits after controlled self-pollination.

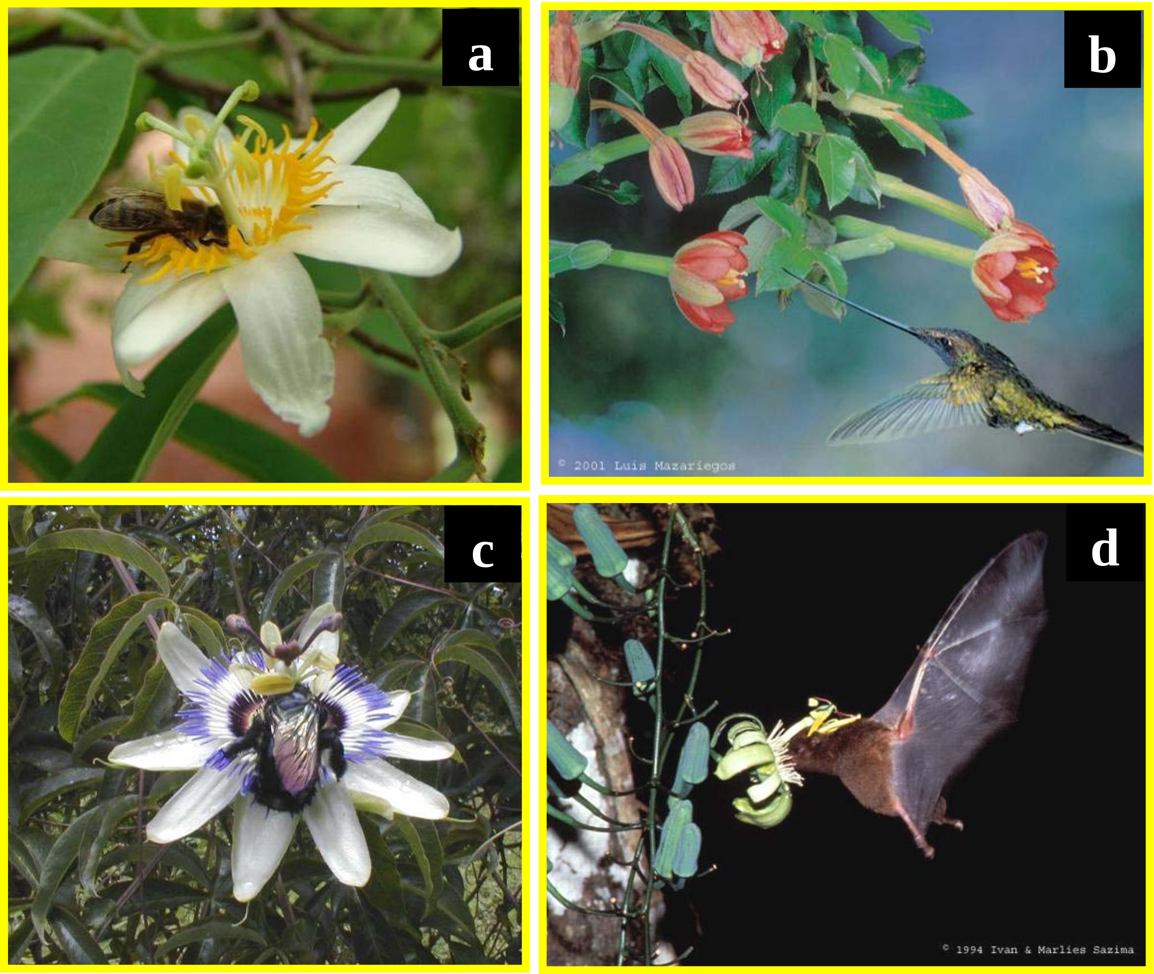


Figure 4. *Passiflora* pollinators: **a.** honey bee on *P. sphaerocarpa*; **b.** sword-billed hummingbird on *P. mixta*; **c.** large wasp on *P. caerulea*; **d.** bat on *P. ovalis*.

As for self-incompatibility, interspecific compatibility appears to be quite variable among *Passiflora* species. Spontaneous hybrids have been observed in subgenus *Tacsonia* and their experimental obtention is relatively easy (Escobar, 1985; Schöniger, 1986). However fertility may decline considerably in subsequent generations, F_2 and backcrosses (R_1), due to reduced flowering or fruiting, exacerbated by poor seed germination and high mortality (Schöniger, 1986). Nonetheless, interspecific compatibility among the most common species of subgenus *Tacsonia* is consistent with evidences of interspecific introgression (Primot et al., 2005; Segura et al., 2005). Hybridization has also been attempted among species of subgenus *Passiflora* to produce new ornamentals of for resistance breeding. Interspecific incompatibility appears more frequent than in subgenus *Tacsonia*. *P. edulis* has often been crossed with the closely related *P. incarnata*, with variable results. Fertile hybrids have been obtained by some researchers (Beal, 1972; Winks et al., 1988) and sterile hybrids by others (Knight, 1991), who resorted to chromosomal doubling to partially restore fertility. Ruberté-Torres & Martín (1974) obtained hybrids from 42 parental combinations of seven passion fruit species. Most hybrids were vigorous with intermediate characteristics of foliage, flowers and fruits. They varied in degree of sterility of pollen and seeds. Payán & Martín (1975) used double pollinations, with compatible and incompatible pollens on different stigmas of the same flowers, and applied hormones to delay flower abscission and overcome incompatibility barriers in 28 crosses involving nine species. More recent reports by Junqueira et al. (2005) appear more optimistic on the feasibility of interspecific crosses, showing positive results from crosses involving 15 species of subgenera *Passiflora* and *Distephana* (*P. coccinea*).

Chromosome numbers are now available for more than 150 *Passiflora* species (Snow & MacDougal, 1993; De Melo et al., 2001). Most species of *Passiflora* are diploid, with $2n = 12$, 18, 20 or 24 chromosomes, although some tetraploids ($2n = 24$), hexaploids ($2n = 36$) and octoploids ($2n = 72$) have been observed (Snow & MacDougal, 1993; De Melo et al. 2001). Several chromosome base numbers ($n = 3, 6, 9$) have been proposed for the genus, however in the absence of a clear understanding of the phylogenetic relationships among species, there has been no consensus (Storey, 1950; Raven, 1975; Snow & MacDougal, 1993; Yockteng, 2003). According to De Melo et al. (2001), $n = 6$ is the most probable base number for the genus, whereas $n = 9$, $n = 10$ and $n = 12$ were considered secondary. However, the second most probable base number $n = 12$, appears to have played an important role in the evolution of the group because it is better represented in other genera of the family (De Melo & Guerra, 2003). Yockteng (2003) and Yockteng & Nadot (2004) presented an alternative hypothesis where $n = 12$ is the ancestral chromosome number of *Passiflora,* as genus *Adenia* (2*n* = 24) was placed as a sister clade to *Passiflora* in their phylogenetic study of the ncpGS sequences.

In *Passiflora*, biparental plastid genome transmission was first suspected by Corriveau & Coleman (1988), following epifluorescence microscopy observations on *P. edulis*. Do et al. (1992) showed that RFLP markers of cpDNA were mostly inherited maternally in crosses between yellow and purple maracuja when the former (*P. edulis* f. *flavicarpa*) was used as female parent, and biparental in the reciprocal cross, suggesting asymmetric post-fertilization exclusion processes. Transmission was paternal in the hybrid '*P. coccinea* Aubl x *P. edulis* f. *flavicarpa*'. Recently, Mráček (2005) observed biparental transmission between *P. menispermifolia* Kunth and *P. oerstedii* Mast., and Muschner et al. (2006) established paternal transmission of cpDNA in four interspecific hybrids of subgenera *Passiflora* and *Dysosmia* and maternal transmission in an interspecific hybrid of subgenus *Decaloba*. All mtDNA were maternally transmitted in the same five hybrids. More recently, Hansen et al. (2007) found paternal or biparental inheritance of cpDNA, in 16 interspecific crosses and maternal inheritance in an intraspecific progeny of *P. costaricensis*, the only species of subgenus *Decaloba* in their sample.

I.1.5. Uses

The discovery of several thousands years old seeds of *Passiflora* from archaeological sites in Virginia, North America, provides strong evidences of the pre-historic use of the fruits by the Amerindian people (Gremillion, 1989). In Colombia, 200 years before Christ, the Malagana people were inspired by a passion flower for a gold jewel (Figure 5; BRC 2007). Most *Passiflora* species present an ornamental interest, thanks to their spectacular shapes and colors, others are of pharmaceutical interest for their sedative, antispasmodic, antibacterial and insecticidal properties, but they are even more appreciated for their edible fruits, which are consumed *in natura* or in preparations such as juices, sherbets and ice cream.

Several species of *Passiflora* have been used extensively in the traditional therapeutics in many countries. *P. edulis* has been used as a sedative, diuretic, anthelmintic, anti-diarrheal, stimulant, tonic and also in the treatment of hypertension, menopausal symptoms, colic of infants in South America (Chopra et al., 1956; Kirtikar & Basu, 1975; Mowrey, 1993). In Nagaland (India), fresh leaves of *Passiflora edulis* are boiled in a little amount of water and the extract is drunk for the treatment of dysentery and hypertension (Jamir et al., 1999). The extract of *P. alata* (fragrant granadilla) has been used as an anxiolytic, sedative, diuretic and an analgesic in Brazil (Oga et al., 1984). In the West Indies, Mexico, the Netherlands and South America, the roots of *P. caerulea* L., have been used as a sedative and vermifuge. In Italy, the plant has been used as an anti-spasmodic and sedative (Hickey & King, 1988; Dharwan et al., 2004). *P. foetida* L. leaf infusion has been used to treat hysteria and insomnia in Nigeria (Nwosu, 1999). In India this plant (*P. foetida*) is widely cultivated and its leaves are applied on the head for giddiness and headache; a decoction is given in cases of biliousness and asthma and the fruit is used as an emetic (Kirtikar & Basu, 1975). In Brazil, the same herb is used in the form of lotions or poultices for erysipelas and skin diseases with inflammation (Chopra et al., 1944). *P. incarnata* L. is a popular traditional European remedy (Handler, 1962) as well as a homoeopathic medicine (Rawat, 1987) for insomnia, anxiety, and has been used as a sedative tea in North America (Bergner, 1995). The juice of *P. maliformis* L. is used for intermittent fevers in Brazil. *P. quadrangularis* (giant granadilla) is used throughout the Caribbean as a sedative and for headaches. Leaf infusion is taken for high blood pressure and diabetes (Seaforth et al., 1983). In Central America, stems of the aerial parts of *P. sexflora* Juss. and *P. vitifolia* Kunth have been used against snakebites (Morton, 1981).

Figure 5. Flower of *Passiflora* (probably *P. ligularis*) made in gold by a precolombian goldsmith of Malagana culture in Colombia, b.C. 200 - 200 a.C (Banco de la República de Colombia, Museo del Oro, Bogotá D.C).

I.1.6. Cultivated species

More than 80 *Passiflora* species produce an edible fruit, the most interesting ones belonging to subgenera *Passiflora* and *Tacsonia* (Martin & Nakasone, 1970; Coppens d'Eeckenbrugge, 2003). The two botanicals forms of *P. edulis* Sims, *edulis* (purple maracuja) and *flavicarpa* Degener (yellow maracuja), are by far the most important fruit crops in the family, with a world production estimated at ca. 640.000 tons (http://www.passionfruitjuice.com) and a permanent presence on the international market. Other cultivated passion fruits are *P. tripartita* var. *mollissima* (Kunth) Holm-Nielsen & Jørgensen (curuba de Castilla), *P. tarminiana* Coppens & Barney (curuba India), *P. ligularis* (sweet granadilla), *P. maliformis* (granadilla de piedra, cholupa), *P. quadrangularis* (giant granadilla), *P. popenovii* Killip (granadilla de Quijos), *P. alata* (fragrant granadilla) and *P. laurifolia* L. (golden apple) (Annex 3). These eight species are mainly commercialized in South American for the local and national markets, principally in Colombia and Brazil, with incursions on the international market. Passion fruits are consumed fresh or processed into juices, sherbets, ice cream, and components of industrial pastry and candies. The most important commercial species are susceptible to a large number of pests and diseases, with considerable negative effects on production. Thanks to the high number of species producing and edible fruit of commercial size, the genus *Passiflora* has high potential for crop diversification and economic development, which induced research institutions in the Andean countries to prioritize their characterization and the evaluation of wild and cultivated populations (Debouck & Libreros, 1995), and develop strategies for conservation and improvement of these genetic resources.

I.1.7. Breeding

The genetic variability in the genus *Passiflora* is very wide, both within the genus and within the most cultivated species. This variability can be used by breeders in their efforts to improve traits in the species of subgenera *Passiflora* and *Tacsonia*, which are diploid with $2n = 18$ chromosomes. In spite of the success of a few *flag* species, most species with an edible fruit are still poorly known. Few species have diffused out of America and only the maracuja, the sweet maracuja, the granadilla, the stone granadilla and the curubas have been objects of intensive cultivation. Many wild species of *Passiflora* present characteristics of interest for breeding programs but the hybridization of these species with cultivated species is not always possible.

Several levels of passion fruit selection are observed in relation to the coexistence of all domestication stages. Many species, which are rarely cultivated but simply harvested, have never undergone artificial selection. Cultivation of species grown in home gardens has resulted in the creation of some unique types, such as the large-fruited giant granadilla (*P. quadrangularis* var. *macrocarpa*), which bears exceptionally large fruit. In commercialized species, such as the maracuja, sweet granadilla and curubas (*tacsos*), growers carry out phenotypic or mass selection when establishing or renewing new plots, in function of their observations or, sometimes, in function of an ideotype imposed by the local market. Seeds are collected from a small number of good quality fruits plucked from one or two high performing plants. Given the size of the plots, the total population is small and the selection intensity is low, especially if the plantation renewal cycle is long. This practice and seed exchanges maintain considerable variability in the populations.

Modern breeding has been focused on *P. edulis*. The first work took place in the developed tropical or subtropical regions where the commercial cultivation of *P. edulis* was initiated, but with very limited genetic resources and without even knowing the existing variation. These few institutional works concentrated on the clonal propagation of hybrids between yellow and purple maracujas, obtained on a very narrow genetic base, in Australia, Hawai and Florida (Knight, 1992; Vanderplank, 2000; Winks et al., 1988). The main breeding objectives were early flowering, improved yield, resistance to pests and diseases (*Fusarium*, *Phytophthora*, *Alternaria*, *Xanthomonas* and virus), cold tolerance and fruit quality (Table 1). In spite of the lack of basic knowledge on genetic resources, complex technical approaches have been explored directly, including interspecific hybridizations, in Puerto Rico and Australia (Beal, 1972; Payán & Martín, 1975; Winks et al., 1988), biotechnologies, with *in vitro* tissue culture (Drew 1991; Cancino & Hodson, 1994), somatic hybridization (Dornelas et al., 1995; Otoni et al., 1995; Barbosa & Vieira, 1997) and genetic transformation with *A. tumefaciens* (Manders et al., 1994; Silva, 1998; Hall et al., 2000).

As the commercial cultivation of *P. edulis* started in tropical America, their place of origin, with materials repatriated from Hawaii, propagation by seedlings became the rule. This cultural practice, the increase in production areas and the abundance of natural pollinators increased genetic variation, widening the basis for later breeding programs. The most significant ones have taken place in Brazil, first country in production as well as consumption of yellow maracuja and sweet maracuja. The most advanced Brazilian breeding programs have used progeny-testing for the obtention of synthetic populations, aiming at a better productivity, quality and homogeneity of the crop, while maintaining sufficient genetic diversity for efficient cross-pollinations (Coppens d'Eeckenbrugge et al., 2001; Meletti et al., 2005). Several cultivars have been proposed for consumption *in natura* (*e.g.* 'IAC-273' and 'IAC-277'; Meletti et al., 2000) and for the agroindustry (*e.g.* 'IAC-275' and 'CPATU-Casca Fina'; Nascimento et al., 2003).

Table 1: Breeding objectives in passion fruits.

Objective	Selection criteria
Productivity	• Vigor, early production, productivity (flowering, fruiting). • Self-fertility if clonal selections (out of dated).
Fruit quality	• Adequate and uniform size. • Yield of pulp and/or juice. • Sugar/acidity ratio (fresh or processed) and pulp aroma. • Color of pulp, dark yellow for maracujas, orange to salmon for curubas and giant granadilla. • Small seeds. • Pericarp colored, turgescent (smooth), durable and resistant during transportation.
Resistance to fungal diseases	• *Alternaria alternata*, *A. passiflorae* and other species for maracujas and curubas. • *Fusarium oxysporum* and *F. solani* for the purple maracuja and sweet granadilla. • *Phytophtora nicotianae* and *P. cinnamoni* for maracujas. • *Septoria passiflorae* for the purple maracuja • *Oidium* sp. for curubas. • *Colletotrichum gloeosporioides* (anthracnose) and *Cladosporium herborum*, especially for curubas.
Resistance to bacterial diseases	• *Xanthomonas passiflorae* and *X. campestris* pv. *Passiflorae* for maracujas, *P. alata* and giant granadilla.
Resistance to viral diseases	• Potyviruses for maracujas (PMV and SMV) and sweet granadilla (ringspot). • Tymovirus and closterovirus for maracujas.
Resistance to nematodes	• *Meloidogyne incognita* and *M. javanica* for maracujas, giant granadilla, *P. alata* and curubas • *Rotylenchulus reniformis* for the purple maracuja.
Acclimatization	• Cold resistance for yellow and purple maracujas and frost resistance for curubas.

I.1.8. *Passiflora* research and prospects, in Colombia and in the Andean region

There is little factual information available on the Andean passion fruits. This must be generated by comparative tests in the areas where these species are available. Research institutions in Bolivia, Peru, Ecuador, Colombia, and Venezuela could provide information that may be useful as the basis for industrial development. The future of these fruits will depend upon horticultural development. The production of pulp and concentrate has extremely good prospects if commercial-scale production can be established and maintained.

In the last ten years, institutions of Andean countries, grouped in a net promoted by Bioversity International (formerly IPGRI), have started a systematic exploration of the genetic resources of Andean *Passiflora* species, which has allowed the constitution of collections of the most common species. Nowadays, important collections exist in the five countries: Bolivia, Colombia, Ecuador, Peru and Venezuela. Scientists from the region have investigated the genetic variability of the cultivated curubas and related wild species, building the bases for conventional breeding programs. However, similar efforts on the warm climate species have only been carried out in Brazil.

The main problems encountered along these research efforts on passion fruit genetic resources have included the difficulty of approaching such a wide morphological and genetic diversity at both intra- and interspecific levels, with related taxonomical problems and inconsistencies, and practical problems for its effective conservation. The specific adaptations and high level of endemism of species originating from a wide range of habitats impose *in situ* conservation strategies, implying a good knowledge of the distribution of the different species and the repartition of their diversity.

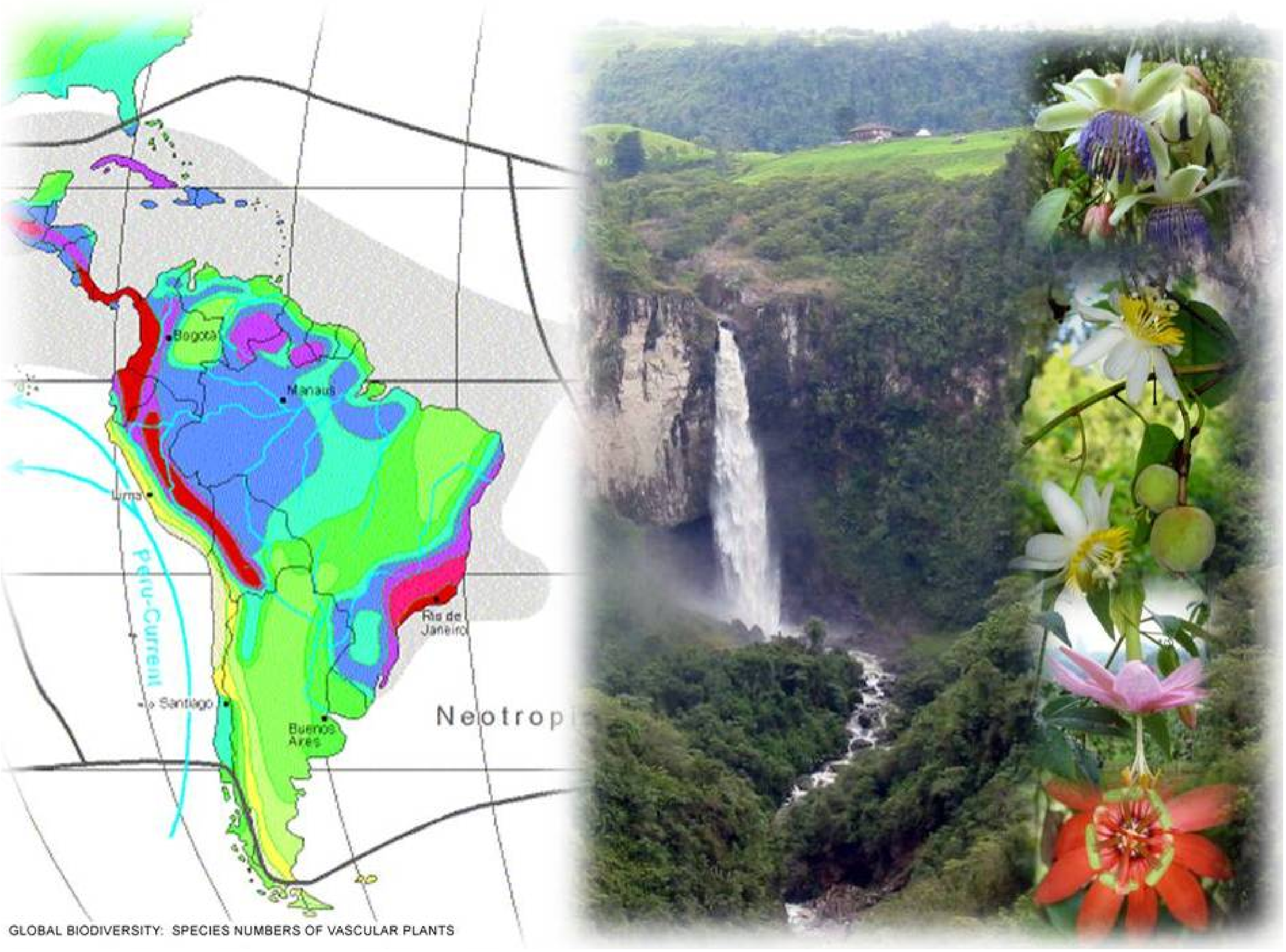
In Colombia, several collaborative projects have been focused on Passifloraceae. The Interamerican Development Bank (BID) has supported a regional project, coordinated by Bioversity International in 1994-1997. Colciencias funded in 1999-2001 the national project “Conservación y utilización de los recursos genéticos de pasifloras”, developed by French and Colombian scientists at the IPGRI-Americas office. In 2004, the same group developed a study of diversity of the *Passifloraceae* and *Caricaceae* in the Colombian coffee growing zone. All these projects have generated a considerable amount of information on morphology, cytology, palynology, molecular diversity, and biogeography of *Passiflora*, strengthening the national collections and providing most of the material for the work presented in this thesis.

I.1.9. Structure of the thesis

Our research is presented in five more chapters. The first two bear on *Passiflora* geography in Colombia. The first one consists of an inventory of species for Colombia, their distribution among biogeographic regions and administrative divisions, and considers their status of conservation. The second presents a more detailed analysis of the ecogeographic drivers of *Passiflora* diversity, through distribution modeling in relation to climatic adaptation of the different species, and gives orientations for their *in situ* conservation. The next two chapters analyze *Passiflora* diversity, the third chapter concerning morphological diversity and the fourth one genetic diversity. Each of these four chapters is treated independently, with the structure of a scientific article. A wider general discussion is the object of the final chapter.

CHAPTER II

Diversity of Colombian Passifloraceae: biogeography and an updated list for conservation



II.1 Diversity of Colombian Passifloraceae: biogeography and an updated list for conservation

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Submitted and accepted in Biota Colombiana

II.1.1. Abstract

The list of Colombian Passifloraceae was revised, using 3,930 records from literature, herbaria, and field observations. It includes 167 species, 165 of them native, which is equivalent to 27% of the family. Our list brings more details on species distribution and presents 26 species new to Colombia. *Passiflora* is the most important genus, with 162 species. When compared with other regions, the Andes of Colombia and Ecuador constitute its center of diversity. Within Colombia, the highest diversity is also concentrated in the Andean region, with 81% of the species, particularly in the departments of Antioquia, Valle del Cauca, Cundinamarca, Quindío, Risaralda, and Caldas. The highest number of species is found at elevations between 1000 and 2,000 m. Most common species thrive in disturbed habitats, such as borders of roads, cultivated plots, and secondary forest. Most of the 58 endemic species are high Andean and belong to subgenera *Tacsonia* and *Decaloba*. Forty-two species produce an edible fruit, and nine are commercially cultivated. Among the species reported, 70% are threatened to some degree and three are considered extinct. Colombia may still harbor many unknown species in poorly explored departments. A better knowledge of *Passiflora* diversity and its distribution is needed to develop its economic potential. The urgent task of conserving this threatened richness must target the conservation of these resources as well as their habitat. Both aspects may be combined if Passifloraceae can be used as an indicator of biodiversity in the Andean region, which seems justified by their multiple ecological interactions with many organisms.

***Keywords*:** biodiversity, Colombia, Neotropics, Passifloraceae, passionflowers.

II.1.2. Introduction

The Passifloraceae consist of 18 genera and approximately 630 species, distributed throughout the tropics from the coastal zones up to 3,800 m in Andean páramos (Holm-Nielsen et al., 1988). In America, it is represented by four genera (*Ancistrothyrsus*, *Dilkea*, *Mitostemma* and *Passiflora*). *Passiflora*, with about 525 species is numerically and economically the most important genus of the family; it is distributed mainly in the New World (Ulmer & MacDougal, 2004), with only 22 Old World species of subgenus *Decaloba* (syn. *Plectostemma sensu* Killip), in the tropical and sub-tropical regions of Southeast Asia and Austral Pacific. Passionflowers are generally perennial lianas or herbaceous vines climbing by tendrils, although some are trees, shrubs, or even annuals. Their wide morphological variation appears to result from the diversity of their habitats as well as their coevolutionary relationships with many organisms, including protective ants (Apple & Feener, 2001), herbivores (particularly *Heliconius* spp. butterflies; Gilbert, 1982), pollinators, and the plant communities providing them physical support and access to sunlight. Pollination is mainly carried out by insects and birds; several species are bat-pollinated (Endress, 1994; Büchert & Mogens, 2001) and a few species exhibit elements of the carnivory syndrome (Radhamani et al., 1995). Many species are cultivated for their edible fruit, as ornamentals, or for their medicinal properties (Ulmer & MacDougal, 2004; Coppens d’Eeckenbrugge, 2003; Martin & Nakasone, 1970; Dharwan et al., 2004). *P. edulis* Sims (maracuja) is by far the best known and economically most important species of the family.

When Spanish missionaries arrived in South America in the 16th century, they felt passionflowers were a good omen for their mission. In their unique morphology, they saw the elements of the Passion of Jesus Christ and a sign that the New World would successfully be converted to Christianity (Killip, 1938; Uribe, 1955a). This religious symbolism gave the plant their common name of *Flos Passionis*, or “passion flowers”. The Latin translation by Pluckenet (1696; cited by Escobar, 1988a) was accepted for the genus *Passiflora* created by Linnaeus in 1753, who described 24 species in his *Species Plantarum* (cited by Killip, 1938), a number increased to 35 by Lamarck (1789; cited by

Killip, 1938). The first extensive monograph of the family was published by Cavanilles in 1780 (cited by Killip, 1938), with 43 species treated. They were followed by authors like Jussieu (1805), De Candolle's (1828), Masters (1872) and Harms (1925), who described about 250 species divided into 21 sections (Killip, 1938). In his 1938 monograph, *The American Species of Passifloraceae*, Killip made the most extensive description of the New World species, classifying 355 species into 17 genera and 22 subgenera, based on floral morphology (Annex 1). In Colombia, the priest Uribe (1954, 1955a, 1955b, 1957, 1958, 1972) described several new species and Escobar (1986, 1987, 1988a, 1988b, 1989, 1990, 1990 inedited, 1994) revised the subgenera *Distephana*, *Manicata* (syn. *Granadillastrum*), *Rathea* and *Tacsonia*, including *Tacsoniopsis* in the latter, and described one additional subgenus, *Porphyropathanthus*. She passed away in 1993, leaving an inedited document on her revision of subgenus *Astrophea*. MacDougal revised Killip's subgenus *Plectostemma* in 1994, restoring its ancient name *Decaloba*. In the last decade, MacDougal and Feuillet have published many papers including the description of about 15 new species, mainly of the subgenera *Decaloba* and *Astrophea* (MacDougal, 1992, 1994, 2006; Feuillet, 2002, 2004). Recently, Feuillet & MacDougal (2003; Annex 2) proposed a new infrageneric classification in *Passiflora*. According to this proposal, only based on morphological characters, four subgenera would be recognized: *Astrophea* and *Deidamioides*, from South and Central America, *Decaloba*, from America, Southeast Asia and Australia, and *Passiflora*, exclusively from America (Ulmer & MacDougal, 2004). Additionally, they proposed to downgrade genus *Tetrastylis* as a section of subgenus *Deidamioides*. Recent molecular analyses partly support the reduction in the number of subgenera (Muschner et al., 2003; Yockteng, 2003; Yockteng & Nadot, 2004; Hansen et al., 2006; see Annex 4a-d), with the existence of at least three major groups, corresponding globally to subgenera *Decaloba*, *Passiflora* and *Astrophea* of the new proposal. On the other hand, molecular data from the different studies are not always consistent on the relative placement of these groups, and their results are less clear at lower levels, with inconsistent grouping of particular species and poor correspondence with some well established morphological divisions. In addition, the monophyly of *Passiflora* has not been established, and the study of Muschner et al. (2003) even raises some doubts about it. Clearly, more studies, involving more numerous species samples, are needed before re-evaluating such a complex and fast evolving group as *Passiflora*.

Colombia's location and variety of ecosystems places it in second position for biodiversity (MacNeely et al., 1990). The country is divided into five main biogeographic regions: Amazonian, Andean, Caribbean, Orinoquian, and Pacific. The Andean region presents a highly varied topography (100-5,400 m) with three main mountain ranges. Thus, the Eastern, Central and Western Cordilleras separate two large inter-Andean valleys from the Pacific Coast to the West and the Orinoquian 'Llanos' to the East. The uplift of the Andes created new habitats and increased local isolation, favoring high speciation rates in many taxa. In *Passiflora*, a particularly striking example is given by subgenus *Tacsonia*, whose beautiful and large-flowered species are strictly adapted to high altitudes in cloud forest (2,000-3,800 m) and pollination by the sword-billed hummingbird *Ensifera ensifera* Lesson, which shows the same distribution (Büchert & Mogens, 2001). As a result of this habitat diversification, the Colombian flora includes one of the world most diverse groups of vascular plants, with 51,220 documented species (May, 1992; UNEP-WCMC, 2004). However, Colombia has undergone recent transformation of large parts of its natural ecosystems, in particular in the Andean region. Seventy percent of the Andes, an area that is vital to the conservation of Colombia's water supply, have been deforested as a result of both agricultural colonization and human migration (World Press Review, 1993). Destruction of natural habitats has drastically affected many species distributions, often reducing their historical ranges to a set of small, fragmented populations (Brooks et al., 2002). Such habitat alteration is predicted to lead to substantial extinction in the near future.

In this context of rapid erosion of biodiversity, Passifloraceae are highly interesting, not only for their fast radiation and spectacular variation in morphology and reproductive biology. Indeed, as stated above, this family is exemplative from the standpoint of coevolution in many respects, such as their particular relationship with specialized herbivores, ants and other nectar feeding insects; most importantly, they are parasites of structure, as they depend on many very different species for their support, from low shrubs in disturbed habitats to high trees in primary forests. They are mainly perennials, but their life cycle is much shorter than that of their support. They are sensitive to long-term changes in the ecosystem (dependence on trees) as well as short-to medium-term changes (by their other adaptive traits). Thus, they should constitute an excellent indicator group for the monitoring of biodiversity in Colombia. In addition, Colombia presents a long tradition of diversity in fruit production and consumption, and it is the country with the highest number of marketed passion fruit species, so the study of *Passiflora* diversity must also be thought in terms of conservation of genetic resources of important or promising fruit crops.

The last inventory by Hernández & Bernal (2000) recorded 141 Passifloraceae species distributed in all the biogeographic regions. Forty-eight of them are endemic to Colombia, mostly living in the Andean region. This inventory was based on the study of specimens from five herbaria (COL, HUA, JAUM, MEDEL and MO) and the citations made in publications compiled by several authors that have worked on the family.

Several recent, collaborative projects have been focused on Passifloraceae. The Interamerican Development Bank (BID) has supported a regional project, coordinated by IPGRI (currently Bioversity International) in 1994-1997. Colciencias funded in 1999-2001 the national project “Conservación y utilización de los recursos genéticos de pasifloras”, developed by French and Colombian scientists at the IPGRI Americas office. In 2004, the same group developed a study of diversity of the *Passifloraceae* and *Caricaceae* in the Colombian coffee growing zone. All these projects have generated a considerable amount of information on morphology, cytology, palynology, molecular diversity, and biogeography of *Passiflora*, providing most of the material for the present inventory and allowing us to supplement and update the list of Hernández & Bernal (2000) with new information, such as species new to science or to the country and elements of ethnobotanical information. In addition, the use of a Geographic Information System (GIS) allowed us to re-assess the conservation status of Colombian Passifloraceae.

II.1.3. Materials and methods

II.1.3.1. *Study area*

Colombia is situated in the north of South America, between 12° 26’ 46” N and 4° 13’ 30” S and between 66° 50’ 54” W and 79° 02’ 33” W, covering an area of 1,141,748 km^2, with an altitudinal range from the sea level to 5,775 m (http://www.igac.gov.co). The main administrative division defines 32 departments and geographers recognize five biogeographic regions (Hernández et al., 1991).

II.1.3.2. *Herbarium and literature data*

The data set consists of information gathered from specimen labels from 18 Colombian herbaria (AFP, CAUP, CDMB, CHOCO, COL, COAH, CUVC, FAUC, FMB, HUA, HUQ, JAUM, MEDEL, PSO, SURCO, TOLI, VALLE, UIS) and five herbaria in other countries (K, MA, MO, NY, P). These collections were gathered between 1750 and 2006. Most specimens were verified or identified, using the keys and descriptions of Killip (1938), and amendments by Holm-Nielsen et al. (1988), Escobar (1988a, 1994), MacDougal (1994) and Tillet (2003). A synonymy list, based on the general list of Feuillet & MacDougal (2003), is given in the Appendix. When possible, voucher label information was used to assign geographic coordinates to specimens, using gazetteers and topographic maps of Colombia (scale 1:50,000 and 1:250,000). The database was supplemented with materials mentioned in species descriptions, essentially those of Killip (1938, 1960), Uribe (1955a), and Escobar (1988a,b, 1989, 1990, 1990 inedited, 1994). Collection records with obviously inaccurate or doubtful data were excluded from the analysis. Coordinates were further checked by plotting all species on a dot map, using the DIVA-GIS 5.2 software (Hijmans et al., 2001). Finally, we followed the infrageneric classification by Killip (1938) with the amendments of Escobar (1988, 1989) and MacDougal (1994).

II.1.3.3. *Expeditions and samples collected*

The dot map of all geo-referenced specimens was used to plan germplasm collecting trips. The prioritization of explored areas followed three criteria: permission of access (unfortunately not obtained for protected areas), richness of species and collection gaps. The collecting trips were carried out during 2003-2006, covering 555 localities in 17 departments, between 0 and 4,200 m of altitude. The explorations were concentrated in the Andean region, in watersheds, wild forest areas, cultivated fields and road borders. Data were recorded for each collected specimen, including locality names, elevation, geographic coordinates using a hand-held GPS device, status (wild, cultivated or introduced), and ethnobotanical information (if any). These passport data were recorded and tabulated. Finally, the Geographic Information System software DIVA-GIS 5.2 was used to generate a dot map of the distribution of accessions collected/observed during the expedition.

II.1.3.4. *Threat status of Passifloraceae*

The distribution area of each native species was characterized by the maximum distance (MaxD) and the circular area (CA_{50}), following the method of Hijmans et al. (2001). This methodology has been applied in a number of studies to provide quantitative assessment of the distribution area required by the Red List criteria, for example by Maxted et al. (2005). MaxD is the largest distance between any pair of observations of one species. CA_{50} is the total surface within a 50-km radius around all the observations for a same species. These methods were supplemented with historical records of each taxon and subjected to the Red List criteria of the World Conservation Union (IUCN 2003, 2004), involving complex combinations of quantitative observations concerning the size and structure of the population, the range and fragmentation of its distribution (extent of occurrence and area of occupancy), as well as the intensity of their past or foreseeable variation. Along these lines, we considered that CA_{50} under 20,000 km2, MaxD under 100 km and number of observations under six, as well as the absence of records younger than 100 years, are critical.

II.1.4. Results

II.1.4.1. *Data collecting*

A total of 3,330 herbaria and 45 literature data, concerning 120 species, were gathered and georeferenced when coordinates were not directly available. The highest number of species and specimens were found in the Colombian herbaria COL and HUA, with 1,056 and 976 records, respectively. During the collecting trips, most specimens were observed in forest fragments, gallery forest and forest and road edges, mainly in the watersheds of the coffee growing zone, between 1000 and 2,000 m. In all sites visited during the expeditions, 87 Passifloraceae species were recorded. Five individuals could not be identified. The dot map of Figure 1 shows the spatial distribution of our final dataset of 3,930 records for herbarium (3,330), literature (45) and field collections (555) of Passifloraceae in the different biogeographic regions.

II.1.4.2. *Distribution of species richness*

The number of observations and species richness was highest on the Andean slopes (123 species), followed by the Amazonian region with 45 species (Table 1). The Orinoquian was the poorest region, with only 19 species. The Andean and Caribbean regions share the highest number of species (27). By contrast, the Pacific and Caribbean regions only present four species in common. Figure 2 gives a synthetic image of the similarities in species occurrence among regions, confirming a relative similarity between the Amazonian and Orinoquian as well as between the Andean and Caribbean regions. The Pacific Coast Passifloraceae appear relatively divergent. In the Andean region, Antioquia, Valle del Cauca, Cundinamarca and Santander were the departments that displayed the highest richness of specimens and species (Table 2). Considering their area, Quindío, Risaralda and Caldas are even more diverse. The department of San Andrés and Providencia (Caribbean islands) is only represented by *P. biflora* Lam. and *P. pallida* L.

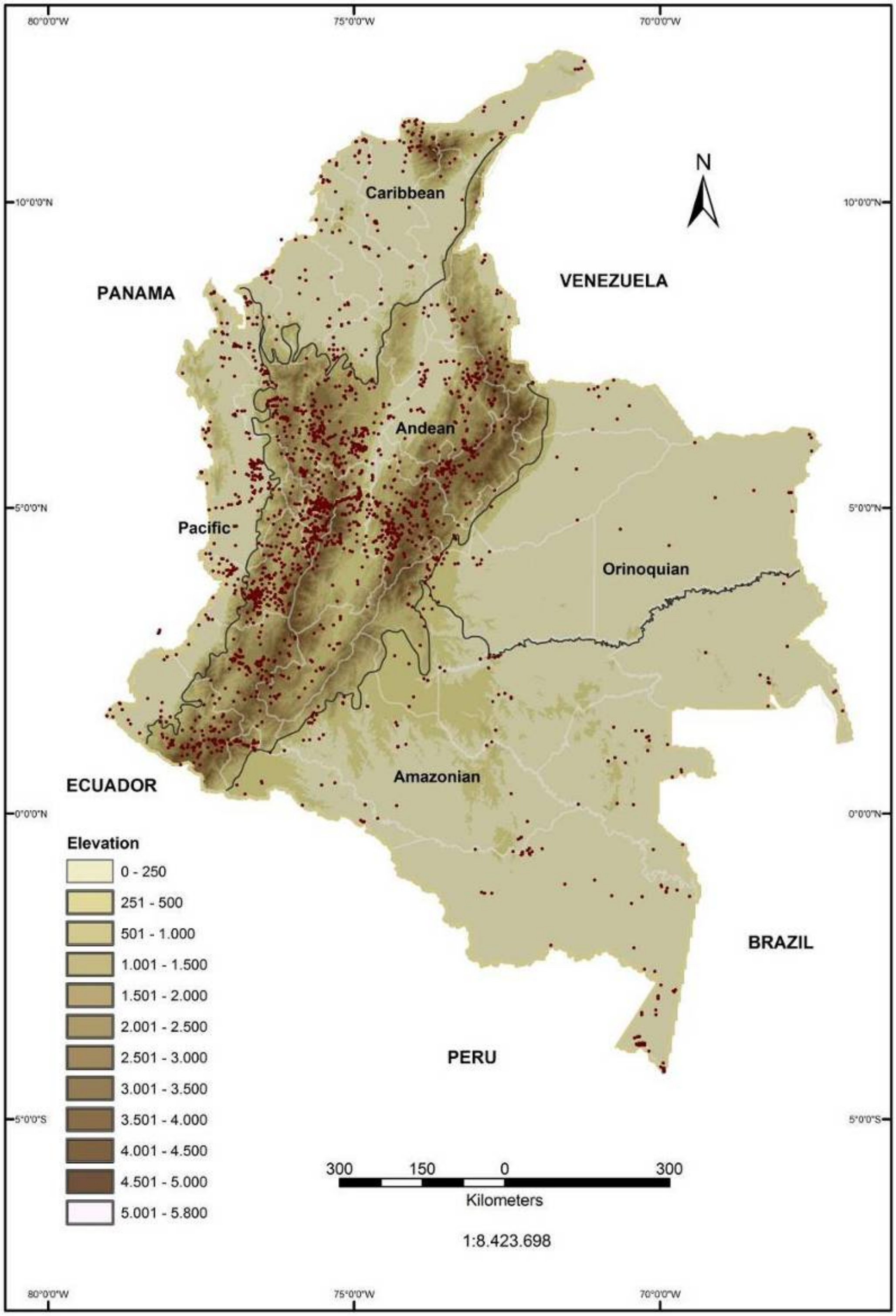

Figure 1. Map of distribution of Passifloraceae specimens for 3,930 collections in the five biogeographic regions in Colombia. Points on the map represent sites of collection.

Table 1. Distribution of Passifloraceae by biogeographic region. The diagonal gives their contribution in species number (**bold**) and contribution to the country's total. The other cells give the number and proportion of shared species for each pair of regions.

Biogeographic region	amz	and	car	ori	pac
Amazonian	**45** (28%)	21 (14%)	9 (12%)	15 (31%)	15 (23%)
Andean		**123** (76%)	27 (20%)	7 (5%)	14 (10%)
Caribbean			**38** (23%)	9 (19%)	4 (6%)
Orinoquian				**19** (12%)	9 (14%)
Pacific					**36** (22%)

II.1.4.3. *New Passifloraceae checklist for Colombia*

Table 3 gives the number of species for each genus and subgenus present in Colombia in relation with the number of species present in the Neotropics. The updated inventory of the Colombian species (Table 4) includes a total of 167 Passifloraceae species, representing three genera, *Ancistrothyrsus*, *Dilkea* and *Passiflora*. This is equivalent to 27% of all Passifloraceae. The genus *Passiflora* is by far the most important with 162 species, representing 11 of Killip's subgenera, and all the four subgenera defined in the classification proposed by Feuillet & MacDougal (2003). The most abundant species were *P. vitifolia* Kunth (359 specimens) and *P. mixta* L. (162 specimens), while 67 species (23%) were represented by a single specimen.

Figure 2. Diagram comparing the similarity in contribution of Passifloraceae species to the floras of the Colombian biogeographic regions (Jaccard distance).

In the expeditions, we found some species that had not been collected in the last decades, such as *P. erytrophylla* Mast., *P. guazumaefolia* Juss., and the semi-arborescent *P. mariquitensis* Mutis *ex* Uribe. The latter was described in 1783 by José Celestino Mutis during the Botanical Expedition of the "Nuevo Reino de Granada" in Mariquita (Tolima). It was considered extinct by Uribe (1955a) and a synonym of *P. pittieri* Mast. by Escobar (1990 inedited). However, we could verify that *P. mariquitensis* still exists, as three specimens that we have collected in highly disturbed forest near Mariquita corresponded very well to the type specimen, while they appeared morphologically distinct from *P. pittieri* specimens from Costa Rica, Panama, and northwestern Colombia in several traits (*e.g.* nectar shape, peduncle length, nerve shape). Similarly, we maintained other species that had been considered synonyms by Hernández & Bernal (2000), such as *P. mollis* H.B.K. (vs. *P. cuspidifolia* Harms), and *P. hahnii* Mast. (vs. *P. guatemalensis* S. Watson), after checking the collected materials against the type specimens. Ours list presents 26 species new to Colombia, from those recognized by Killip (1960), Feuillet & MacDougal (2003) and Ulmer & McDougal (2004) and three inedited from Escobar (1990) and Hernández (2003): *Ancistrothyrsus antioquiensis* L.K Escobar (ined.), *P. alata* Curtis, *P. andina* Killip, *P. bucaramangensis* Killip, *P. candollei* Tr. & Planch., *P. chocoensis* Gerlach & Ulmer, *P. cincinnata* Mast., *P. hahnii* (Fourn.) Mast., *P. hirtiflora* Jørgensen & Holm-Nielsen, *P. killipiana* Cuatrecasas, *P. lyra* Planch. & Linden & *ex* Killip, *P. megacoriacea* Porter-Utley (ined.), *P. mollis* Kunth, *P. monadelpha* Jørgensen & Holm-Nielsen, *P. munchiquensis* Hernández (ined.), *P. occidentalis* Hernández (ined.), *P. pallida* L. (clearly separated from *P. suberosa* by Porter-Utley, 2003), *P. pillosissima* Killip, *P. popenovii* Killip, *P. sodiroi* Harms, *P. tuberosa* Jacq., *P. rigidifolia* Killip, *P. tricuspis* Mast., *P. truxillensis* Planch. & Lind. *P. caerulea* L., recently introduced from Brazil and Argentina and cultivated as an ornamental, was not included in the counts of each department. *P. alata* was not counted for Quindío and Valle del Cauca either, as the material under cultivation was also introduced from Brazil. Nine more species occur close to the Colombian international border (less than 100 km), and possibly exist also in the country, although they have not been included in this inventory. Another important result is the presence of the genera *Ancistrothyrsus* and *Dilkea* in the Andean and Pacific regions, the former following the mention of *A. antioquiensis* by Escobar (1990 ined.). Unfortunately, she passed away before publishing her monograph on arborescent Passifloraceae.

Several botanical forms and varieties are mentioned for *P. edulis* Sims, *P. cumbalensis* (Karst.) Harms, *P. foetida* L, *P. ligularis* Juss., *P. longipes* Juss., *P. rugosa* (Mast.) and *P. tripartita* (Juss.) Poir. A total of 42 species with edible fruit are reported. Nine of them are sold on the international, national and/or local markets, *P. edulis* f. *flavicarpa* Degener and *P. edulis* f. *edulis* (introduced), *P. ligularis*, *P. tripartita* var. *mollissima*, *P. tarminiana* Coppens & Barney, *P. quadrangularis* L., *P. maliformis* L., *P. popenovii* Killip, *P. nitida* Kunth, and *P. alata* Curtis. Other species, such as *P. antioquiensis* H. Karst., *P. cumbalensis*, *P. laurifolia* L., P. *nitida* Kunth, *P. palenquensis* Holm-Niels. & Lawesson *P. tiliifolia* L., and *P. pinnatistipula* Cav. are cultivated in home gardens. Some commonly cultivated species seem to depend on human activity for their propagation, which suggests an advanced stage of domestication and/or an incomplete acclimatisation following an ancient introduction. Thus, *P. edulis* f. *flavicarpa*, *P. ligularis*, *P. quadrangularis* L., *P. popenovii P. tripartita* var. *mollissima*, and *P. tarminiana,* are exceptionally found as feral plants. On the other hand, let us remind that the latter has pullulated as an invasive plant in Hawaii and New Zealand. Another particular case is *P. edulis* f. *edulis*, introduced from southern South America, which has naturalized at intermediate to high altitudes, where it is not uncommon in the wild.

Table 2. Number of observations and species of Passifloraceae in the 32 Colombian departments.

Department	**Abbreviation**	**Biogeographic region**	**Observation number**	**Species number**
Amazonas	ama	amz	87	19
Antioquia	ant	and car pac	784	70
Arauca	ara	and ori	10	6
Atlántico	at	Car	18	7
Bolívar	bl	and car	33	17
Boyacá	by	and ori	145	36
Caldas	cl	And	245	36
Caquetá	cq	amz and	47	18
Casanare	cs	and ori	4	4
Cauca	cau	amz and pac	161	42
Cesar	ce	and car	13	10
Chocó	cho	and pac	211	40
Córdoba	cor	and car	33	9
Cundinamarca	cun	and ori	419	53
Guainía	gn	amz	16	10
Guaviare	gv	amz	27	14
Huila	hu	and	62	22
La Guajira	lg	and car	21	12
Magdalena	ma	car	71	31
Meta	met	amz and ori	85	24
Nariño	na	and pac	170	44
Norte de Santander	ns	and	79	36
Putumayo	pu	amz and	56	26
Quindío	qu	and	150	38
Risaralda	ri	and pac	68	24
S. Andrés y Prov.	sp	car	4	2
Santander	snt	and	203	48
Sucre	suc	car	6	3
Tolima	to	and	213	44
Valle del Cauca	vc	and pac	420	56
Vaupés	va	amz	35	20
Vichada	vch	ori	16	9

The vernacular names are very diverse for each species. In the Amazonian region, we noted several indigenous names for the species *P. foetida* var. *gossypiifolia* Desv. (Iñana-leeg, Murulale), *P. holtii* Killip (Guachique), *P. nitida* (Burucuña, Gemarundare, Tuchica, Jino-Gojé), *P. serratodigitata* L. (Cipo-Cipo), *P. vitifolia* (Maloca de Fisi). In the Cauca and Nariño departments (south of the Andean region) *P. fimbriatistipula* Harms and *P. ligularis* are named Pachuaca and Awapit in the indigenous languages.

Table 3. Number of Passifloraceae species in Colombia and the Neotropics.

Genus	Subgenus	Colombia	Neotropics
Ancystrothyrsus		2	3
Dilkea		3	5
Mitostemma		0	3
Passiflora	*Astrophea*	22	57
	Decaloba	52	190
	Dysosmia	2	20
	Distephana	6	15
	Manicata	1	5
	Passiflora	38	156
	Porphyropathanthus	1	1
	Psilanthus	3	4
	Rathea	2	3
	Tacsonia	30	55
	Tryphostemmatoides	4	7
All Passifloraceae		**167**	**533**

Among the species collected in our expeditions, we found several species growing very commonly in disturbed habitats like road borders, secondary forest margins, and especially riverbanks between 1000 and 2,000 m: *P. adenopoda* Moc, & Sessé *ex* DC., *P. alnifolia* Kunth, *P. coriaceae* Juss., *P. capsularis* L., *P. rubra* L, and *P. suberosa* L. The latter two can even be considered weeds in the coffee plantations. At higher altitudes (above 2,500 m), *P. mixta* is also very common in disturbed habitats.

II.1.4.4. *Endemism*

Among the 165 native species, 58 (36%) are endemic to the country. The largest concentration of these occurs in the Andean region, principally in the Cordillera Central, in the departments of Antioquia and Tolima. The elevation belt between 1,500 and 2,500 m presents the highest richness of endemic and rare species (≤ 5 observations). Only eight of these were represented with only one specimen (*e.g. P. cremastantha* Harms), while *P. bogotensis* Benth and *P. antioquiensis* were the most collected endemic species, with 23 recorded specimens each. The proportion of endemic species varied considerably among taxonomic groups, especially among the subgenera of *Passiflora* (Table 4). Thus, *Tacsonia* (21), *Decaloba* (13), *Passiflora* (9) and *Astrophea* (7) present the highest number of endemic species. Subgenus *Tacsonia* displays the highest richness of endemic species in the Cordillera Central with eight species, mainly of the section *Colombiana* characterized by a very long peduncle (*P. flexipes* Triana & Planch., *P. linearistipula* L.K. Escobar, *P. quindiensis* Killip and *P. tenerifensis* L.K. Escobar). Twenty-one species (37%) are restricted to very small areas of one department. These are located mainly in the departments of Antioquia (6), Tolima (4), Santander (3), Cauca (2), while only one such narrow endemic is found for the departments of Bolivar, Boyacá, Chocó, Caldas, Cauca, and Magdalena. Figure 3 shows 15 endemic species from five subgenera.

Figure 3. Colombian endemic species (a) *P. antioquiensis*; (b) *P. parritae*; (c) *P. flexipes*; (d) *P. linearistipula*; (e) *P. lanata*; (f) *P. tenerifensis*; (g) *P. trinervia*; (h) *P. longipes*; (i) *P. erytrophylla*; (j) *P. bogotensis*; (k) *P. magdalenae*; (l) *P. smithii;* (m) *P. arborea*; (n) *P sphaerocarpa*; (o) *P. emarginata*.

II.1.4.5. *Threatened species*

Figure 4 shows the distribution of the 165 Colombian Passifloraceae native species, according to their threat status under the criteria of the IUCN (2003, 2004). Seventy-one percent of them present some threat degree, 10% being critically endangered (**CR**), 6.1% vulnerable (**VU**) or endangered (**EN**). Four of the 16 critically endangered species are endemic. All three extinct species (**EX**) belong to the Andean subgenus *Tacsonia*. Unfortunately, the only two species of genus *Ancistrothyrsus* are included in the category CR. Only 16% of the species were placed in the two categories **LC** and **NT**, 'least concern' and 'near threatened'. The species *P. alata*, *P. megacoriacea* and *P. rigidifolia* are placed in the **DD** category because of deficient data. The 29.3% classified in 'least concern', belong mostly to subgenera *Decaloba* and *Passiflora* with 18 and 14 species, respectively.

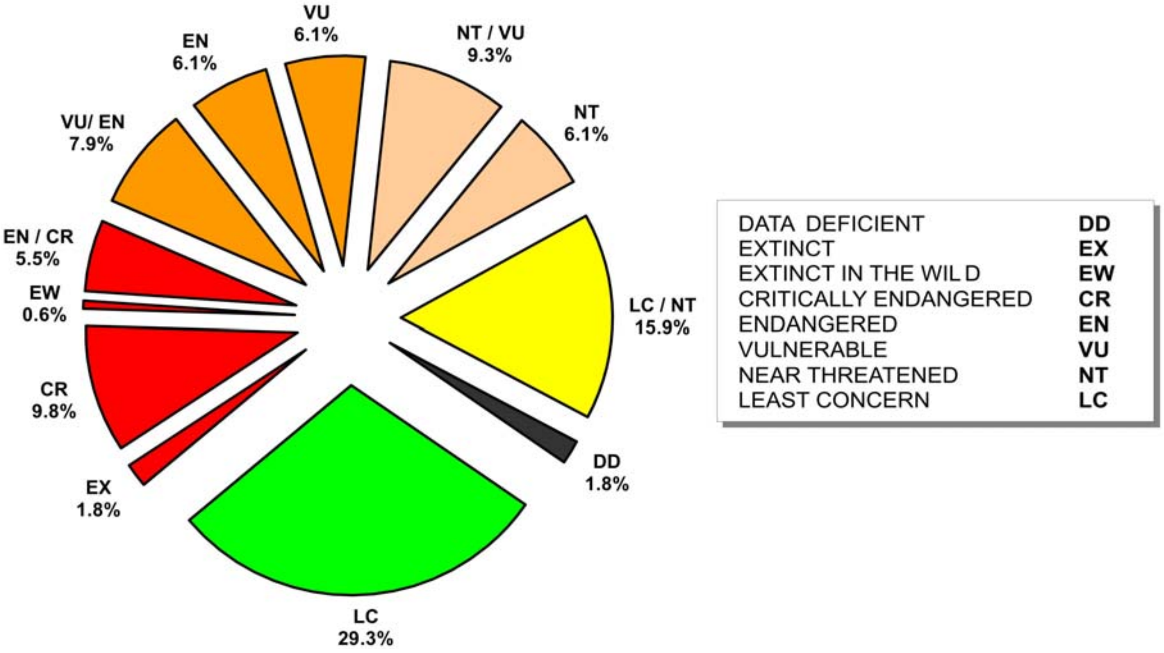

Figure 4. Percentual number of the threat status of 165 Passifloraceae native species under the IUCN criteria.

II.1.5. Discussion

Colombia has been subject to many studies focused on inventories of plant species groups (Gentry, 1993; Silverstone-Sopkin & Ramos, 1995; Galeano et al., 1998; Rangel, 1995, 2002). Passifloraceae have been inventoried in taxonomical works by Escobar (1998a, 1989, 1990 inedited) and Hernández & Bernal (2000). As compared to the latter, we have added new information on geographical distribution of each taxon and extended the list to a total of 167 Passifloraceae species, from three genera and the five biogeographic regions, with reports of 26 species new to Colombia.

For obvious reasons, the quality of botanical inventories depends on the quality of taxonomical work in this complex family. While the definition of genera and subgenera should not affect significantly studies of the distribution of its diversity across the Colombian territory, such work may be affected to some extent by poor definitions below the subgenus level. Indeed, several morphological groups include species that are very similar, and regularly reported as very difficult to distinguish from each other. In several cases, experts may have underestimated intraspecific variation in widely distributed species, or even intra-individual variation, splitting well known species in several new species only distinguished by a few quantitative or color traits. Among the difficult groups, let us mention particularly subgenus *Astrophea*, whose species tend to be less well differentiated, at least in sterile specimens, by nectar gland position and number, having only two at the junction of the lamina and petiole, while they may show impressive intraspecific variation in pubescence and intra-individual variation in leaf size and shape according to light exposure and whole tree development (heteroblasty). In subgenus *Decaloba* also, several morphological groups demand great experience and caution for their identification, even in the most common species such as *P. capsularis* and *P. rubra*, which can be found in the same habitats. In the most difficult cases, several species have even changed status several times. For instance, Killip merged *P. bauhinifolia* H.B.K. with *P. andreana* Mast. in 1938, and restored it as a distinct species in 1960, while Holm-Nielsen et al. (1988) merged *P. bauhinifolia* with another close relative, *P. alnifolia*, a position that we have adopted here. On the other hand, a couple of other species may also show very little morphological differentiation, as *P. mollis* and *P. cuspidifolia* or *P. hahnii* and *P. guatemalensis*, but differ in their altitudinal distribution, which confirms that they are distinct entities. Many new species of subgenus *Distephana* are also questionable, as one of its two most common species, *P. coccinea* Aubl., distributed in most of the Amazon, has been split in several species on the basis of bract size, nectar gland numbers, and small variation in numbers and respective colors of the corona series. Concerning Colombia, Vanderplank (2006) underlined that the description of *P. coccinea* by Escobar (1988) matches perfectly that of *P. miniata* Vanderplank, so he considered the latter a Colombian species. However, we have not adhered to this opinion for several reasons. Vanderplank described it on material grown in glasshouse and his report does not refer to the examination of Colombian materials. The type and level of the differentiation described between the different new species and *P. coccinea* is at most of the same order as morphological variation in other common widespread species (*e.g. P. vitifolia, P. foetida*, *P. suberosa*, *P. alnifolia, P. capsularis, P. mixta, P. cumbalensis, P. maliformis,* or *P. emarginata*). He reported a high level of sexual compatibility with the other common *Distephana* species, *P. vitifolia*, which raises the expectation of sexual compatibility with the even closer "true" *P. coccinea*. Thus we have stuck to the treatment of *P. coccinea* by Escobar (1988), whose quantitative description is more precise than the original by Aublet (1775) but not fundamentally different. Within subgenus *Passiflora*, *P. maliformis*, *P. serrulata* and *P. multiformis* constitute other cases of possible overclassification, as they are mostly differentiated by the degree of lobation of their leaves, a trait that is quite variable in many other species, including other *Tiliifoliae*, such as *P. ligularis* (Killip, 1938; *obs. pers.*). A wider problematic group is the series *Laurifoliae*, with ten species in Colombia, always difficult to identify from incomplete specimens. Although they probably constitute a very young group and they exhibit a high number of common traits, species of subgenus *Tacsonia* are relatively easy to differentiate. Particularly interesting are the endemics of section *Colombiana*, from the center of the cordilleras, often characterized by a very long peduncle and linear-lanceolate stipules, and from the northeast and up to the Venezuelan Andes. Several authors have reported easy interspecific hybridization in subgenus *Tacsonia*, involving cultivated as well as wild materials (Escobar, 1985). This phenomenon, by producing spontaneous off-types, may have led to some overclassification in this subgenus. Indeed, of the 30 species reported here for Colombia, five (*P. cremastantha* Harms, *P. formosa* Ulmer, *P. pamplonensis* Planch. & Linden *ex* Triana & Planch., *P. purdiei* Killip, *P. rigidifolia* Killip) are known only from the type material. Whether this is due to high endemism, ancient extinction, or off-types resulting from hybridization cannot be ascertained, unless a second specimen is recorded, as we did for *P. linearistipula*. It is important to note that *P. formosa* was described as a new species from the same specimen considered as an off-type of *P. lanata* (Juss.) by Escobar (1988). Overclassification may be suspected even in better-known species, as *P. parritae* (Mast.) Bailey, and *P. jardinensis* L.K. Escobar. Indeed, in populations of the former, we have observed sufficient morphological variation to include the few known specimens of the latter species, which might simply represent a small isolated population. On the other hand, most endemics of subgenus *Tacsonia* were found in highlands of difficult access, and more species can reasonably be expected to be described from relatively poorly explored areas such as the South of Tolima, Santander and Norte de Santander departments.

Our list ranks Colombia as the country with the highest richness of Passifloraceae, followed by Brazil with 127 species. Figure 5 allows comparisons for species richness and relative diversity of passion flowers in the Neotropics, showing the strong influence of latitude (typical of a tropical distribution) and topography on *Passiflora* diversity. Colombian species richness and diversity is more than twice that of Peru and Venezuela, two countries of similar surface and latitude. Given its much smaller area, Ecuador also presents an impressive diversity. Thus, the northern Andes of Colombia and Ecuador clearly constitute the center of diversity for the genus *Passiflora*. This is probably due to the greater availability of habitats, especially at high elevations, in these two countries. The presence of three Andean cordilleras in Colombia very probably played a significant role. Indeed, radiation has been very active in the northern Andes, with particular contribution of recent and fast evolving groups, such as subgenera *Rathea* and *Tacsonia*, accounting for more than 41 highland species in Colombia and Ecuador. Among them, 21

(14%) species are endemic to Colombia. Colombian highlands are also rich in representatives of subgenus *Decaloba*.

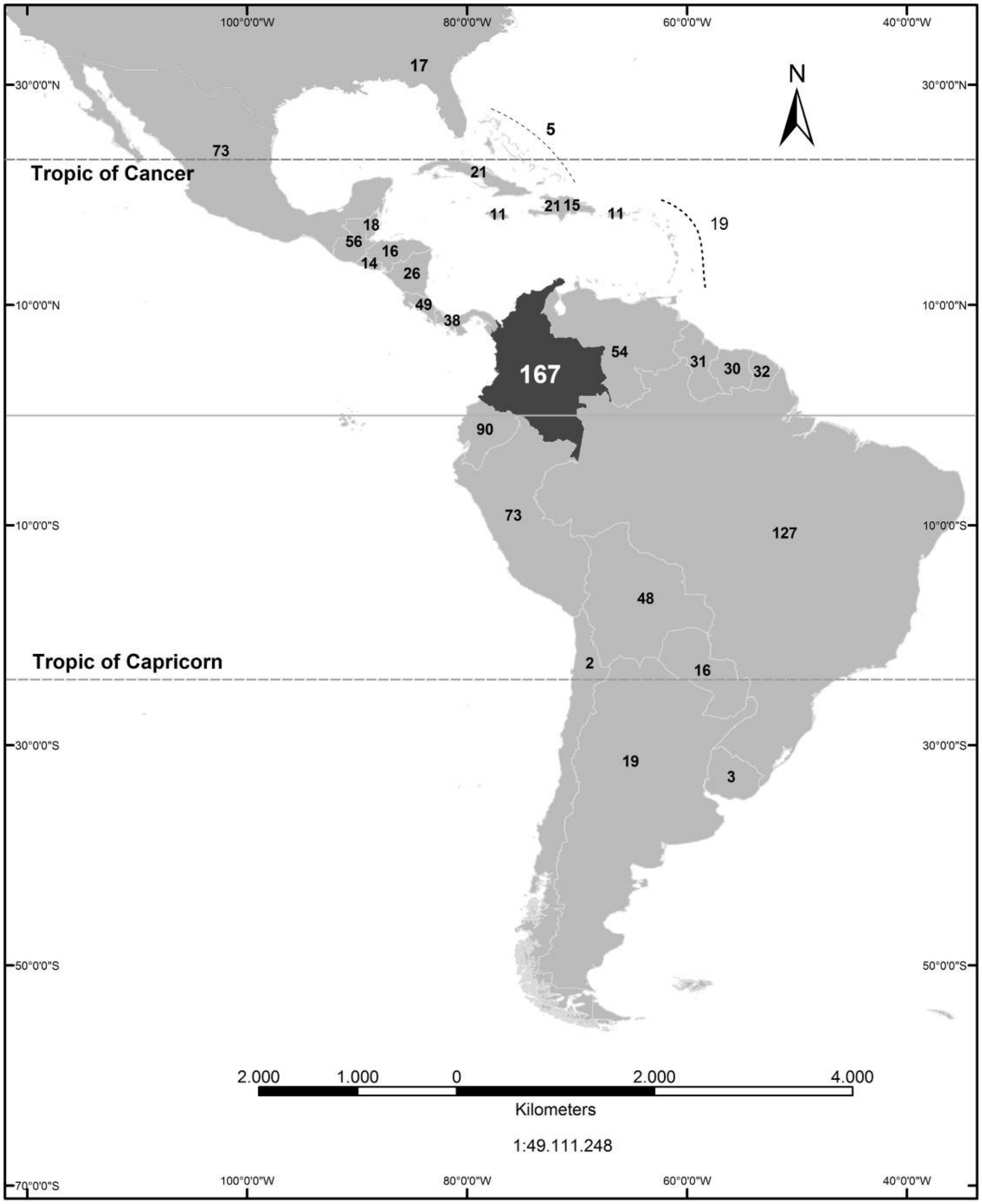

Figure 5. Distribution of Passifloraceae species richness in American countries, according to information gathered from Killip (1938, 1960), Escobar (1988, 1989, 1990 inedited, 1994), Holm-Nielsen et al. (1988), Jørgensen & León (1999), MacDougal (1994), Vanderplank (2000), Deginiani (2001), Tillet (2003), Ulmer & MacDougal (2004), records of the herbaria cited in this study and many journal articles related with the description of new species present in the America.

According to Escobar (1988a), 40% of the New World Passifloraceae are found in the Andes. In Colombia, habitats between 1000 and 3,000 m account for only 27% of the land area, yet 81% of the species of Passifloraceae are found there. With 123 species, the Andean region concentrates the highest richness, mainly between 1000 and 2,000 m. The Caribbean region shares the highest proportion of species (27) with the Andean region (Table 1), which is mostly due to the presence of the Sierra Nevada de Santa Marta mountain range in northern Colombia, with a steep gradient of elevation from the Caribbean Sea to summits at 5,775 m. The increase of species richness and endemism with the elevation is generally interpreted as a result of the increasing isolation and decreasing habitat surface in high mountain regions, leading to small, fragmented populations which are prone to speciation (Simpson, 1975; Jørgensen et al., 1995).

Another contribution to the particular species richness in Colombia and Ecuador is that of the Pacific Coast region, continuous with the similar highly diverse ecosystems of Central America (Chocó-Darién/Western Ecuador hotspot of Myers et al., 2000), and receiving one of the highest rainfalls in the world, in strong contrast with the conditions prevailing in the westerns Andes and coast of Peru that are arid or semi-arid, or the drier and more contrasted climate of Venezuela. The Passifloraceae species composition of this region appears both diverse and well-differentiated when compared with that of the other biogeographic regions (Figure 2), heightening its interest. This is not surprising, as the Chocó region is recognized as one of the most diverse biotas in the world, with nearly 40% endemism (Gentry, 1986).

Until recently, the genera *Dilkea* and *Ancistrothyrsus* were only known from the Amazon basin. The description of *A. antioquiensis* by Escobar (1990 ined.) in the Andes and the observation of *Dilkea retusa* in the Andes and Pacific regions extend their distribution to other important biota.

The distribution of Passifloraceae has been drastically affected by deforestation, principally in the Andean region. Its historical range corresponds to a region with a long history of livestock and agriculture that now supports extensive plantations of coffee, sugar cane, rice, bananas, and potatoes. According to our field observations, very common species, such as *P. adenopoda*, *P. alnifolia*, *P. capsularis*, *P. coriaceae*, *P. rubra*, *P. suberosa*, and *P. mixta*, are mostly species that thrive in secondary forest or disturbed old-growth forest. Human disturbances may even have contributed to extend their distribution, as reported in other plants (Svenning, 1998).

According to Myers et al. (2000) and Robbirt et al. (2006), rarity and endemism represent two factors of particular significance in the consideration of risk of decline and extinction. In this context, most Colombian Passifloraceae (70.7%) are under some threat degree according to IUCN criteria. Only 29.3% fall in the 'least concern' category (**LC**), which clearly illustrates the alarming situation for the family (Figure 3). Our results are consistent with the Red List of plants published by the von Humboldt Institute (Calderón, 2005), based on the 141 species listed by Hernández & Bernal (2000), with similar percentages for each category. However, this list only includes *P. colombiana* L.K Escobar under the category of critically endangered species (**CR**), while ours places 16 species in this category.

Exploration for Passifloraceae was not possible in the protected areas of Colombia that are of essential importance for the conservation of the country's biodiversity, as we lacked permission of access by the Colombian Ministry for Environment (MMA). Another limiting factor of research for conservation purposes is the conflict situation in many areas (Martin & Szuter, 1999; Dévalos, 2001).

Forests in the northern Andes are currently one of the major conservation priorities on a global scale due to their fragility, biological richness, high rates of endemism and multiple anthropogenic threats (Olson & Dinerstein, 1998). As Passifloraceae display very high species richness, endemism and extinction risk in this area, and given their multiple ecological interactions with many organisms, as well as their economic potential, this family should constitute both an important target of conservation efforts and a good indicator of their success.

Table 4. List of 167 Passifloraceae species of Colombia. Fifty-eigth endemic species are marked by an asterisk (*); twenty-six species new to Colombia by the abbreviation ‘nr’; nine species probably present in the country are indicated between square brackets. New records, for a given biogeographic region, department (abbreviated as in Tables 1 and 2) or elevation-range are indicated by **bold** letters. Abbreviations in **bold** letters in the ‘Notes’ column correspond to the plant habits: shrub (**Ab**), tree (**Ar**), and climber (**Tr**). V.N and I.N. indicate vernacular and indigenous names, respectively.

Taxon	Biogeographic Region	Geopolitical Distribution	Elevation	Collection for Reference	Bibliographic Reference	IUCN Category	Notes
Genus *Ancistrothyrsus* Harms, 1931							
Ancistrothyrsus antioquiensis L.K Escobar (ined), 1988 * nr	**and**	**ant**	**90-800**	Escobar & Roldán 8819 (HUA) - Type	F.J Roldán (*com. pers*), Escobar (1990 inedited)	CR	**Tr**
[*Ancistrothyrsus hirtellus* A.H. Gentry, 1992]	amz		**150-350**	Gentry & Stein 47114 (MO) - Isotype	Gentry 1992		**Tr** Reported in the Ecuadorian, Peruvian and Venezuelan Amazon.
Ancistrothyrsus tessmannii Harms, 1931	amz	**ama** pu	50-400	Vester & Matapi 639 (COAH)	Holm-Nielsen *et al.* 1988	CR	**Tr**
Genus *Dilkea* Mast., 1871							
Dilkea johannesii Barb. Rodr., 1885	amz	va	100-500	Soejarto 2461 (HUA)	Killip 1938	CR	**Tr**
Dilkea parviflora Killip, 1938	amz	ama cq va	100-500	Gentry 64981 (MO)	Holm-Nielsen *et al.* 1988	LC	**Tr** V.N.: Canilla de Tente, Tripa de Tente (ama). Edible fruit
Dilkea retusa Mast.,1871	amz **and pac**	ama **ant cho cq gv** met **pu snt** va **vc**	100-500	López *et al.* 5947 (COAH)	Killip 1938; Uribe 1955b; Holm-Nielsen 1974; Holm-Nielsen *et al.*1988	LC	**Tr**

Genus *Passiflora* L., 1753 **Subgenus *Astrophea* (DC.) Masters, 1871** **Section *Astrophea***							
Passiflora callistema L.K. Escobar, 1994 *	car	bl	100	E. Forero 487 (COL) - Type	Escobar 1990 Inéd., 1994	CR	**Tr** Only known from the type.
Section *Botryastrophea*							
Passiflora holtii Killip, 1938	amz	ama **cq** gn va	**150**-500	Jaramillo 7890 (COL)	Killip 1938; Escobar 1990 Inéd., 1994	LC/NT	**Tr** I.N: Guachique, Bejuco (ama). Edible fruit
Passiflora pyrrhantha Harms, 1926	amz	va	400-1000	Shultes & Cabrera 12693 (COL)	Killip 1938; Holm-Nielsen *et al.*1988; Escobar 1990 Inéd., 1994	EN/CR	**Tr**
Passiflora securiclata Mast., 1893	amz ori	ara by **gv va** vch	**150**-500	Betancourt *et al.* 9753 (COAH)	Killip 1960; Escobar 1990 Inéd., 1994	LC	**Tr**
Passiflora spicata Mast., 1872	amz	gv	**150**-500	Cuatrecasas 7397 (COL)	Killip 1938; Holm-Nielsen *et al*. 1988; Escobar 1990 Inéd, 1994	VU	**Tr**
Passiflora spinosa (Poepp. & Endl.) Mast., 1871	amz and ori **car**	ama ant **by cq cor** cun gn **met pu** snt **va** vch	**150**-500	Zarucchi 4279 (COL)	Killip 1938; Holm-Nielsen 1974; Holm-Nielsen *et al.*1988; Escobar 1990 Inéd., 1994	VU	**Tr** V.N.: Cocorella (bl), Bejuco campano (snt)
Section *Dolichostemma*							
Passiflora citrifolia (Juss.) Mast.,1871	amz	va vch	**85**-500	Barbosa & Zurucchi 2989 (COAH)	Killip 1838; Escobar 1990 Inéd.	LC	**Tr**

Passiflora haughtii Killip, 1938 *	and	snt	100-**700**	Haught 1635 (COL)	Killip 1938; Escobar 1990 Inéd., 1994	CR	**Ab**
Passiflora mariquitensis Mutis *ex* Uribe, 1954 *	and	**to**	**420-700**	Ocampo *et al*. 55 (TOLI)	Killip 1938; Escobar 1990 Inéd., 1994	CR	**Ab** Formerly considered extinct.
Passiflora mutisii Killip, 1938 *	and	to	**600**	Mutis 2279 (MA) - Type	Killip 1938; Escobar 1990 Inéd., 1994	EX	**Tr**
Passiflora pittieri Mast., 1897	**pac**	ant cho	50-1000	Gentry & Aguirre 15318 (COL)	Killip 1938; Escobar 1990 Inéd., 1994; Gentry 1976	VU	**Ab**
Section *Euastrophea*							
Passiflora arborea Spreng., 1826	and **car**	ant **bl by cau cl cun** hu ma **na** qu **ri to** vc	1000-2300	Humboldt & Bonpland 5864 (P) - Type	Killip 1938; Pérez 1956; Holm-Nielsen *et al*. 1988; Escobar 1990 Inéd.	NT	**Ar** V.N: Cherimoyo (vc), Granadillo arboreo (cun). Edible fruit
Passiflora lindeniana Planch. *ex* Triana & Planch., 1873	and	cun **ns** snt	1000-2700	Linden 1409 (P) - Type	Escobar 1994	NT	**Ab**
Passiflora emarginata Humb. & Bonpl., 1813 *	and **pac**	**cau cl** cho na vc	1500-2000	Humboldt & Bonpland (P) - Type	Killip 1938; Escobar 1990 Inéd., 1994	LC	**Ar** Edible fruit
Passiflora engleriana Harms, 1894 *	and	ant	1500-2500	Escobar 8853 (COL)	Killip 1938; Escobar 1990 Inéd., 1994	VU/EN	**Ar**
Passiflora macrophylla Spruce *ex* Mast., 1883	amz **and** pac	**ant cau** cho pu na	60-**1800**	Alcázar & Salgado 1203 (CAUP)	Killip 1938; Holm-Nielsen *et al*. 1988; Escobar 1990 Inéd., 1994	LC	**Ab** V.N: Acaba familia (cho)

Passiflora putumayensis Killip, 1938	and	pu	**1350**-2500	Mora-0. 3438 (PSO)	Killip 1938; Escobar 1990 Inéd., 1994	EN/CR	**Ab**
Passiflora sphaerocarpa Triana & Planch., 1873 *	and	**ant ce** cun **na ns** qu **ri snt** to **vc**	400-**1700**	Schlim 285 (P) - Type	Killip 1938; Uribe 1972; Escobar 1990 Inéd., 1994	LC/NT	**Ar** V.N: Gulupo de Arbol (cun), Capafraile (to). Edible fruit
Passiflora tica Gomez-Laur. & L.D. Gómez, 1981	pac	ant cho	450-1500	Escobar 2192 (HUA)	Escobar 1990 Inéd., 1994	LC/NT	**Ar**
Section *Pseudoastrophea*							
[*Passiflora costata* Mast., 1872]	amz		**50-350**	Spruce 1670 (K) - Type	Killip 1938; Escobar 1990 Inéd., 1994		**Tr** Reported in the Amazon of Peru, Brazil, Guianas, and Venezuela) (confluence of the rivers Rio Negro and Casiquiare).
Passiflora grandis Killip, 1938 *	and	ns snt	1000-2000	Schlim 585 (K)	Escobar 1990 Inéd., 1994	EN/CR	**Ar**
[*Passiflora ovata* Martin *ex* DC., 1828]	**ori**		**0-150**	Colector n.v.	Killip 1938; Escobar 1990 Inéd., 1994		**Tr** Reported in the Amazon of Venezuela.
Passiflora phaeocaula Killip, 1927	amz **ori**	gn va **vch**	**150-1100**	Madriñan 893 (MO,GH)	Killip 1938; Holm-Nielsen 1974; Escobar 1990 Inéd., 1994	LC/NT	**Tr Ab**
Passiflora skiantha Huber, 1960	amz	gv	**150**-500	Cuatrecasas 7366 (COL)	Killip 1938; Escobar 1990 Inéd.	NT/VU	**Tr**

[*Passiflora tessmannii* Harms,1926]	amz		50-500	Tessmann 4385 (N) - Type	Killip 1938; Escobar 1990 Inéd., 1994		**Tr** Reported in the northern Amazon of Peru.
Passiflora venosa Rusby	and pac	cho	**50-450**	Juncosa s.n. (JAUM) n.v.	Killip 1938; Escobar 1990 Inéd.	VU/EN	**Tr**
Subgenus *Decaloba* (DC.) Rchb., 1828							
Section *Cieca*							
Passiflora apoda Harms,1929	and	ant cau **cl** qu **na** ri to vc	**1900-3260**	Hazen 9688 (MO) - Isotype	Killip 1938; Hernández 2003	LC/NT	**Tr**
Passiflora coriacea Juss.,1805	and **car pac**	ant **by** cau **cl** cho cun **hu** ma **ns** qu **ri** **snt** to vc	**250**-1500	Uribe 2565 (COL)	Croat 1978; Holm-Nielsen *et al.* 1988	LC	**Tr** V.N.: Ala de Murcielago
Passiflora holosericea L.,1753	car	at bl **ce**	0-**1400**	Cuadros-H 1882 (COL)	Killip 1938	LC/NT	**Tr**
Passiflora megacoriacea Porter-Utley, 2003 nr	**car**	**bl**	**100-200**	Killip & Smith 14415 (US)	Porter-Utley 2003	DD	**Tr**
*Passiflora pallida*L., 1753 nr	**car**	**at bl ma sp**	**0-200**	Dugand & Jaramillo 2844 (COL)	Porter-Utley 2003	LC	**Tr** Appel Monkey (sp)
Passiflora sodiroi Harms, 1922 nr	**and**	**cau**	**1850-2150**	Escobar *et al.* 4368 (PSO)	Holm-Nielsen *et al.* 1988	EN/CR	**Tr**
Passiflora suberosa L., 1753	and car	ant cau cl cun **gv na ns qu** **snt** suc to **vc**	200-**2200**	Cuatrecasas 15930 (VALLE)	Holm-Nielsen *et al.* 1988	LC	**Tr** V.N.: Curubita de Monte (ant)
Section *Decaloba*							
Series *Auriculatae*							
Passiflora auriculata Kunth, 1817	amz and car ori pac	ama ant bl by cau **cl** cho **cor** cq cun **gn gv** met na ns pu qu snt **to** va vc vch	0-1500	Killip & Cuatrecasas 58988 (VALLE)	Holm-Nielsen 1974; Holm-Nielsen *et al.* 1988	LC	**Tr** V.N: Rejito (cun)

Series *Sexflorae*							
Passiflora sexflora Juss., 1805	and	ant hu **qu to vc**	**1700**-2300	Zurucchi *et al.* 5813 (CHOCO)	Holm-Nielsen *et al.* 1988	NT/VU	**Tr** V.N.: Corvejo (na)
Series *Luteae*							
Passiflora filipes Benth., 1843	and	**qu** ri **vc**	**950**-1250	Silverstone 7205 (CUCV)	Holm-Nielsen *et al.* 1988	VU	**Tr**
Series *Miserae*							
Passiflora misera Kunth, 1817	and car **ori pac**	ant at **ara** bl by cau cl cho cor **cun cs** lg **ma met vc ns**	0-**1050**	E. Forero 9936 (COL)	Killip 1938	LC	**Tr**
Passiflora tricuspis Mast., 1872 nr	**and**	**met**	**1220-2000**	Estrada *et al.* 146 (MA)	Killip 1938	CR	**Tr**
[*Passifora trifasciata* Lemaire, 1868]	**amz**	**ama pu**	**130-1100**	Brandbyge *et al.*33556 (AAU)	Killip 1938; Nielsen *et al.* 1988		**Tr** Reported in the Amazon of Ecuador, Brazil and Peru. Ornamental (qu)
Series *Punctatae*							
Passiflora alnifolia Kunth, 1817	and **car**	ant **by cau** cl cun ma na **pu** qu ri **snt to** vc	**1400**-2500	Hno. Daniel 2803 (MEDEL)	Holm-Nielsen *et al.* 1988	LC	**Tr**
Passiflora andreana Mast., 1883	and	ant cau cun ma na qu ri	**1500-3150**	Garcia-B.12949 (COL)	Holm-Nielsen *et al.* 1988	CR	**Tr**
Passiflora azeroana L. Uribe, 1955 *	and	by **cun** hu snt	2500-3000	Lozano 3718 (COL)	Uribe 1957	NT/VU	**Tr**
Passiflora biflora Lam., 1789	and car	ant **at bl ce cl** cho cun hu ma **met** na **ns** ri sp snt to **vc**	0-1500	Garcia-B. 11720 (COL)	Killip1938; Holm-Nielsen 1974; Croat 1978	LC	**Tr** V.N.: Peyen Papaya (sp), Desjarretadera (cun)

Passiflora bogotensis Benth., 1845 *	and **car**	**by** cun **hu lg ma ns snt vc**	2000-3700	Garcia-B. 15291 (COL)	Killip 1938; Holm-Nielsen 1974	LC	**Tr** V.N.: Curubo macho (cun)
Passiflora bucaramangensis Killip, 1930 * nr	**and**	**snt**	**1500-2600**	Killip & Smith 16787 (MO) - Isotype	Killip 1930, 1938	EN	**Tr**
Passiflora candollei Tr. & Planch., 1873 nr	**amz**	**ama**	**100**	Rudas *et al.* 2180 (COL)	Killip 1938	NT	**Tr**
Passiflora chelidonea Mast., 1979	and **car pac**	**ant ara cau** cho na ns **pu ri** snt vc	**900**-3000	Cuatrecasas 12526 (COL)	Holm-Nielsen *et al.* 1988	LC	**Tr**
Passiflora cuneata Willd.,1809	and **car**	**ant by** cho **cun ma met** ns snt vc	**900**-3000	Uribe 5973 (COL)	Killip 1938; Hno. Daniel 1968; Holm-Nielsen 1974	LC	**Tr** V.N.: Granadillita de Monte (ant)
Passiflora cuspidifolia Harms, 1893	and	by cun snt	2000-3200	Prieto 302 (UIS)	Holm-Nielsen *et al.* 1988	LC	**Tr**
Passiflora dawei Killip, 1930 *	and	cun **snt**	**900**-1600	Idrobo 2037 (COL)	Killip 1930, 1938; Hernández 2003	VU/EN	**Tr**
Passiflora erytrophylla Mast.,1872 *	and	**by** cun	**1600-2790**	Ocampo *et al.* 54 (HUA)	Killip 1938; Uribe 1955a	EN	**Tr** Not collected since 1938.
Passiflora lyra Planch. & Lind. *ex* Killip, 1846 nr	**and**	**ant**	**400-840**	MacDougal 4161 (HUA)	Killip 1938	NT/VU	**Tr**
Passiflora magdalenae Triana & Planch., 1873 *	and	cl **cun** to	**200-1200**	Uribe 2568 (COL)	Killip 1938; Pérez 1956	NT/VU	**Tr** V.N.: Granadillo del Magdalena.
Passiflora micropetala Mast., 1872	**amz** and	**ama** ant **by** cho cq met pu vc	0-**710**	Perez-A.669 (COL)	Holm-Nielsen *et al.* 1988	LC	**Tr**
Passiflora mollis HBK., 1817 * nr	**and**	**ant cl cho qu lg snt to vc**	**1400-2500**	Humboldt & Bonpland (P) - Type	Killip 1938; Hno. Daniel 1968	LC/NT	**Tr**

Passiflora monadelpha Jørgensen & Holm-Nielsen, 1987 nr	**and**	**to vc**	**2800-3310**	Escobar 4859 (HUA)	Holm-Nielsen *et al.* 1988; Hernández 2003	VU/EN	**Tr**
*Passiflora munchiquensis.*Hernández (ined), 2003 * nr	**and**	**cau vc**	**1900-3200**	Vargas 3909 (HUA)	Hernández 2003; A.Hernández (*com. pers*).	NT/VU	**Tr**
Passiflora occidentalis Hernández (ined), 2003 * nr	**and pac**	**cau cho na pu vc**	**50-1200**	Killip 39025 (COL)	Hernández 2003; A.Hernández (*com. pers*).	LC/NT	**Tr**
Passiflora panamensis Killip, 1922	pac car	ant bl cho **cor**	0-500	Zarucchi *et al.* 5107 (CHOCO)	Killip 1938	NT	**Tr** V.N.: Gulupa (ant)
Passiflora pilosissima Killip, 1931 * nr	**and**	**ant vc**	**1500-2100**	Lehmann 7630 (US)	Killip 1938	CR	**Tr**
Passiflora popayanensis Killip, 1930 *	and	cau	2400-2900	Lozano 6472 (COL)	Killip 1938	VU/EN	**Tr**
Passiflora punctata L., 1753	**and** pac	**cau cun** na **vc**	**20-1750**	Romero-C. 3150 (COL)	Croat 1978; Holm-Nielsen *et al.* 1988	LC/NT	**Tr**
[*Passiflora sandrae* J. MacDougal, 2006]	**pac**	**cho**	**800-1100**	Garwood 1178 (MO) - Type	MacDougal 2006		**Tr** Collected in the border of Panama and Colombia (cho)
Passiflora tribolophylla Harms, 1922 *	pac	ant cau cho	50-**1820**	Lehmann 5420 (foto, COL)	Killip 1938; Hno. Daniel 1968	LC/NT	**Tr**
Passiflora tuberosa Jacq., 1804 nr	**and**	**vc**	**1200**	Cuatrecasas 15930 (VALLE)	Killip 1938	EN	**Tr**
Passiflora ursina Killip & Cuatrec., 1960	and	ant na vc	**2100-3100**	Roldán 2345 (HUA)	Killip 1960; Holm-Nielsen *et al.* 1988; Hernández 2003	VU/EN	**Tr**
Passiflora vespertilio L.,1753	amz **and** ori	ama met na	**150**-500	Plowman 2425 (COL)	Holm-Nielsen *et al.* 1988	LC/NT	**Tr**

Section *Hahniopathanthus*							
Passiflora guatemalensis S. Watson, 1887	and car	ant **cl** lg ma **qu ri** to **vc**	0-**1580**	Uribe 2532 (COL)	Killip 1938; Ulmer & MacDougal 2004	LC	**Tr**
Passiflora hahnii (Fourn.) Mast., 1872 nr	**and car**	**ant cl lg ma to vc**	**100-1250**	Killip & Hazen 8670 (Y)	Uribe 1955b; Holm-Nielsen 1974; Ulmer & MacDougal 2004	CR	**Tr** V.N.: Granadilla Abroquelada (ant)
Section *Pseudodysosmia*							
Passiflora adenopoda Moc. & Sessé *ex* DC., 1828	and **car**	ant by cl cun **cau** ma qu ri to vc	100-**2100**	Cuatrecasas 15703 (VALLE)	Holm-Nielsen *et al*. 1988; MacDougal 1994	LC	**Tr** V.N: Pegajosa (qu), Granadilla Culebra (vc), Gulupo (cun). Edible fruit
Passiflora lobata (Killip) Hutch. *ex* J.M. MacDougal,1986	pac	ant cho	0-1200	Gentry 23791 (COL)	MacDougal 1994; Ulmer & MacDougal 2004	NT	**Tr**
Passiflora morifolia Mast., 1872	and	na	**500-1000**	Karsten s.n. (W) n.v.	Killip 1938; MacDougal 1994.	EN	**Tr**
Section *Pseudogranadilla*							
Passiflora bicornis Mill., 1768	car	ant at bl lg ma	0-500	Saravia 3643 (COL)	Killip1938; Holm-Nielsen 1974	LC	**Tr** V.N.: Cachito de Venado (bl), Cinco Llagas (at)
Passiflora hirtiflora Jørgensen & Holm-Nielsen, 1987 nr	**and**	**ns**	**2650**	Escobar 3152 (HUA)		CR	**Tr**
Passiflora kalbreyeri Mast., 1883 *	and **car**	**ce** ns **snt**	**1100-3100**	Killip 20284 (COL)	Killip 1938	LC/NT	**Tr**
Passiflora menispermacea Triana & Planch., 1873 *	and	to	**1400**-3000	Cuatrecasas 9247 (MA)	Killip 1938	LC	**Tr**
Section *Xerogona*							

Passiflora capsularis L., 1753	and **car** pac	**ant cl** cun cho hu **lg ma na ns** qu snt to **vc**	100-**2000**	Uribe 2566 (COL)	Killip 1938; Holm-Nielsen 1974; Holm-Nielsen *et al*. 1988	LC	**Tr**
Passiflora costaricensis Killip, 1922	pac	cho	**20-1500**	Croat 42591 (HUA)	Holm-Nielsen 1974; Holm-Nielsen *et al*. 1988	NT	**Tr**
Passiflora escobariana J.M. MacDougal, 1992	and	ant	**1090**-1100	MacDougal 3823 (HUA) - Isotype	MacDougal 1992; Ulmer & MacDougal 2004	VU	**Tr**
Passiflora rubra L., 1753	and car	**ant cl cau** cun **hu** lg pu **na pu qu** ri to **vc**	500-2000	Garcia-B. 17279 (COL)	Holm-Nielsen *et al*. 1988	LC	**Tr** V.N.: Chulupa de Monte (cl)
Subgenus *Dysosmia* (DC.) Killip, 1938							
Passiflora foetida var. *eliasii*Killip, 1938	**car**	**at bl ma**	**0-500**	Penell 12029 (N)	Kiliip 1938	VU	**Tr** V.N.: Flor de la Pasión, Pasionaria (at)
Passiflora foetida var. *gossypiifolia* (Desv.) Mast. 1872	**amz** and car ori **pac**	ama ant **ara at** bl by cau **ce** cor **cq** cs cun **cho** gn **gv hu** lg ma met **na** ns **qu snt suc to va vc**	**0-1500**	Schultes 22576 (COL)	Killip 1938; Martin & Nakasone 1970; Romero-C. 1991; Ulmer & MacDougal 2004; Ulmer & Ulmer, 2005	LC	**Tr** V.N.: Granadilla (cho), Flor de la Pasión (at), Gulupo (cun), Bejuco Canastilla (met), Chulupa de Loma (ant hu), Cinco Llagas (cor). I.N.: Iñana-leeg murulale (ama). Edible fruit

Passiflora foetida var. *hispida* (DC.) Killip *ex* Gleason, 1931	**and car**	**ant bl cun ns to**	**0-1500**	Killip & Smith 21000 (N)	Killip 1938; Ulmer & Ulmer, 2005	LC	**Tr** V.N: flor de la pasión (ma), gulupo (cun)
Passiflora foetida var. *isthmina* Killip, 1938	**and pac**	**na snt vc**	**0-1200**	Killip 5289 (N)	Killip 1938	VU	**Tr** V.N.: Flor de la Pasión (vc)
Passiflora foetida var. *moritziana* (Planch.) Killip *ex* Pull, 1937	**car**	**ma**	**0-500**	Killip & Smith 21088 (N)	Killip 1938	VU	**Tr** V.N.: Flor de la Pasión (ma)
Passiflora foetida var. *sanctae-martae* Killip, 1938 * nr	**car**	**ma**	**0-500**	Smith 1532 (P)	Kiliip 1938	EN	**Tr** Flor de la Pasión (ma)
Passiflora vestita Killip, 1938	amz	pu	0-500	Betancourt 5164 (MO) n.v.	Killip 1938; Holm-Nielsen *et al.* 1988	VU/EN	**Tr**
***Distephana* (Juss.) Killip, 1938**							
Passiflora coccinea Aubl.,1775	amz **ori**	**ama cs** gn gv met na va vch	**150**-1500	Davidse 5321 (COL)	Escobar 1988a	LC	**Tr** V.N.: Lluvia Padie, Granadillo de Conga (ama), Granadilla colorada (cs). Edible fruit
Passiflora involucrata (Mast) A.H. Gentry, 1981	amz	ama cq **va**	**150-350**	Schultes 6923 (COL)	Escobar 1988a	LC	**Tr**
Passiflora glandulosa Cav., 1790	amz	va	**150**-500	Romero-C. 3668 (AAU) n.v.	Killip 1938; Holm-Nielsen 1974	EN	**Tr**
Passiflora quadriglandulosa Rodschied, 1796	amz	ama gu	**150**-500	Lozano 604 (COL)	Escobar 1988a; Holm-Nielsen *et al.* 1988	LC/NT	**Tr**

Passiflora variolata Poepp. & Endl., 1838	amz	ama cq va	**150**-500	Zarucchi 2197 (COL)	Escobar 1988a	LC/NT	**Tr** V.N.: Granadilla, Oncilla, Parcha de Culebra de Agua (ama)
Passiflora vitifolia Kunth, 1817	amz and **car ori** pac	ama **ant bl** by **cau ce cl** cho **cor cq** cun **lg** gv **ma met na pu ri snt to** va **vc vch**	0-**1800**	Cuatrecasas 15740 (VALLE)	Killip 1938; Romero C. 1956, 1991; Martin & Nakasone 1970; Holm-Nielsen 1974; Holm-Nielsen *et al.* 1988	LC	**Tr** V.N.: Chulupo (cq), Granadilla de Monte (cho), Granadillo (met cq), Gulupa (to). I.N.: Maloca de Fisi (ama). Edible fruit
Subgenus *Manicata* (Harms) Escobar, 1988 (Syn. *Granadillastrum*)							
Passiflora manicata (Juss.) Pers., 1807	and	by cau cl **cun** na ns qu snt to vc	**1400**-2700	Richter s.n. (COL)	Jussieu 1805; Holm-Nielsen 1974; Escobar 1988a	LC	**Tr** V.N.: Tacso (na), Curubo de Monte (qu ns).
***Passiflora* (Medik.) Mast., 1871 (Syn. *Granadilla*)**							
Series *Digitatae*							
Passiflora serratodigitata L.,1753	amz **and** pac	ama cho **ns ant**	0-1000	Renteria 3542 (COL)	Killip 1938; Holm-Nielsen 1974; Holm-Nielsen *et al.* 1988; Romero-C. 1991	LC	**Tr** V.N.: Cocorilla (cho). Granadilla, Naracujinha (ama). N.I.: Cipo-Cipo Naracujinha (ama).
Series *Laurifoliae*							

Passiflora ambigua Hemsl. *ex* Hook., 1902	**amz** and **ori** pac	ant **by** cl cho **cun** hu ma met **pu** snt vc	0-2000	Fuchs 21744 (COL)	Holm-Nielsen *et al*. 1988	LC	**Tr** Edible fruit
Passiflora gleasonii Killip, 1924	ori	gn	**150**-500	Madriñán 1014 (COL)	Killip 1938	EN	**Tr**
Passiflora guazumaefolia Juss., 1805	**and** car	**ce** cor bl ma **snt**	0-500	Uribe 2405 (COL)	Killip 1938; Coppens 2003	LC/NT	**Tr** V.N: La Parcha (ce), Cocorilla (ma). Edible fruit
Passiflora killipiana Cuatrecasas, 1960 nr	**amz**	**cq**	**250-500**	Schultes 5875 (US)	Killip 1960	CR	**Tr**
Passiflora laurifolia L., 1753	**and** amz **pac**	ama **cho** cq **gv hu** met **snt** va	0-**1700**	Zarucchi 1824 (COL)	Killip 1938	LC	**Tr** Edible fruit
Passiflora nitida Kunth, 1817	amz **and car** ori **pac**	ama **ant** cho **cq cun cs gn** gv **ma** met **na** pu va **vc**	0-**1940**	Triana 2931 (P)	Killip 1938; Romero-C. 1956, 1991; Holm-Nielsen 1974; García-B. 1975; Croat 1978	LC	**Tr** V.N.: Granadilla (cho met), Granadilla Babosa (na). N.I.: Burucuña, Gemarundare, Tuchica, Jino-Gojé (va). Edible fruit
[*Passiflora phellos* C. Feuillet, 2004]	amz		**90-150**	Wurdack & Addeley 43479 (NY) - Holotype	Feuillet 2004		**Tr** Reported in the Amazon of Brazil, Peru and Venezuela

Passiflora popenovii Killip, 1922 nr	**and**	**cau na vc**	**1200-2050**	Escobar & Escobar 1017 (HUA)	Killip 1938; Holm-Nielsen *et al*. 1988; Romero-C. 1991; Ulmer & MacDougal 2004	EW	**Tr** V.N: Granadilla de Quijos (na), granadilla caucana, curubejo (cau). Cultivated. Edible fruit
Passiflora riparia Mart. *ex* Mast., 1872	amz	cq **pu va**	**300-400**	Smith 3157 (US)	Killip 1960	LC/NT	**Tr** Edible fruit
Passiflora tolimana Harms, 1894 *	and	**ant** to vc	**820**-2000	Echeverry 3627 (TOLI)	Killip 1938	NT/VU	**Tr** Edible fruit
Series *Incarnatae*							
Passiflora cincinnata Mast., 1868 nr	**and**	**ns**	**1200**	Killip & Smith 20879 (Y)	Killip 1938	CR	**Tr** Ornamental (qu). Edible fruit
Passiflora edulis f. *edulis* Sims, 1818	amz and pac	ant **cl** cau cho cun gv **met na** qu **ri snt to** vch vc	**1100-2750**	Idrobo 1637 (COL)	Holm-Nielsen *et al*. 1988; Vanderplank 2000; Ulmer & MacDougal 2004	NE	**Tr** Introduced from Brazil in the 1950s. V.N: Curuba Redonda (ant cl ri qu), Gulupa (cun). Cultivated or feral. Edible fruit
Passiflora edulis f. *flavicarpa* Degener, 1932 nr	**amz and car ori pac**	**ant ara bl ce cl cho cun gn hu met pu qu snt ri to vc**	**0-1800**	Silvestone 14399 (CUVC)	Killip 1938; Ulmer & MacDougal 2004	NE	**Tr** Introduced from Brazil in the 50s. V.N.: Maracuyá. Cultivated. Edible fruit
Series *Kermesinae*							

Passiflora lehmanni Mast., 1885 *	**amz** and	**ant cau cl** cun hu **pu** qu **ri snt vc**	1000-2000	Uribe 2588 (COL)	Killip 1938; Holm-Nielsen 1974	LC	**Tr**
Passiflora smithii Killip, 1930	and **car**	cun ma **qu** snt to **vc**	500-2000	Killip & Smithii 15015 (MO) - Holotype	Killip 1938; Holm-Nielsen 1974	LC	**Tr** V.N.: Curuba Silvestre (to).
Passiflora trisulca Mast., 1887 *	and	ant **cl vc**	**1300**-1800	Marulanda 91 (HUA)	Killip 1938; Hno. Daniel 1968	NT	**Tr**
Series *Lobatae*							
Passiflora caerulea L., 1753 nr	**and**	**cl cun qu**	**1000-2700**	Ocampo 83 (VALLE)	Deginani 2001		**Tr** Introduced from Argentina. Ornamental. Edible fruit
Passiflora gritensis H. Karst., 1859	and	by ns	**2450**-2500	Cuatrecasas 1808 (COL)	Killip 1938	LC/NT	**Tr**
[*Passiflora montana* Holm-Nielsen & Lawesson, 1987]	**and**		**2600**	Holm-Nielsen *et al*. 6200 (AAU)	Holm-Nielsen *et al.* 1988		**Tr** Collected on the border of Ecuador and Colombia (na)
Passiflora picturata Ker, 1822 nr			**450**	Uribe 1334 (US)	Killip 1938, 1960	DD	**Tr**
Passiflora pennellii Killip, 1924 *	and	**ant** cun	1200-**1600**	Uribe 4827 (COL)	Killip 1938	NT/VU	**Tr**
Passiflora resticulata Mast. & André, 1884	**amz** and **pac**	cau **gv na vc**	0-2000	Marulanda & Márquez 1665 (HUA)	Killip 1938; Holm-Nielsen 1974;Holm-Nielsen *et al.* 1988	NT/VU	**Tr**
Passiflora semiciliosa Planch & Linden, 1873 *	and **car**	**ma** ns	**1850-3000**	Garcia-B. 20749 (COL)	Killip 1938	VU	**Tr** V.N.: Gulupa, Palcha (ns)

Passiflora subpeltata Ortega, 1798	**amz** and car ori	ant bl **cau** ce **cor cq cs** cun ma **suc** to vc	0-2400	Ramírez *et al.* 11507 (CAUP)	Killip 1938; Holm-Nielsen 1974	LC	**Tr** V.N.: Cocorilla (bl)
Series *Quadrangulares*							
Passiflora alata Curtis, 1788 nr	**amz**	**ama**	**200**	Ocampo 82 (VALLE)	Killip 1938; Ulmer & MacDougal 2004	DD	**Tr** Introduced (qu vc) from Brazil in the 90s. V.N.: Maracúa. Cutivated. Edible fruit
Passiflora quadrangularis L.,1759	amz and **car ori** pac	ama ant **bl** cau **cl** cho cq cun gn **hu** ma met **na** ns **qu** va **ri** snt **to vc**	0-**1500**	Gentry 15371 (COL)	Killip 1938; Romero-C. 1956, 1991; Holm-Nielsen1974; Holm-Nielsen *et al.* 1988	LC	**Tr** V.N.: Badea (ant cl hu cun met qu ri), corvejo (snt), Granadillo Grande (cau), curuba (vc), Motorro (gn). Cultivated. Edible fruit
Series *Menispermifoliae*							
Passiflora chocoensis G. Gerlach & T. Ulmer, 2000 * nr	**pac**	**cho**	**0-100**	Gerlach 434917 (COL) - Holotype	Gerlach & Ulmer, 2000; Ulmer & MacDougal 2004	CR	**Tr**
Passiflora menispermifolia Kunth, 1817	amz **car** and pac	ant **bl by** cho **cor** cq cun met **na ns snt** to **vc**	0-**2140**	Cuatrecasas 15541 (VALLE)	Croat 1978; Holm-Nielsen *et al.* 1988	LC	**Tr** V.N.: Chulupe (cq)
Series *Simplicifoliae*							
Passiflora danielii Killip, 1960 *	and	ant	**1300-2600**	Hno. Daniel 1536 (MEDEL) - Isotype	Killip 1960; Hno. Daniel 1968	VU/EN	**Tr**
Passiflora longipes Juss., 1805 *	and	cun by **qu** snt **to**	2500-3500	Sanchez 17 (COL)	Killip 1938	NT	**Tr**

Passiflora longipes var. *oxyphylla* L. Uribe, 1977 *	and	by **ns** snt	2000-2600	Cadena 83 (UIS)	Uribe 1977	NT	**Tr**
Passiflora oerstedii Mast., 1872	and ori pac	**ant** cau cho cun **cau** met na qu **ri** vc	0-**2000**	Romero-C. 6141 (COL)	Killip 1938; Holm-Nielsen 1974; Holm-Nielsen *et al.* 1988	LC	**Tr**
Series *Tiliaefoliae*							
Passiflora ligularis f. *lobata* (Mast.) Killip, 1938 nr	**and**	**ant**	**1800-2000**	Archer 1498 (COL)	Killip 1938	NT	**Tr** V.N: Granadilla. Cultivated. Edible fruit
Passiflora ligularis Juss., 1805	and	ant **cl** cun **cau** by **cho hu met** na ns **pu qu ri snt to** vc	**1550**-2500	Dombey 739 (P) - Type	Killip 1938; Romero-C. 1956, 1991; Holm-Nielsen *et al.* 1988	LC	**Tr** V.N: Granadilla; Granadilla Pipo (na). N.I.: Awapit (na). Cultivated. Edible fruit
Passiflora magnifica L.K. Escobar, 1990 *	and	ant	1250-1750	Callejas 6586 (HUA) n.v.	Escobar 1990; Ulmer & MacDougal 2004	VU	**Tr** Edible fruit
Passiflora maliformis L.,1753	and **car pac**	**ant** by **cl cau** cun **cho** hu ma na **qu snt** to vc	0-**2200**	Humboldt & Bonpland 1804 (P) - Type	Killip 1938; Romero-C, 1956, 1991; Holm-Nielsen, 1974; García-B. 1975; Holm-Nielsen *et al.* 1988	LC	**Tr** V.N: Gulupa, Granadilla de Piedra, o de Hueso (cu, na vc), Gurapa (snt), Chulupa (hu). Cultivated. Edible fruit
Passiflora multiformis Jacq.,1809	**and** car	**lg** ma **ns**	0-**1300**	Romero-C. 8992 (COL)	Killip 1938	NT/VU	**Tr** V.N: Palchita (ns). Edible fruit

Passiflora palenquensis Holm-Niels. & Lawesson, 1987	pac	ant cau cho na vc	0-**1200**	Espina & Garcia 1951 (COL)	Holm-Nielsen & Lawesson 1987; Holm-Nielsen *et al.* 1988	LC	**Tr** V.N.:ranadilla (cho), "Camelo" (vc). Cultivated. Edible fruit
Passiflora platyloba Killip, 1922	pac	cho	0-1050	Gentry & Juncosa 40946 (COL)	Gentry 1976	NT/VU	**Tr** Edible fruit
Passiflora seemannii Griseb.,1858	**amz** and pac ori	ant **by** cho cun gn **gv** met ns snt va vc vch	0-**1300**	MacDougal 4144 (HUA)	Croat 1978	LC	**Tr** V.N.: Palcha, Chulupa (met), Granadilla Montañera (cun). Edible fruit
Passiflora serrulata Jacq., 1767	car	at **ma lg**	0-500	Bunch 601 (FMB)	Killip 1938; Coppens 2003	NT/VU	**Tr** V.N.: Guayabita Cimarrona (ma). Edible fruit
Passiflora tiliifolia L., 1753	and pac	ant cau cho **cl na qu vc to**	**1100-2500**	González 1411 (CAUP)	Killip 1938; Holm-Nielsen 1974; Holm-Nielsen *et al.*1988; Coppens 2003	LC/NT	**Tr** V.N.: Granadilla, Machimbi (Colombia). Cultivada. Fruto comestible.
Subgenus *Porphyropathanthus* L.K Escobar, 1989							
Passiflora sierrae L.K. Escobar, 1989 *	**car**	ma	3000-3700	Cuatrecasas 24375 (COL)	Escobar 1989	EN/CR	**Tr**
Subgenus *Psilanthus* (DC.) Killip, 1938							
Passiflora bicuspidata (H.Karst.) Mast.,1872 *	and	by cun ns snt	2500-3500	Rojas 138 (CDMB)	Uribe 1972; Killip 1978	VU	**Tr**

Passiflora hyacinthiflora Planch. & Linden, 1873 *	and	**by** ma ns	2900-**3300**	Garcia-B. 20700 (COL)	Killip 1938	LC/NT	**Tr**
Passiflora trinervia (Juss.) Poir., 1811 *	and	cl qu to vc	**2500-3700**	Cuatrecasas 20241 (VALLE)	Jussieu 1805; Killip 1938	VU	**Tr**
Subgenus *Rathea* (Karst.) Killip, 1938							
Passiflora andina Killip, 1938 nr	**and**	**na**	**2800**	Karsten (V)	Killip 1938; Holm-Nielsen *et al.*1988	CR	**Tr**
Passiflora colombiana L.K. Escobar, 1986 *	and	na **pu**	3000-**3600**	Mora 6175 (PSO) - Paratype	Escobar 1986, 1988	CR	**Tr**
Subgenus *Tacsonia* (Juss.) Tr. & Planch, 1873							
Section *Bracteogama*							
Passiflora cumbalensis var. *caucana* L.K. Escobar, 1987 *	and	cau	2300-2800	Tryon 6001 (COL)	Escobar 1987, 1988b	LC	**Tr** V.N.: Curuba de Monte. Edible fruit
Passiflora cumbalensis var. *cumbalensis* (H. Karst.) Harms,1894	and	na pu	3000-3800	Fernandez 5834 (COL)	Romero-C. 1956; Holm-Nielsen 1974; Escobar 1987, 1988; Holm-Nielsen *et al.* 1988	LC/NT	**Tr** V.N.: Curuba Roja, Tauso (na). Edible fruit
Passiflora cumbalensis var. g*oudotiana* (Triana & Planch.) L.K. Escobar, 1987	and **car**	ant by **cl** cq cun **hu ma** na **pu** qu **ri snt** to **vc**	**1800-3300**	Uribe 2593 (COL)	Escobar 1987, 1988; Holm-Nielsen *et al.* 1988	LC	**Tr** V.N.: Curuba bogotana (cun), Curubo mucura, curuba rosada, Tausa (na). Cultivated. Edible fruit
[*Passiflora sanctae-barbarae* Holm-Nielsen & Jørgensen, 1987]	**and**		**2200-2700**	Harling & Andersson 12445 (AAU) - Isotype	Holm-Nielsen *et al*. 1988		**Tr** Reported in the northern Andes of Ecuador

Passiflora tripartita var. *azuayensis* Holm-Nielsen & Jørgensen, 1988 nr	and car	**ant by cun ma ns**	**2000-2610**	Escobar 19999 (HUA)	Holm-Nielsen *et al*. 1988	LC/NT	**Tr** V.N.: Curuba. Edible fruit (by cun)
Passiflora tripartita var. *mollissima* Holm-Nielsen & Jørgensen, 1988	and **car**	**ant** by **cau cl** cun **ma na ns pu snt vc**	**2200**-3500	Romero-C 8007 (PSO)	Holm-Nielsen *et al*. 1988; Romero-C. 1991; Ulmer & MacDougal 2004	LC	**Tr** V.N.: Curuba de Castilla (ant by cu cl); Tauxso (na). Cultivated. Edible fruit
Passiflora tarminiana Coppens & Barney, 2001	**and**	**ant by cau cl cun hu na qu snt to vc**	**2000-2900**	Coppens 72 (COL) - Type	Coppens *et al*. 2001; Campos 2001	LC	**Tr** V.N.: Curuba India. Cultivated. Edible fruit.
Section *Colombiana*							
Series *Colombianae*							
Passiflora adulterina L.f.,1781 *	and	by cun **snt to**	**2600-3600**	Barclay 4517 (COL)	Escobar 1988a	NT	**Tr**
Passiflora crispolanata L.Uribe, 1954 *	and	by cun	2500-3500	Uribe 6773 (COL)	Uribe 1954; Escobar 1988a	NT	**Tr** V.N.: Curuba Paramera (cun)
Passiflora cuatrecasasii Killip, 1960 *	and	by cun met **snt**	2200-3500	Cuatrecasas 9479 (foto, MEDEL)	Killip 1960; Escobar 1988a	VU	**Tr**
Passiflora formosa T. Ulmer, 1999 *	and	by	3000-3100	Uribe 5945 (COL)	Ulmer 1999	EN	**Tr**
Passiflora lanata (Juss.) Poir., 1811 *	and	cun by snt to	2200-3500	Uribe 2587 (COL)	Jussieu 1805; Holm-Nielsen 1974; Escobar 1988a	NT/VU	**Tr** V.N.: Granadilla (cun)
Passiflora pamplonensis Planch.& Linden *ex* Triana & Planch., 1873 *	and	snt	2000-3000	Funck & Schlim 1385 (foto, VALLE)	Escobar 1988a	EN/CR	**Tr** Curubita de Piñuela (snt)

Passiflora rigidifolia Killip, 1960 * nr	**and**	**ant**	**3750**	Burke 185 (K) - Type	Killip 1960	DD	**Tr** Known only from the type.
Passiflora rugosa var. *rugosa* (Mast.) Triana & Planch., 1873	and	**cun** met ns	3000-3500	Peñuela 008 (COL)	Escobar 1988a	LC/NT	**Tr**
Passiflora rugosa var. *venezolana* L.K. Escobar, 1986	and	ns snt	2500-3500	Garcia-B. 20001 (COL)	Escobar 1988a	LC/NT	**Tr**
Passiflora trianae Killip, 1938 *	and	ns **snt**	3000-3500	Escobar 569 (COL)	Escobar 1988a	VU/EN	**Tr**
Passiflora truxillensis Planch. & Linden, 1873 nr	and	**ns**	1800-3000	V. Barney & G. Coppens (foto), com. Personal	Escobar 1988a; Ulmer & Ulmer 2005	EN	**Tr**
Series *Leptomischae*							
Passiflora antioquiensis H. Karst., 1859 *	and	ant **cau** cl cun **hu pu qu** ri **to** vc	1800-2700	Escobar 2133 (HUA)	Hno. Daniel 1968; Uribe 1972; Garcia- B. 1975; Escobar 1988a	LC/NT	**Tr** V.N.: Granadilla (vc), Curuba Antioqueña (ant). Wild or cultivated in home gardens. Edible fruit
Passiflora cremastantha Harms, 1922 *	and	cau	2000-2500	Lehmann 5421 (F) - Type	Escobar 1988a	EX	**Tr** Known only from the type.
Passiflora flexipes Triana & Planch., 1873 *	and	**cl** qu ri	2500-**3380**	Vargas 626 (FAUC)	Escobar 1988a	NT/VU	**Tr** V.N.: Curuba de Monte (cl qu ri). Edible fruit
Passiflora leptomischa Harms, 1922 *	and	ant cau qu vc	2000-2800	Escobar *et al.* 4421 (PSO)	Escobar 1988a	LC/NT	**Tr** Edible fruit
Passiflora tenerifensis L.K. Escobar, 1988 *	and	vc	2800-3100	Escobar 4853 (COL)	Escobar 1988a, 1989b; Campos 2001	EN/CR	**Tr** V.N.: Curuba de Monte (vc). Edible fruit

Series *Quindiensae*							
Passiflora linearistipula L.K. Escobar, 1988 *	and	cl	**2650-3170**	Ocampo *et al*. 56 (HUA)	Escobar 1988a	EN/CR	**Tr** Not collected since 1984.
Passiflora quindiensis Killip, 1938 *	and	to	2900-3100	Uribe 3320 (COL)	Escobar 1988; Campos 2001	VU/EN	**Tr**
Section *Fimbriatistipula*							
Passiflora fimbriatistipula Harms, 1894 *	and	cau hu	**2130-3240**	Fernandez *et al.* 30182 (AFP)	Escobar 1988a	NT/VU	**Tr** I.N.: Pachuaca (cau)
Passiflora uribei L.K. Escobar, 1988 *	and	**na** pu	2500-2700	Escobar *et al.* 2896 (HUA)	Uribe 1958; Escobar 1988a	EN	**Tr**
Section *Parritana*							
Passiflora jardinensis L.K. Escobar, 1988 *	and	ant	**2750**-3000	Zarucchi 6963 (COL)	Escobar 1988b	VU/EN	**Tr**
Passiflora parritae (Mast.) L.H. Bailey, 1916 *	and	**cl qu ri** to	**2500-3020**	Sánchez 15 (FAUC)	Escobar 1988a	VU/EN	**Tr** Curuba de Monte (to). Edible fruit
Section *Poggendorffia*							
Passiflora pinnatistipula Cav.,1799	and	ant by cun **na** ns	2000-3600	Uribe 6643 (COL)	Escobar 1988b; Holm-Nielsen 1974; Holm-Nielsen *et al.* 1988; Campos 2001	LC/NT	**Tr** V.N.: Curuba Redonda, Gulupa (cun) Cultivated. Edible fruit
Passiflora x *rosea* (H. Karst.) Killip, 1938	and	**by** cun	2500-3500	Uribe 3941 (COL)	Escobar 1988a	VU	**Tr** Natural hybrid of *P. pinnatistipula* x *P. tripartita* var. *mollissima.* Edible fruit (when fertile)
Section *Tacsonia*							

Passiflora mixta L. f., 1781	and	**ant cl** by cau cun **na ns qu ri snt to vc**	1700-3700	Humboldt & Bonpland (P) - Type	Escobar 1988a; Holm-Nielsen 1974; Holm-Nielsen *et al.* 1988; García-B. 1975	LC	**Tr** V.N.: Curuba de Monte (vc), Curubo de Páramo (cun), Palchuaca (cau), Curubito de Indio (cl). Edible fruit
Passiflora schlimiana Triana & Planch., 1873 *	**car**	**ce lg** ma	2400-**3220**	Romero-C. 7407 (COL)	Holm-Nielsen 1974; Escobar 1988a; Romero-C. 1991; Coppens 2003	VU/EN	**Tr** V.N.: Curuba. Edible fruit
Section *Tacsoniopsis*							
Passiflora bracteosa Planch. & Linden, 1873	and	ns snt	2200-3000	Garcia-B. 20745 (COL)	Escobar 1988a	EN	**Tr** V.N.: Palchoaca (ns, snt)
Passiflora purdiei Killip, 1938 *	and	cun ma		Purdie s.n. (K) n.v.	Escobar 1988a	EX	**Tr** Known only from the type.
Subgenus *Tryphostemmatoides* (Harms) Killip), 1938							
Passiflora tryphostemmatoides Harms, 1894	and	**ant** cau hu qu ri vc	1000-**2700**	Lehmann 5662 (K) - Isotype	Killip 1938; Holm-Nielsen *et al.* 1988	NT	**Tr**
Passiflora gracillima Killip, 1924	and	ant **cau cl hu na qu** to	2000-**3150**	Penell 9393 (MO) - Isotype	Killip 1924, 1938	LC	**Tr** V.N.: Golondrina (cho)
Passiflora arbelaezii L. Uribe, 1957	**and** pac	ant **cau** cho **cun** na vc	0-**2300**	Roldán 1162 (COL)	Uribe 1957	LC/NT	**Tr**
Passiflora pacifica L.K. Escobar, 1988 *	pac	cho na vc	0-**1800**	Escobar 2143 (HUA)	Escobar 1988b	LC/NT	**Tr**

II.1.6. Conclusions

With 167 reported species, Colombia is the country with the highest Passifloraceae richness. This richness is concentrated in the Andean region, particularly in the departments of Antioquia, Valle del Cauca and Cundinamarca. Comparing with other countries indicates that the northern Andes of Colombia and Ecuador constitute the center of diversity for the most important genus, *Passiflora*. The low level of exploration in parts of the Andes, the Amazonian and the Orinoquian raises expectations that Colombia may still harbor many unknown species. Future studies should encompass new regions, including protected areas and conflict zones. Indeed, a better knowledge of this diversity, and its distribution, is urgent for the *in situ* conservation of this threatened richness, targeting the conservation of these resources as well as their habitat. Both aspects may even be combined if the genus *Passiflora* can be used as an indicator of biodiversity in the Andean region, as was the objective of a project in the coffee growing zone. Another important aspect is its direct valorization as a germplasm resource for crop diversification programs, implying the need for a better understanding of its morphological and genetic diversity.

II.1.7 Acknowledgements

The authors wish to thank the herbaria that provided specimens or collection data, and particularly Francisco J. Roldán (HUA) and Alexandra Hernández (COL), as well as Colciencias, the Colombian Ministry for Environment (MMA) and the Research Center of the Colombian Coffee Grower Federation (Cenicafé) for funding the collecting missions. The first author gratefully acknowledges financial support from the Gines-Mera Fellowship Foundation (CIAT-CBN). We are indebted also to José O. Velásquez (Casa Mutis, Mariquita), Hernando Criollo (U.Nariño), Mauricio Villegas (Cenicafé), Vicky Barney (Bioversity International), Alvinxon Castro (U.Chocó), Robinson Galindo (PNN Catatumbo) and Carolina Alcazar (Proselva) for assistance in obtaining plant data for this study. We are extremely grateful to Colombian farmers contacted in the fieldwork for

their continuous help and availability in localizing a great part of the observed plant material.

II.1.8. Appendix 1. Synonymy = valid name

Cieca auriculata M. Roemer, 1846 = *Passiflora auriculata* Kunth, 1817
Cieca coriacea (Juss) M. Roemer, 1846 = *Pasiflora coriacea* Juss., 1805
Cieca discolor M. Roemer, 1846 = *Passiflora misera* Kunth., 1817
Cieca pallida (L.) M. Roemer, 1846 = *Passiflora pallida* L., 1753
Decaloba alnifolia M. Roemer, 1846 = *Pasiflora alnifolia* Kunth, 1817
Decaloba biflora (Lam.) M. Roemer., 1846 = *Pasiflora biflora* Lam., 1789
Decaloba bogotensis (Benth.) M. Roemer, 1846 = *Passiflora bogotensis* Benth., 1845
Decaloba cuneata M. Roemer., 1846 = *Passiflora cuneata* Willd., 1809
Decaloba filipes M. Roemer, 1846 = *Pasiflora filipes* Benth, 1843
Decaloba holosericea M. Roemer, 1846 = *Passiflora holosericea* L., 1753
Decaloba jacquini M. Roemer, 1846 = *Passiflora pulchella* Kunth, 1817
Dilkea johannesii var. *parvifolia* Hoehne, 1915 = *Dilkea johannesii* Barb.Rodr., 1885
Dilkea acuminata Mast., 1871 = *Dilkea retusa* Mast., 1871
Dilkea magnifica Steyerm., 1968 = *Dilkea retusa* Mast., 1871
Dilkea wallisii Mast., 1872 = *Dilkea retusa* Mast., 1871
Disemma hahnii E. Fourn., 1869 = *Passiflora hahnii* Mast., 1872
Disemma hahnii Fourn., 1869 = *Passiflora hahnii* (Fourn.) Mast., 1872
Distephana cuneata M. Roemer, 1846 = *Passiflora bicuspidata* (H.Karst.) Mast., 1872
Distephana spinosa (Poeep. & Endl.) M. Roemer, 1835 = *Passiflora spinosa* (Poepp. & Ende.) Mast., 1871
Granadilla rubra Moench, 1802 = *Passiflora rubra* L., 1753
Grandilla vespertilio Moench, 1802 = *Passiflora vespertilio* L., 1753
Passiflora erubescens Triana & Planch., 1873 = *Passiflora erytrophylla* Mast., 1872
Passiflora velata Mast., 1872 = *Passiflora serrulata* Jacq., 1767
Passiflora williamsii Killip, 1922 = *Passiflora platyloba* var. *williamsii* (Killip) A.H. Gentry, 1976
Passiflora adenophylla Mast., 1872 = *Passiflora subpeltata* Ortega, 1798
Passiflora alba Link & Otto, 1798 = *Passiflora subpeltata* Ortega, 1798
Passiflora albicans L. Uribe, 1958 = *Passiflora uribei* L. K. Escobar, 1988
Passiflora angustifolia Swartz, 1788 = *Passiflora suberosa* L., 1753
Passiflora appendiculata G.F.W. Mey., 1818 = *Pasiflora auriculata* Kunth, 1817
Passiflora bauhinifolia Kunth, 1817 = *Passiflora alnifolia* Kunth, 1817
Passiflora bifurca Mast., 1873 = *Passiflora cuneata* Willd., 1809
Passiflora bilobata Vell., 1827 = *Passiflora rubra* L., 1735
Passiflora boyacana Killip, 1960 = *Passiflora crispolanata* L. Uribe, 1954
Passiflora capsularis var. *geminifolia* DC., 1828 = *Passiflora sexflora* Juss., 1805
Passiflora caucaense Holm-Niels., 1974 = *Passiflora emarginata* Humb. & Bonpl., 1813
Passiflora chilensis Miers, 1826 = *Passiflora pinnatistipula* Cav., 1799
Passiflora cisnana Harms, 1894 = *Passiflora rubra* L., 1753
Passiflora corumbaensis Barb., 1898 = *Passiflora cincinnata* Mast., 1868
Passiflora cualiflora Harms, 1906 = *Passiflora citrifolia* (Juss.) Mast., 1871
Passiflora difformis Kunth, 1817 = *Passiflora coriaceae* Juss., 1805
Passiflora digitata L., 1763 = *Passiflora serratodigitata* L., 1753
Passiflora elegans Triana & Planch., 1873 = *Passiflora quindiensis* Killip, 1938
Passiflora emiliae Sacco, 1966 = *Passiflora ambigua* Hemsl. *ex* Hook., 1902
Passiflora eminula Mast., 1883 = *Passiflora costata* Mast., 1872
Passiflora eriocaula Harms, 1922 = *Passiflora rugosa* (Mast.) Triana & Planch.var. *rugosa,*1873
Passiflora erosa Rusby, 1907 = *Passiflora morifolia* Mast., 1872
Passiflora erosa Rusby, 1906 = *Passiflora morifolia* Mast., 1872
Passiflora fulgens Wallis *ex* Morren, 1866 = *Passiflora coccinea* Aubl., 1775
Passiflora gigantifolia Harms, 1894 = *Passiflora macrophylla* Spruce *ex* Mast., 1883
Passiflora glauca Humb. & Bonpl., 1813 = *Passiflora arborea* Spreng., 1826

Passiflora goudotiana Triana & Planch., 1873 = *Passiflora cumbalensis* (H. Karst.) Harms var. *goudotiana* (Triana & Planch.) L. K. Escobar, 1987
Passiflora heydei Killip, 1922 = *Passiflora morifolia* Mast., 1872
Passiflora hydrophila Barb Rodr., 1891 = *Passiflora costata* Mast., 1872
Passiflora incana Seemann *ex* Mast., 1883 = *Passiflora seemanni* Griseb., 1858
Passiflora inundata Ducke, 1925 = *Passiflora costata* Mast., 1872
Passiflora laticualis Killip, 1924 = *Passiflora misera* Kunth., 1817
Passiflora longipes var. *retusa* Triana & Planch., 1873 = *Passiflora longipes* Juss., 1805
Passiflora lorifera Mast, & André, 1883 = *Passiflora macrophylla* Spruce *ex* Mast., 1883
Passiflora lunata J.E. Smith., 1790 = *Passiflora biflora* Lam., 1879
Passiflora macrocaropa Mast., 1869 = *Passiflora quadrangularis* l., 1759
Passiflora micrantha Killip, 1938 = *Passiflora erythrophylla* Mast., 1872
Passiflora miraflorensis Killip, 1924 = *Passiflora sexflora* Juss., 1805
Passiflora mollis var. *integrifolia* Planch. *ex* Mast., 1872 = *Passiflora cuspidifolia* Harms, 1893
Passiflora nympheoides Karst., 1859 = *Passiflora nitida* Kunth, 1817
Passiflora oblongifolia Pulle, 1906 = *Passiflora laurifolia* L., 1753
Passiflora ocanensis Planch. & Linden, 1873 = *Passiflora lindeniana* Planch. *ex* Triana & Planch., 1873
Passiflora ornata Kunth, 1817 = *Passiflora maliformis* L., 1753
Passiflora pala Planch. & Linden, 1873 = *Passiflora bogotensis* Benth., 1845
Passiflora paraguayensis Chad., 1899 = *Passiflora capsularis* L., 1753
Passiflora pennipes Sm., 1819 = *Passiflora pinnatistipula* Cav., 1799
Passiflora praeacuta Mast., 1887 = *Passiflora oerstedii* Mast., 1872
Passiflora pubera Planch. & Linden, 1873 = *Passiflora sphaerocarpa* Triana & Planch., 1873
Passiflora pulchella Kunth,1817 = *Passiflora bicornis* Mill., 1768
Passiflora quadriglandulosa var. *involucrata* (Mast.) Killip, 1938 = *Passiflora involucrata* (Mast.) A.H. Gentry, 1981
Passiflora reticulata Sauv., 1873 = *Passiflora holosericea* L.,1753
Passiflora salmonea Harms, 1894 = *Passiflora parritae* (Mast.) Bailey, 1916
Passiflora sanguinea J.E. Smithi, 1819 = *Passiflora vitifolia* Kunth, 1817
Passiflora schultzei Harms, 1929 = *Passiflora arborea* Spreng., 1826
Passiflora spherocarpa var. *pilosula* Mast., 1883 = *Passiflora pubera* Planch. & Linden, 1873
Passiflora stipulata Aubl., 1858 = *Passiflora subpeltata* Ortega, 1798
Passiflora suberosa var. *pallida* (L.) Mast. = *Passiflora pallida* L., 1753
Passiflora tomentosa Lam. var. *mollissima* Triana & Planch., 1873 = *Passiflora mollissima* (Kunth) L.H. Bailey, 1916
Passiflora trisecta Planch. & Linden *ex* Triana & Planch., 1873 = *Passiflora trianae* Killip, 1938
Passiflora Van-Volxemii Triana & Planch., 1893 = *Passiflora antioquiensis* Karst., 1859
Passiflora var. *cuellensis* Goudot *ex* Triana & Planch., 1873 = *Passiflora menispermifolia* Kunth, 1817
Passiflora vesicaria L., 1753 = *Passiflora foetida* L., 1753
Passiflora vitifolia var. *involucrata* Mast., 1872 = *Passiflora involucrata* (Mast.) A.H. Gentry, 1981
Passiflora weberiana André, 1885 = *Passiflora morifolia* Mast., 1872
Passiiflora acerifolia Schlecht. & Cham., 1830 = *Passiflora adenopoda* Moc. & Sessé *ex* DC., 1828
Rathea floribunda Karst., 1859 = *Passiflora andina* Killip, 1938
Tacsonia adulterina Juss., 1805 = *Passiflora adulterina* L. f., 1781
Tacsonia bicuspidata H. Karst., 1859 = *Passiflora bicuspidata* (H. Karst.) Mast., 1872
Tacsonia cumbalensis H. Karst., 1859 = *Passiflora cumbalensis* var. *cumbalensis* (H. Karst.) Harms, 1894
Tacsonia cuneata Benth, 1845 = *Passiflora bicuspidata* (H. Karst.) Mast., 1872
Tacsonia flexipes (Triana & Planch) Mast., 1883 = *Passiflora flexipes* Triana & Planch., 1873
Tacsonia glandulosa Juss., 1805 = *Passiflora glandulosa* Cav.,1790
Tacsonia infundibularis Mast., 1883 = *Passiflora bracteosa* Planch. & Linden, 1873
Tacsonia lanata Juss., 1811= *Passiflora lanata* (Juss.) Poir., 1811
Tacsonia mixta (L.f.) Juss., 1805 = *Passiflora mixta* L.f., 1781
Tacsonia mollissima Kunth var. *glabrescens* Mast.,1872 = *Passiflora mollissima* (Kunth) L.H. Bailey, 1916
Tacsonia mollissima Kunth, 1817 = *Passiflora mollissima* (Kunth) L.H. Bailey, 1916
Tacsonia parritae Mast., 1882 = *Passiflora parritae* (Mast.) L.H. Bailey, 1916
Tacsonia pinnatistipula var. *pennipes* (Sm.) DC., 1828 = *Passiflora pinnatistipula* Cav., 1799
Tacsonia pinnatistipula (Cav.) Juss., 1805 = *Passiflora pinnatistipula* Cav.,1799
Tacsonia quadriglandulosa (Rodschied) DC., 1828 = *Passiflora quadriglandulosa* Rodschied, 1796
Tacsonia rosea (H. Karst.) Sodiro, 1903 = *Passiflora* x *rosea (*H. Karst.) Killip, 1938
Tacsonia rugosa Mast., 1872 = *Passiflora rugosa* (Mast.) Triana & Planch, 1873 var. *rugosa*
Tacsonia spinescens Klotsch in Schomb., 1848 = *Passiflora securiclata* Mast., 1893
Tacsonia spinosa Poepp. & Endl., 1835 = *Passiflora spinosa* (Poepp. & Ende.) Mast., 1871
Tacsonia trinervia Juss., 1805 = *Passiflora trinervia* (Juss.) Poir., 1811
Tetrastylis lobata Killip, 1926 = *Passiflora lobata* (Killip) Hutch. *ex* J.M. MacDougal, 1986

CHAPTER III

Distribution, diversity and *in situ* conservation of Colombian Passifloraceae

III.1. Distribution, diversity and *in situ* conservation of Colombian Passifloraceae

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III.1.1 Abstract

Analysis was made of 3,930 records of 165 wild Passifloraceae to assess the distribution of their diversity in Colombia, identify collection gaps, and explore their potential as indicator species. Despite variable collecting density among and within biogeographic regions, the Andean region clearly presents a higher species richness, particularly in the central coffee growing zone and the departments of Antioquia, Cundinamarca and Valle del Cauca. The elevational distribution of diversity shows a small peak below 500 m, and two higher ones between 1000-2,000 and 2,500-3,000 m. This pattern corresponds to divergent adaptive trends among genera and infrageneric divisions. The analysis on 19 climatic variables showed that the two principal variance components, explaining 77% of the total, are respectively associated with temperature and precipitation, without influence of seasonality. Distribution parameters allow recognizing more than 36 narrow endemics. Prediction of species distribution showed nine areas with very high richness (predicted sympatry of 41 to 54 species) in the Andean region, three of which correspond to collection gaps. Endemics were not particularly frequent there, so a prioritization of protected areas based on species richness would not favor their conservation. The sites with high *Passiflora* diversity are poorly represented in the current system of protected areas. Instead their striking correspondence with ecotopes of the coffee growing zone imposes a conservation strategy integrating agricultural and environmental management at the landscape level. Reciprocally, several traits of *Passiflora* species make them particularly suited as indicators for any effort of conservation or restoration in this region of importance for the country.

***Keywords*:** Andes, Colombia, coffee growing zone, distribution, geographic information systems, Passifloraceae diversity, endemism.

III.1.2. Introduction

New World Passifloraceae include four tropical genera (*Ancistrothyrsus*, *Dilkea*, *Mitostemma* and *Passiflora*) and about 550 species (Ulmer & MacDougal, 2004). The largest genus of the family is *Passiflora* L., with ca. 525 species distributed in a wide range of habitats, essentially tropical, ranging from humid rain forests to semi-arid subtropics. Most of them are herbaceous or woody vines, usually climbing by tendrils, while a few are trees or shrubs. More than 80 species produce an edible fruit, the most interesting ones belonging to subgenera *Passiflora* and *Tacsonia* (Coppens d'Eeckenbrugge, 2003). Among them, is the maracuja, *P. edulis* Sims, and its yellow-fruited form, *P. edulis* f. *flavicarpa* Degener, with a world production estimated at more than 640.000 tons (Passionfruit, 2006). In Colombia, ten more species/forms are cultivated. The fruits of the purple maracuja (*P. edulis* f. *edulis* Sims.), the sweet granadilla (*P. ligularis* Juss.), the giant granadilla (*P. quadrangularis* L.), the stone granadilla (*P. maliformis* L.), the granadilla de Quijos (*P. popenovii* Killip), the sweet maracuja (*P. alata* Curtis), and the banana passion fruits, 'curuba de Castilla' (*P. tripartita* var. *mollissima* (Kunth) Holm-Nielsen & Jørgensen), 'curuba quiteña' (*P. tarminiana* Coppens & Barney) are common on the national or regional markets. Those of the 'granadilla de clima frío' (*P. pinnatistipula* Cav.), the 'curuba roja' or rosy passion fruit (*P. cumbalensis* Karst.), the 'curuba antioqueña' (*P. antioquiensis* (Karst) Harms.), *P. nitida* Kunth and *P. palenquensis* Holm-Niels. & Lawesson are also cultivated, at a very local scale. These and other *Passiflora* species may be used for other purposes, such as garden ornamentals or pharmaceuticals (Coppens d'Eeckenbrugge et al., 2001). Killip in 1938 classified the genus *Passiflora* in 22 subgenera, including 355 American species (Annex 1). This classification has been amended by Escobar (1988, 1989, 1994) who merged subgenera *Tacsioniopsis* and *Tacsonia*, and proposed a new subgenus, *Porphyropathanthus*, and MacDougal (1994), who reinstated the name *Decaloba* for Killip's subgenus *Plectostemma*. More recently, Feuillet & MacDougal (2003; Annex 2) proposed a much deeper revision, reducing the number of subgenera to only four (*Astrophea*, *Decaloba*, *Deidamioides* and *Passiflora*), and downgrading most of Killip's divisions to lower levels. This proposal has been partially justified by recent molecular data (Muschner et al., 2003; Yockteng, 2003, Annexe Ib;

Yockteng & Nadot, 2004; Hansen et al., 2006, see Annex 4a-d), however it still needs to be more clearly supported by further studies.

Colombia's geographic location and its variety of ecosystems place it as the second most biodiverse country in the world (McNeely et al., 1990). It is divided into five main biogeographic regions: Amazonian, Andean, Caribbean, Orinoquian, and Pacific (Hernández et al., 1991). The Andean region presents a highly diverse topography (100-5,400 m), with three long mountain ranges, the Eastern, Central and Western Cordilleras, which separate two main inter-Andean valleys from the other regions. The uplift of the Andes created new habitats and increased local isolation, favoring high speciation rates in many taxa (Gentry, 1986). The continuously humid climate of the Amazonian and Orinoquian lowlands and the extremely wet climate of the Pacific region contrast with the dryer and more seasonal climate of the Caribbean. As a result, the Colombian flora includes some of the world most diverse groups of vascular plants, with 51,220 documented species (May, 1992; UNEP-WCMC, 2004). It is hoped that most of the floristic richness is located in the protected areas that cover 365,120 km^2, approximately 32% of the territory (Parques Naturales de Colombia, 2006), falling under different categories of protection, including Natural National Parks, Flora and Fauna Sanctuary, Natural National Reserves, Unique Natural Area, Park Way and Indigenous Areas. Smaller forest reserves have also been created to protect river basins for water supply. On the other hand, destruction of many natural habitats has drastically affected species distributions, often reducing their historical ranges to a set of small, fragmented populations (Brooks et al., 2002). Such habitat alteration is predicted to lead to substantial extinction in the near future.

Many conservation biologists have focused their attention on areas presenting high levels of endemism and diversity, and that are also experiencing a high rate of loss of ecosystems. Such regions, characterized by localized concentrations of biodiversity under threat, and representing priorities for conservation actions, are defined as biodiversity hotspots (Myers et al., 2000; Sechrest et al., 2002). The application of this concept in the case of Colombia implies very wide studies to investigate the distribution of biodiversity and endemism across the country. Complete inventories are not realistic at that scale, so other approaches have been taken to exploit incomplete biodiversity data, combining remote sensing and field sampling/inventories of indicator taxa at different scales (Villareal et al., 2006). We proposed here to use climatic niche modeling and test the potential of Passifloraceae as an indicator of biodiversity in Colombia, as this family represents several interesting traits in terms of diversity, adaptation and evolution.

Indeed, Colombia is particularly rich in Passifloraceae. The family is represented by 167 species (about 27% of the total), grouped in three genera, *Ancistrothyrsus*, *Dilkea*, and *Passiflora*, with greatest diversity in the Andean region (123 species). The country has 58 endemic Passifloraceae species, 95% of them exclusively Andean, implying a high extinction risk, as the Andes region is the most densely populated and hence disturbed of the country (Ocampo et al., 2007). According to the categories and criteria of IUCN Red List of threatened species (IUCN, 2003) and Ocampo et al. (2007) have established that more than 100 Colombian species of Passifloraceae are threatened to some degree, while three species are considered extinct.

As vines, most *Passiflora* species have adapted to many different habitats, particularly for their support. They are medium-lived organisms depending on longer-lived trees and shrubs, which makes them responsive to both medium and long-term changes of their ecosystems. They also show high levels of co-evolution with their herbivores, the best-known example being that of *Heliconius* butterflies (Gilbert, 1982), and some species even exhibit elements of the carnivory syndrome (Radhamani et al., 1995). They have developed mutualism with protector insects as nectar-feeding ants (Apple & Feener, 2001), and with a wide range of pollinators, including small and large insects, birds, and even bats (Büchert & Mogens, 2001; Sazima & Sazima, 1978).

Finally, given the economic importance of several of its representatives, the genus *Passiflora* constitutes an important genetic resource, and the characterization and evaluation of wild and cultivated populations is seen as a high priority for Andean countries because of its clear potential for development and crop diversification (Debouck &

Libreros, 1995). Strategies for conservation and improvement are needed to optimize the use and conservation of this resource.

Biodiversity data have been traditionally produced through a variety of complementary approaches using field survey and sampling, museum records, botanical collections, and, in recent times, spatial analysis of digital data integrated within a Geographical Information System (GIS). In each area, the combination of geological, edaphic, climatic, ecological, historical and anthropic factors produce a unique range of constraints defining unique patterns of genetic diversity (Maxted et al., 1995). GIS makes it possible to build maps of species richness, potential distribution and endemism, to prioritize areas for conservation based on principles such as complementarity, and to assess the completeness of existing protected areas networks (Peterson, 2001). Applications have been developed in recent years that offer new possibilities for understanding biological diversity. Several of these methods use climatic variables as the principal drivers of herbarium or collecting data, often in combination with spatial environmental information, and are generally acknowledged to generate valuable additional information for diversity studies and conservation actions (Franklin, 1995; Skov, 2000; Lehmann et al., 2002). Such modeling tools have been applied to problems of plant biogeography (Hijmans et al., 2001; Hijmans and Spooner, 2001; Midgley et al., 2002; Vargas et al., 2004; Ferguson et al., 2005), conservation (Jones et al., 1997; Hijmans et al., 2000; Jarvis et al., 2002, 2003, 2005; Kingston & Waldren, 2005), evolutionary ecology (Zaharieva et al., 2004), invasive or endemic species management (Peterson & Robins, 2003; Peterson, 2004; Leimberck et al., 2004), and potential areas for plant collection (Rodríguez et al., 2005). In *Passiflora*, Segura et al. (2003) reported a first mapping of the potential distribution of five species of subgenus *Tacsonia* in the Andean countries using the Floramap software of Jones et al. (2002). Their results showed evidence of intra-specific variation in climatic adaptation along the Andes, from Colombia to Peru. Recently, Scheldeman et al. (2006) used the DIVA-GIS computer program to determine the distribution and environmental adaptation of highland papayas (*Vasconcellea* spp.) based on germplasm and herbarium data. The combination of observed diversity maps and potential diversity maps permitted identifying important collection gaps, mainly in Colombia and Ecuador.

The present study of the distribution and diversity of Passifloraceae in Colombia was conducted through sequentially: (1) assessing the geographic distribution of collections, (2) analyzing it in terms of species richness across the Colombian territory, (3) inferring the potential distribution of each species with predictive distribution models, (4) summing these spatial predictions to produce a map of potential diversity, and (5) locating collecting gaps by detecting those areas where Passifloraceae species are likely to occur but have no yet been collected. Combining these results permits an analysis of the current status of *in situ* and *ex situ* conservation of Passifloraceae in Colombia. It also provides elements to evaluate the potential of this group as an indicator for the detection of biodiversity hotspots and monitoring of conservation/restoration efforts.

III.1.3. Materials and methods

III.1.3.1. *Geography and climate*

Colombia is located in the north of South America, between 12° 26’ 46” N and 4° 13’ 30” S and between 66° 50’ 54” W and 79° 02’ 33” W, covering an area of 1,141,748 km^2, with altitudes ranging from the sea level to 5,775 m (IGAC, 2006). It is divided in 32 departments. Its natural habitat diversity is distributed among five main biogeographic regions (Amazonian, Andean, Caribbean, Orinoquian and Pacific). Figure 1 shows the distribution of the 32 departments and the five biogeographic regions of the country. Colombian climates are tropical, with relatively uniform temperatures throughout the year. Precipitations vary greatly, with some of the wettest parts of the world in the Pacific lowlands (average annual rainfall reaching 10,000 mm) contrasting with extremely dry areas in the coast (< 500 mm per year), and show a tendency to increase with altitude in the Andean region.

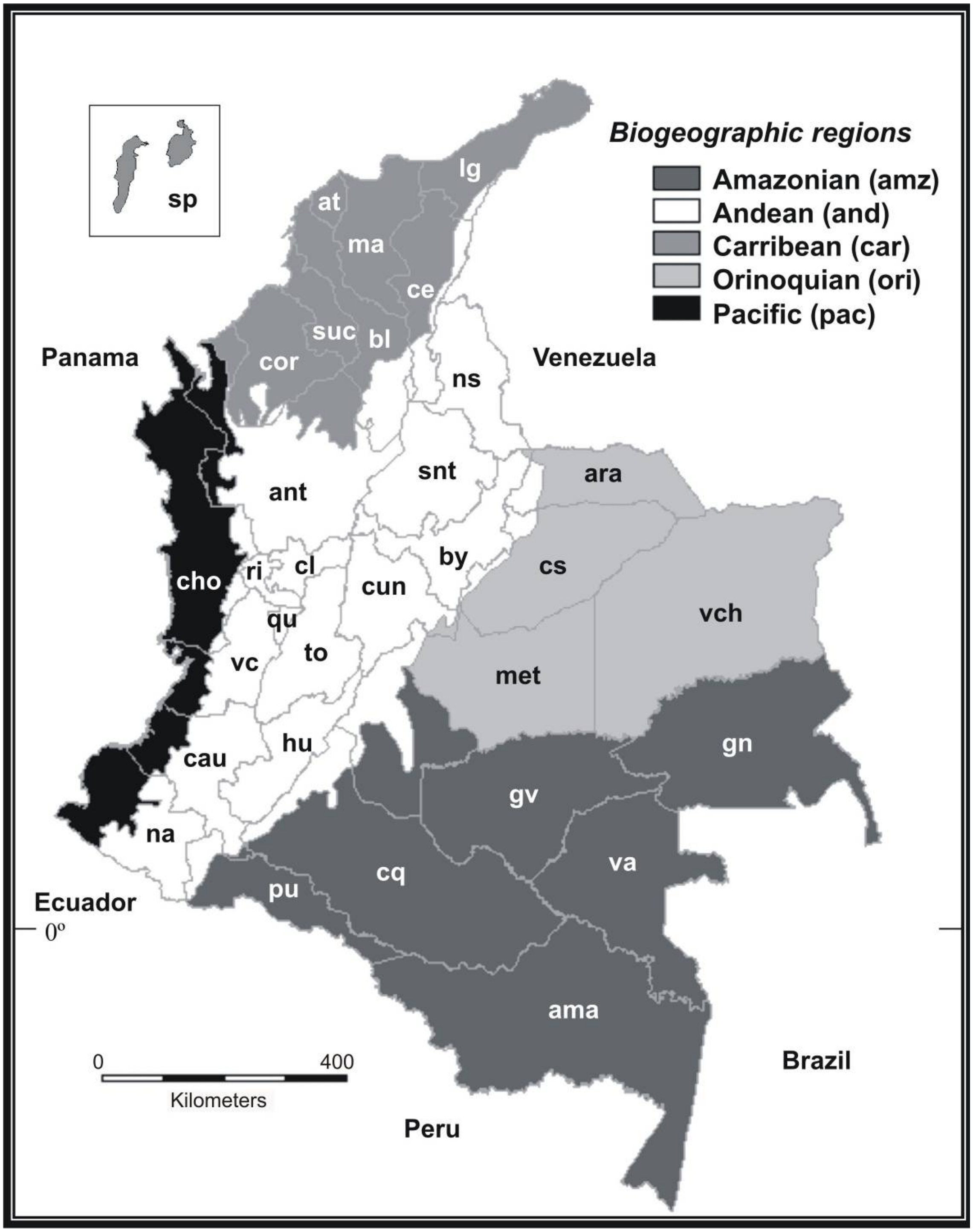

Figure 1. Colombia's geopolitical division in 32 departments and biogeographic division in five regions. Amazonas (**ama**), Antioquia (**ant**), Arauca (**ara**), Atlántico (**at**), Bolívar (**bl**), Boyacá (**by**), Cauca (**cau**), Cesar (**ce**), Caldas (**cl**), Córdoba (**cor**), Caquetá (**cq**), Casanare (**cs**), Cundinamarca (**cun**), Chocó (**cho**), Guainia (**gn**), Guaviare (**gv**), Huila (**hu**), La Guajira (**lg**), Magdalena (**ma**), Meta (**met**), Nariño (**na**), Norte de Santander (**ns**), Putumayo (**pu**), Quindío (**qu**), Risaralda (**ri**), Santander (**snt**), San Andrés y Providencia (**sp -** Island), Sucre (**suc**), Tolima (**to**), Vaupés (**va**), Valle del Cauca (**vc**), Vichada (**vch**).

III.1.3.2. *Herbarium, field and literature data*

The dataset used in this analysis consists of the information gathered and georeferenced by Ocampo et al. (2007), from 3,930 individuals belonging to 167 Passifloraceae species, consisting of 3,330 specimens from 23 herbaria (AFP, CAUP, CDMB, CHOCO, COL, COAH, CUVC, FAUC, FMB, HUA, HUQ, JAUM, K, MA, MEDEL, MO, NY, P, PSO, SURCO, TOLI, VALLE, UIS), 555 records from explorations in localities of 17 departments, and 45 records of specimens mentioned by Killip (1938, 1960), Uribe (1955a,b) and Escobar (1988a,b, 1989, 1994).

III.1.3.3. *Species distribution and richness*

The number of observations and their elevation range were tabulated for each species. The distribution of species was plotted on dot-maps using the DIVA-GIS software. To quantify the area over which each species is distributed, the maximum distance (MaxD) and circular area (CA_r) were calculated, following the method of Hijmans et al. (2001), and compared. MaxD is the longest distance between any pair of observations of one species. CA_r is calculated by assigning a circle of radius r to each observation and calculating the area covered by all circles for each species. In this case, a radius of 50 km was used (CA_{50}).

Species richness was calculated as the number of species within a defined area, superimposing species location maps, using the point-to-grid richness analysis tool in DIVA-GIS, with a 0.1 x 0.1° grid (corresponding to 12 x 12 km at the equator). The circular neighborhood option was applied with a 2° radius (Hijmans & Spooner, 2001) to eliminate border effects due to the assignation of the grid origin. Species richness was used as a measure of taxonomic diversity because it is a simple, useful, and widely used parameter (Gaston, 1996).

III.1.3.4. *Description of climatic preferences*

In order to highlight the factors that may influence species geographic distribution, and provide an indication of their tolerance to abiotic stress, climate data were extracted for each collection point. DIVA-GIS was used to develop climatic models for predicting the occurrence/diversity of Passifloraceae species in the study area. This package uses

WorldClim climate data (Hijmans et al., 2005), which consists of global surfaces of climate with a 30” grid resolution (corresponding to 1 x 1 km at the equator) derived from a network of over 12,500 meteorological stations across Latin America, 1,479 of which are located in Colombia. For each collection site, 19 bioclimatic variables (derived from 12 monthly means for temperature, rainfall and diurnal temperature range according to Busby (1991) were extracted from the WorldClim data set. Principal components analysis (PCA) was performed on climatic variables from the collection sites where at least one specimen was present. A varimax normalized rotation was applied with the STATISTICA® 6.0 software. To promote readability, the centroid, i.e. the arithmetic average of the factor scores, was used to represent each species general climatic preferences.

III.1.3.5. *Potential species distribution*

Maps of potential species distribution were produced using the BioClim method inside DIVA-GIS for those species with more than 10 observations. Predictive distribution modeling (also termed ecological niche modeling) attempts to predict the geographic distribution of a species using sites of known existence to understand the environmental adaptation of the species, and extrapolating this knowledge to other regions with similar conditions, where no collection has been made. BioClim was chosen because it is a robust methodology, requiring presence-only data (Hijmans & Graham, 2006). It was run using the 19 bioclimatic variables from WorldClim (Hijmans et al., 2005) with 30” resolution (equivalent to 1 km at the equator). Eighty-six species with fewer than 10 observations were omitted from the analysis, as the number of points was too low for reliable results. Unfortunately, this excluded many of the endemic and rare species. Whilst soils and habitat are likely to be also important in determining the geographic distribution of these species, they were not included in the model due to a lack of consistent, continuous data at the country level. Finally, an analysis of complementarity (Rebelo, 1994) was applied to identify the lowest number of protected areas needed for the conservation of native Passifloraceae.

III.1.4. Results and discussion

III.1.4.1. *Distribution of observations*

Figure 2 and Table 1 show the distribution of collection/observation points for all specimens. The Andean region of Central Colombia is by far the most densely explored, particularly in the central coffee growing zone (Quindío, Caldas and Risaralda; 18.93 to 77.20 observations/1000 km²) and the three large departments of Antioquia, Valle del Cauca and Cundinamarca (12.49 to 19.82 observations/1000 km²). By comparison, the northeastern Andes (Boyacá, Santander, Norte de Santander) and the central department of Tolima appear less well explored (3.59 to 9.39 observation/1000 km²). The situation is more difficult to appreciate in the southern Andes, as the departments of Cauca and Nariño also belong in good part to the Pacific region. However, they show a collection density only slightly superior to that of Chocó, which indicates that they have also been less explored than the central departments of the Andean region. The situation is heterogeneous in the Caribbean region, with only two of its seven departments exhibiting more than 3 observations/1000 km² (excluding the atypical case of the small San Andrés and Providencia islands). Finally, the Amazonian and the Orinoquian are by far the less explored biogeographic regions of the country, although they cover half of its area.

The mean number of observations per species also reflects variation in exploration among departments (Table 1), confirming the much denser exploration in the Andes of Antioquia, Cundinamarca and Valle del Cauca (more than 7 observations per species) and in the Pacific region, while this ratio takes much lower values in the other biogeographic regions. However, the relation between exploration density and this indicator is not simple, as the numerous observations in the central coffee growing zone (Caldas, Quindío and Risaralda) are distributed among a very wide diversity of species, so the mean number of observations per species is not as high as could be expected for such densely explored areas.

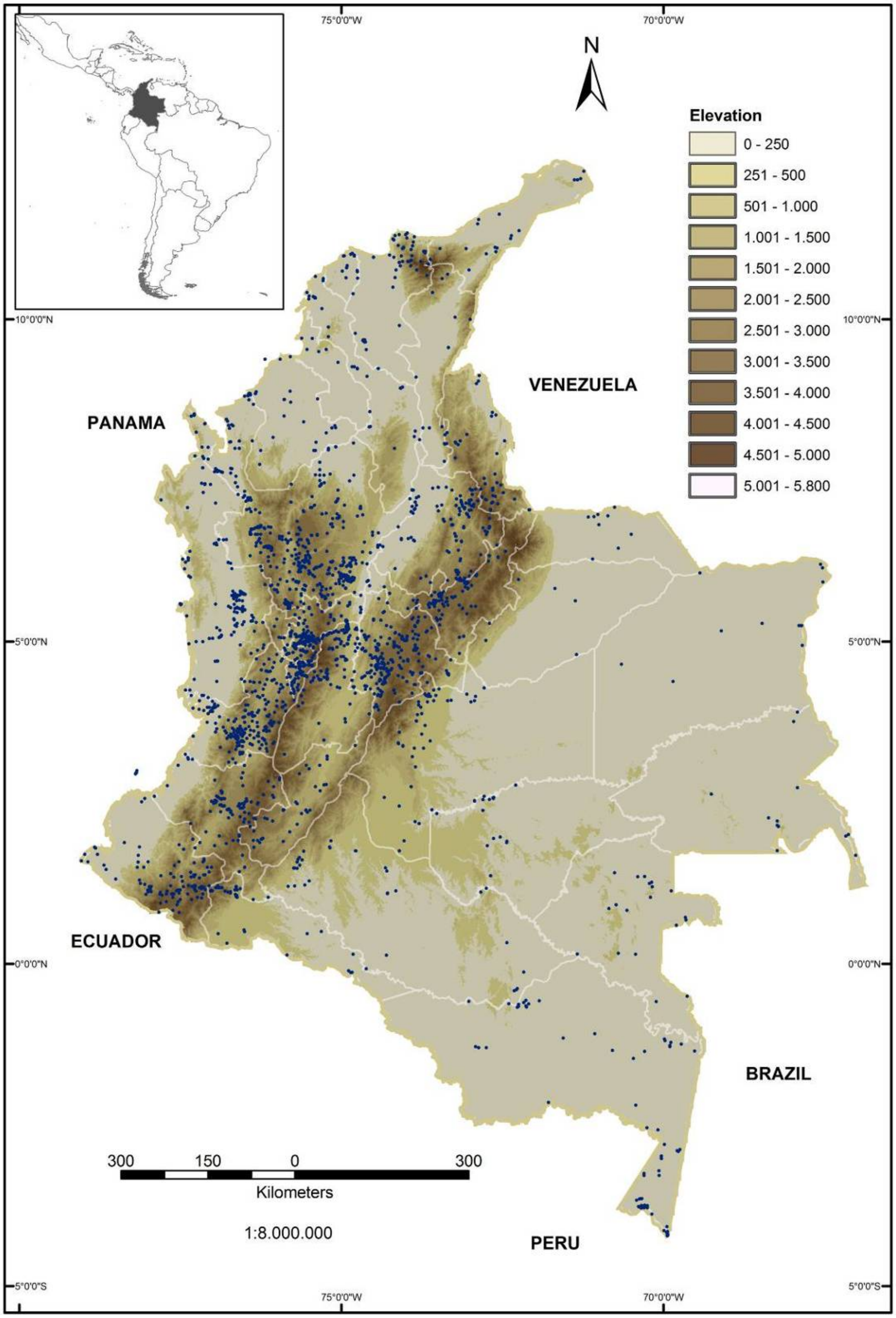

Figure 2. Collection localities of Passifloraceae specimens used in this study, among Colombian departments. Points on the maps represent sites of collection.

This variation in exploration of the Colombian territory can be related in good part to human geography. The superposition of roads and rivers on the map (not presented here) shows that collections were mostly made along rivers in the Orinoquian and Amazonian regions, and roads in other regions, which is a very common and self-explained observation (Hijmans et al. 2000). This is likely why regions with poor infrastructure (*e.g.* Amazonian, Orinoquian and Pacific) have been little explored. An aggravating factor is collector safety. Most of these areas also suffer from chronic political conflict. However other areas are affected although better equipped in infrastructure.

Table 1. Number of observations, species, rare and endemic Passifloraceae species by Colombian division. Source for department areas: IGAC (2005, http://www.igac.gov.co).

Predominant region / department	**Area (km^2)**	**Nb. observ.**	**Nb. observ. /1000km^2**	**Total species**	**Total species /1000km^2**	**Total species/Log. area**	**Observ. / species**	**Rare species**	**Endemic species**
Andean									
Antioquia	62.869	785	12.49	70	1.11	14.588	11.21	28	6
Boyacá	23.012	145	6.30	36	1.56	7.502	4.03	14	1
Caldas	7.291	245	33.60	36	4.94	7.502	6.81	14	1
Cundinamarca	23.942	419	17.50	53	2.21	11.045	7.91	23	0
Huila	18.331	62	3.38	22	1.20	4.585	2.82	18	0
Quindío	1.943	150	77.20	38	19.56	7.919	3.95	25	0
Norte de Santander	22.007	79	3.59	36	1.64	7.502	2.19	25	0
Risaralda	3.592	68	18.93	24	6.68	5.002	2.83	20	0
Santander	30.537	207	6.78	48	1.57	10.003	4.31	31	3
Tolima	22.672	213	9.39	44	1.94	9.169	4.94	27	4
Andean and Pacific									
Cauca	30.985	161	5.20	42	1.36	8.753	3.83	24	1
Nariño	32.046	170	5.30	44	1.40	9.170	3.79	27	0
Valle del Cauca	21.195	420	19.82	56	2.69	11.670	7.38	28	1
Pacific									
Chocó	46.530	211	4.53	40	0.86	8.336	5.28	23	1
Caribbbean									
Atlántico	3.319	18	5.42	7	2.11	1.459	2.57	5	0
Bolívar	26.469	33	1.25	15	0.57	3.126	2.20	9	1
Cesar	22.213	13	0.59	10	0.45	2.084	1.30	9	0
Córdoba	25.020	33	1.32	9	0.36	1.876	3.67	6	0
La Guajira	20.848	21	1.01	12	0.58	2.501	1.75	9	0
Magdalena	22.742	84	3.69	31	1.36	6.460	2.71	19	1
S. Andrés y Providencia	53	4	75.47	2	37.74	0.417	2.00	2	0
Sucre	10.917	6	0.55	3	0.27	0.625	2.00	2	0
Orinoquian									
Arauca	23.393	10	0.43	6	0.26	1.250	1.67	3	0
Casanare	44.428	4	0.09	4	0.09	0.834	1.00	4	0
Meta	85.286	85	1.00	24	0.28	4.930	3.56	14	0
Vichada	100.242	16	0.16	9	0.09	1.876	1.78	6	0
Amazonian									
Amazonas	109.665	87	0.79	19	0.17	3.751	4.05	16	0
Caquetá	91.725	47	0.51	18	0.20	3.751	2.61	13	0
Guainía	70.691	16	0.23	10	0.14	2.084	1.60	9	0
Guaviare	55.391	27	0.49	14	0.25	5.418	1.93	11	0
Putumayo	24.885	56	2.25	26	1.04	2.918	2.15	20	0
Vaupés	54.135	35	0.65	20	0.37	4.168	1.75	10	0

This is particularly obvious in the less explored Andean departments (Tolima, Santander, Norte de Santander and part of Boyacá) and in most departments of the Caribbean. Conversely, most densely populated areas, particularly those around main cities and their universities (Bogotá, Medellín, Cali, central coffee growing zone), have been much more densely explored. This high heterogeneity in exploration must be taken into account to avoid a sampling bias when comparing the situation among departments (Table 1). However, even doing so, Figure 2 and Table 1 show a clear concentration of collection density in the Andean departments. Furthermore, a closer look at the heterogeneity of collection density within these departments, as shown in Figure 1, confirms the association between topography and the density of botanical observations. The most likely explanation is simply that the higher *Passiflora* diversity in the Andes made their exploration more rewarding and stimulating for its students. The distribution of species richness clearly confirms this view.

III.1.4.2. *Species richness*

Departments of the Andean region present a higher species richness (Table 1). The only non-Andean department showing a comparable value for this parameter is Chocó. Among the Andean departments, Antioquia has by far the highest number of species (70 species; 43% of the total), followed by Valle del Cauca and Cundinamarca. These three departments also show the three highest mean numbers of observations per species, which confirms that they are much better explored than the others. Concerning rare species (≤ 5 observations, ≤ 100 km of MaxD and ≤ 20,000 km^2 of CA_{50}), Santander (northeast) occupies the first place, with 31 species, followed by Valle del Cauca (28), and Antioquia (28), Nariño (27), and Tolima (27). Thus, there is little doubt that a more thorough exploration north of the Eastern Cordillera (Santander) and south of the Central Cordillera (Tolima) would discover more specimens per observed species and/or more species. This problem is similar in the departments of the Amazonian, Orinoquian and Pacific regions, where species richness is very poor in relation to their surface. The number of rare species is abnormally high as compared to the total number, indicating a sampling bias due to very poor exploration in these regions. In the case of Chocó (Pacific region) collecting efforts have been practically limited to the borders of the main access road.

III.1.4.3. *Species diversity*

When species richness is related to department size, the most diverse area clearly corresponds to the central coffee growing zone, as this ratio appears to be several times higher in Caldas, Risaralda and Quindío than in the other Andean departments. A precise comparison with departments of other regions is only possible if the species are equally sampled, i.e. if the number of observations per species is equivalent. This is the case for Chocó, Amazonas, and Córdoba, all of them showing a much lower diversity. The map of Passifloraceae diversity, as produced by the GIS analysis (Figure 3), confirms the importance of the Andes and the special contribution of the central coffee growing zone. This correspondence is so striking that one can wonder if, in addition to the highly variable topography, the soil fertility of this area has particularly contributed to its biodiversity.

III.1.4.4. *Distribution by altitude*

The genera *Ancistrothyrsus* and *Dilkea* reach altitudes of 800 m, mostly in the Amazonian region. In contrast, the genus *Passiflora* is distributed between sea level and 3,700 m. Figure 4 presents the relationship between elevation range and species diversity (species number related to diversity) for genus *Passiflora*, which appears trimodal, with maximal values below 500 m and in the ranges 1000-1,500 and 2,500-3,000 m. The species number decreases sharply after 3,500 m until the limit of 4,000 m. With the aim of understanding better this very particular altitudinal distribution, we have taken into account the complexity of this genus, gathering the sixteen subgenera of *Passiflora* present in Colombia into five groups defined on morphological and molecular grounds (cfr. chapters IV and V), and analyzed altitudinal distribution of richness in these species subsets. This grouping is similar to that of the proposal of Feuillet & McDougal (2003), except that Killip’s subgenera *Rathea* and *Tacsonia* are maintained as a distinct fifth group, because of its large and elongated flowers, mostly with red or pink color and very reduced crown, specifically adapted to pollination by the sword-hummingbird. The four others correspond to (1) subgenus *Astrophea* (trees and shrubs), (2) a *Decaloba*-like group, equivalent to subgenus *Decaloba sensu* Feuillet & McDougal (subgenera *Apodogyne, Decaloba*, *Murucuja, Porphyropathanthus*, *Pseudomurucuja* and *Psilanthus*; mostly species with laminar nectaries, small apetalous flowers, pollinated by bees and small insects, and small fruits),

(3) a *Deidamioides*-like group, equivalent to subgenus *Deidamioides sensu* Feuillet & MacDougal (subgenera *Deidamioides* and *Tryphostemmatoides*), and (4) a *Passiflora*-like group gathering subgenera *Calopathanthus*, *Distephana*, *Dysosmia*, *Dysosmioides*, *Passiflora*, and *Manicata*, i.e. species with large flowers, pollinated by large bees or hummingbirds, and large fruits.

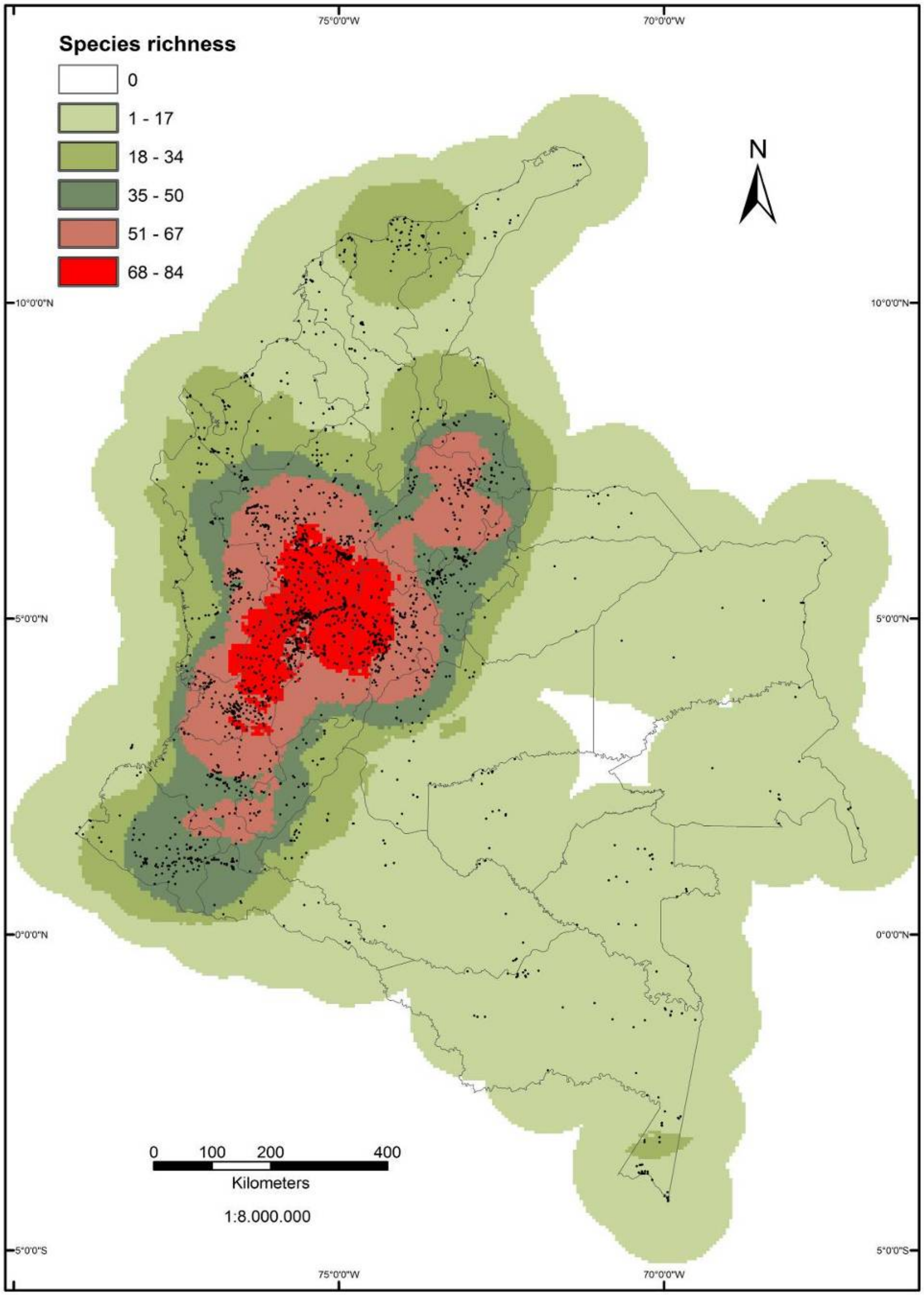

Figure 3. Species richness observed for Passifloraceae in 1x1 km grid cells in Colombia (165 species). Points on the maps represent sites of collection.

The comparison between partial curves clearly shows three distinct patterns in the adaptive potential of these five groups. *Astrophea* and the *Passiflora*-like group present a bimodal distribution with a first cohort of species adapted to tropical lowlands below 500 m, with 16 and 28 species respectively, and a second one adapted to medium elevations (from 1000 to 2,000 m). Very few species can be found at higher altitudes, with only one record of *P. lindeniana* Planch. *ex.* Triana & Planch. just below 2,700 m for *Astrophea*, and seven species for *Passiflora*. The opposite is true for subgenus *Tacsonia*, which shows exclusive adaptation to cold highland climates, as it is typically concentrated between 2,500 and 4,000 m, with a peak between 2,500 and 3,000 m. The fast radiation of this subgenus is clearly the cause of the peak of the global curve around 2,500-3,000 m. The third pattern is that of the *Decaloba*-like group, whose range of adaptation extends spectacularly from 0 to more than 3,000 m, with no lowland peak and a slight peak around 1000-1,500 m, and the small *Deidamioides*-like group, which shows a similar quite uniform distribution of species richness from 0 to 3,150 m, mostly in the Pacific and Andean regions. An interrogation remains concerning the first inflexion of the global curve and those of *Astrophea* and *Passiflora*-like groups in the range 500-1000 m. Interestingly, Jørgensen & León-Yánez (1999) report a bimodal altitudinal distribution of vines in the Ecuadorian flora, with maximal diversity below 500 m and in the 2,000-3,000 m range, and a maximal diversity for *Passiflora* between 2,500 and 3,000 m. Taking latitudinal variation into account (the same *Tacsonia* species usually show a higher distribution in Ecuador, with a difference of about 300-500 m), this corresponds very well with our observations in Colombia. Considering all Passifloraceae, the variation in number of Ecuadorian species with altitude (Kessler, 2002) follows the same pattern as in Colombia. The Ecuadorian richness and high endemism level for subgenus *Tacsonia* is another strong point of convergence with the Colombian situation. According to Jørgensen & León-Yánez (1999) bimodality in altitudinal vine diversity distribution might be due to differential collecting intensity. However, there is no reason to expect a more continuous pattern. Indeed, Kessler (2002) showed that there is no common elevational pattern for diversity, but a wide variety of independent patterns at all taxonomic levels, with maxima at different elevations, and that endemism appeared highest in the narrowest and most fragmented elevational belts. "The degree to which these influences become visible along the elevational gradient are determined by which combination of species is analysed". Strikingly, the same conclusion may be drawn within Passifloraceae, and particularly within *Passiflora*, taking into account infrageneric divisions. This result restricts the potential use of Passifloraceae as an indicator group to the Andean region, where they have developed most of their diversity.

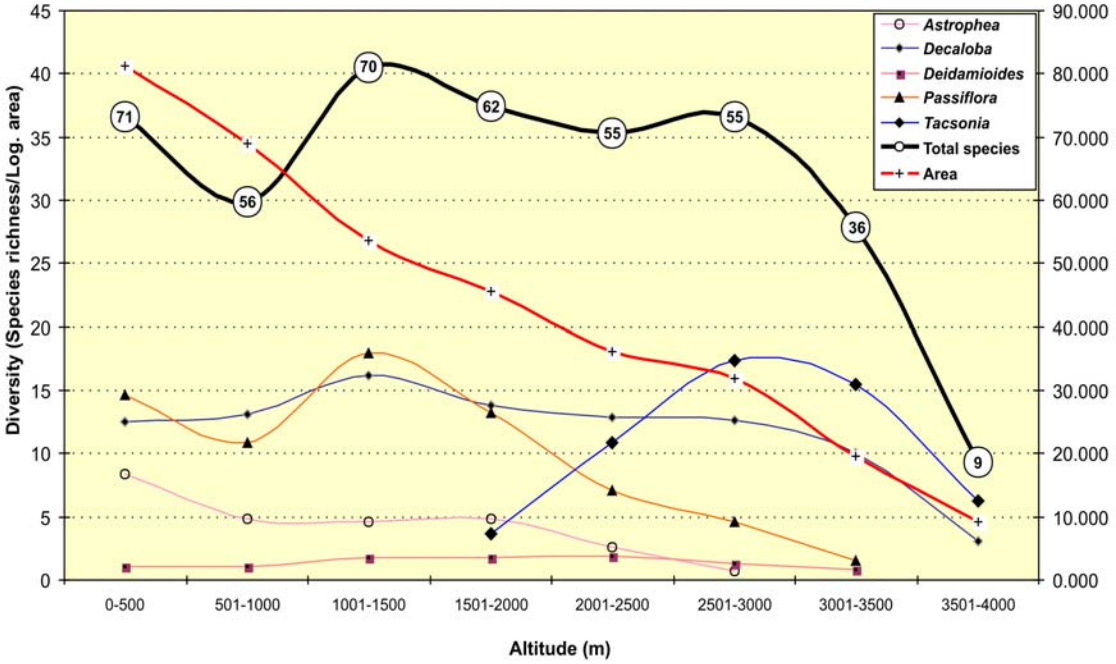

Figure 4. Distribution of total species richness (within circles) and species relative diversity in relation to altitude in Colombia (3,930 observations), for *Passiflora* and five infrageneric groups.

III.1.4.5. *Climatic requirements*

A PCA was carried out on the 19 climatic variables for the 3,930 records of our dataset. The first two principal components explain 77% of the total variance (Table 2). The first one accounts for half of the variation (49%) and is strongly correlated ($r > 0.97$) with variables associated to temperature (maximum, mean and minimal, but not seasonality in temperature). The second one explains 28% of the total variation and is related principally with precipitation in the whole year and in particular seasons (but again, not for seasonality in precipitation). Figure 5 shows the distribution of species in the principal plane. The first axis differentiates Andean species adapted to temperatures below 15 °C (i.e. >2,000 m), on the left side from those growing below 2,000 m, on the right side. Characteristically, these rightmost species originate from the Amazonian and Orinoquian. The second axis separates the species in respect to precipitation. Thus *P. arbelaezii* L. Uribe, *P. costaricensis* Killip, *P. chocoensis* Gerlach & Ulmer, *P. lobata* (Killip) Hutch. *ex* MacDougal, *P. occidentalis* Hernández, *P. pacifica* L.K. Escobar, *P. palenquensis* Holm-Niels. & Lawesson and *P. tica* Gómez-Laur. & L.D. Gómez logically shows preferences for high precipitation, a predominant condition in the Pacific region, and all are predicted to exist sympatrically. At the other extreme of the second axis, are species adapted to lower precipitation levels, specifically to the marked dry season of the Caribbean region, such as *P. bicornis* Mill., *P. serrulata* Jacq., *P. guazumaefolia* Juss. and *P. pallida* L. Amazonian species tend to take an intermediate position.

Table 2. Factor loadings, eigenvalues and percentages of variance for the first four components, resulting from the PCA analysis on 19 bioclimatic parameters for the 3,930 collection points (Colombian Passifloraceae).

Bioclim Parameters	**Principal component**			
	1	**2**	**3**	**4**
Annual Mean Temperature	**0.98**	0.17	0.09	-0.03
Mean Monthly Temperature Range	0.08	-0.21	-0.16	**-0.96**
Isothermality	0.00	0.06	**-0.95**	-0.01
Temperature Seasonality	0.45	0.03	**0.77**	-0.18
Max, Temperature of Warmest Month	**0.97**	0.16	0.12	-0.12
Min, Temperature of Coldest Month	**0.98**	0.20	0.06	0.04
Temp, Annual Range	0.08	-0.22	0.37	**-0.89**
Mean Temperature of Wettest Quarter	**0.98**	0.17	0.09	-0.02
Mean Temperature of Driest Quarter	**0.98**	0.18	0.10	-0.04
Mean Temperature of Warmest Quarter	**0.98**	0.17	0.11	-0.04
Mean Temperature of Coldest Quarter	**0.98**	0.17	0.07	-0.03
Annual Precipitation	0.24	**0.96**	0.04	0.10
Precipitation of Wettest Month	0.29	**0.91**	0.15	0.10
Precipitation of Driest Month	0.09	**0.91**	-0.28	0.13
Precipitation Seasonality	0.23	-0.55	0.60	0.00
Precipitation of Wettest Quarter	0.28	**0.91**	0.17	0.09
Precipitation of Driest Quarter	0.09	**0.93**	-0.25	0.13
Precipitation of Warmest Quarter	0.10	**0.87**	-0.20	0.12
Precipitation of Coldest Quarter	0.29	**0.89**	0.05	0.02
Eigenvalue	9.26	5.37	1.74	1.51
Percentage of variance	48.74	28.26	9.15	7.94

The species repartition in the principal plane consistently reflects the potential for climatic adaptation of the groups that were defined for the analysis of altitudinal distribution. Thus, subgenus *Tacsonia* shows a marked adaptation potential to cool conditions, while subgenus

Astrophea and the *Passiflora*-like group show much higher potential in hot and mild climates. The genera *Ancistrothyrsus* and *Dilkea* are even more clearly adapted to lowlands, mainly in the Amazonian region. The *Decaloba*-like group shows a much broader adaptation range, explaining its quite constant presence across the different biogeographic regions.

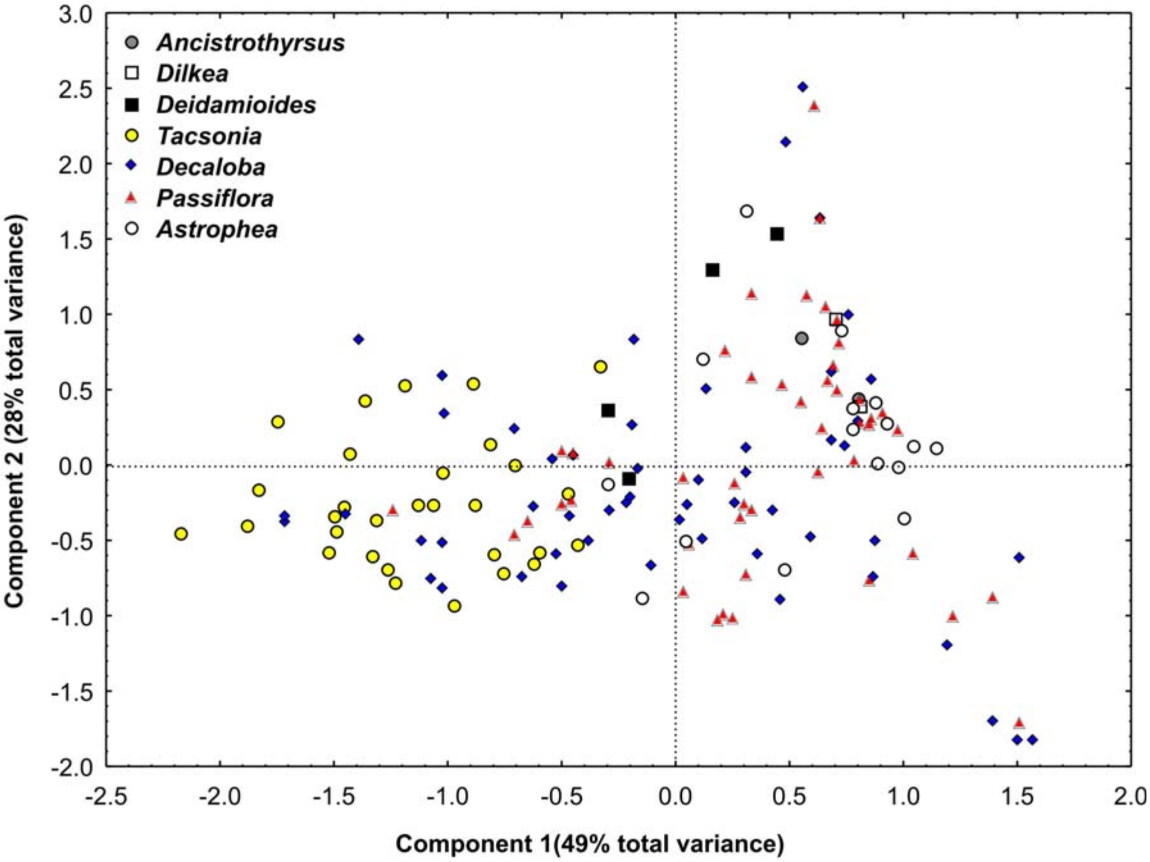

Figure 5. Distribution of Passifloraceae species in the PCA principal plane for climatic variables, with indication of genera (*Ancistrothyrsus* and *Dilkea*) and subgenera of genus *Passiflora*.

III.1.4.6. *Areas of distribution - endemic species*

Table 3 gives MaxD and CA_{50} for the 165 Passifloraceae native species of Colombia. Figure 6 shows a good correspondence ($R^2 = 0.77$) between these distribution parameters, whose comparison also provides information on species dispersion. Species with a high MaxD but relatively low CA_{50} indicate low densities, as a result of biological rarity and/or under-collection, whereas high CA_{50} relative to MaxD indicates high density due to population biology and/or intense collection. The species with the widest distributions in Colombia (more than 1,100 km MaxD) are those that show a very wide distribution including most neotropical regions, such as the very common *P. foetida* L., *P. auriculata*, *P. quadrangularis* and *P. laurifolia* L. (wild and cultivated) *P. suberosa* L, and *P. serratodigitata* L., *P. capsularis* L., *P. rubra* L., and *P. misera* Kunth, and others of still considerable regional distribution, such as *P. vitifolia* Kunth, *P. coccinea* Aubl., *P. spinosa* (Poepp. & Endl.) Mast., *P. nitida*, *P. subpeltata* Ortega, *P. maliformis, P. menispermifolia* Kunth, *P. biflora* Lam., and *Dilkea parviflora* Killip. Only *P. arborea* Spreng (Panamá to Ecuador) and *P. cumbalensis* (Colombia to Peru) show a more restricted distribution. These high-MaxD species are concentrated at low to medium elevations, the only exception being *P. cumbalensis*. According to IUCN criteria, they are not threatened (Least Concern category), except for *P. arborea* (Near Threatened; Ocampo et al., 2007). Between 200 and 1,100 km of MaxD, there are species of regional importance, such as *P. mixta* L.f., *P. ligularis*, and endemics with a relatively wide distribution, such as *P. sphaerocarpa* Triana & Planch. (805 km²), *P. lehmanni* Mast. (878 km²), *P. antioquiensis* and *P. mollis* Kunth. The latter displays a relatively high CA_{50} in its group, as its 17 observations are quite scattered along the Cordillera Occidental. The position of *P. coriacea* Juss. in this group of medium dispersion is very surprising, as it is found in all neotropical countries. The 71 species with MaxD values below 225 km include 36 narrow endemics, 21 of which are exclusive to nine departments, particularly Antioquia (six species), Tolima (four) and Santander (three). The 14 others show similar MaxD and CA_{50} but live across administrative divisions. Only four of these 36 narrow endemics are represented by ten or more observations while ten species are only known from the type collection. Ocampo et al. (2007) considered a MaxD under 100 km as a criterion of rarity and threat, which places 26 endemic species in a very critical situation. The situation of 33 non-endemic species with a MaxD less than 100 km must be examined in relation to their distribution in neighbor countries. *P. truxilliensis* Planch. & Linden *ex* Triana & Planch. is shared with Venezuela, but it is a narrow endemic living around the border. The distribution of 14 species extends to farther places in neighboring countries, and 18 species present a wide distribution, extending to non-neighboring countries. For example, *P. tricuspis* is only reported once, in the Andean foothill, so it has a null MaxD, however its distribution extends south to

Bolivia. Sixteen of these 30 species are adapted to lowland conditions, which suggests that their apparent rarity is in fact due to the poor collecting in the corresponding regions.

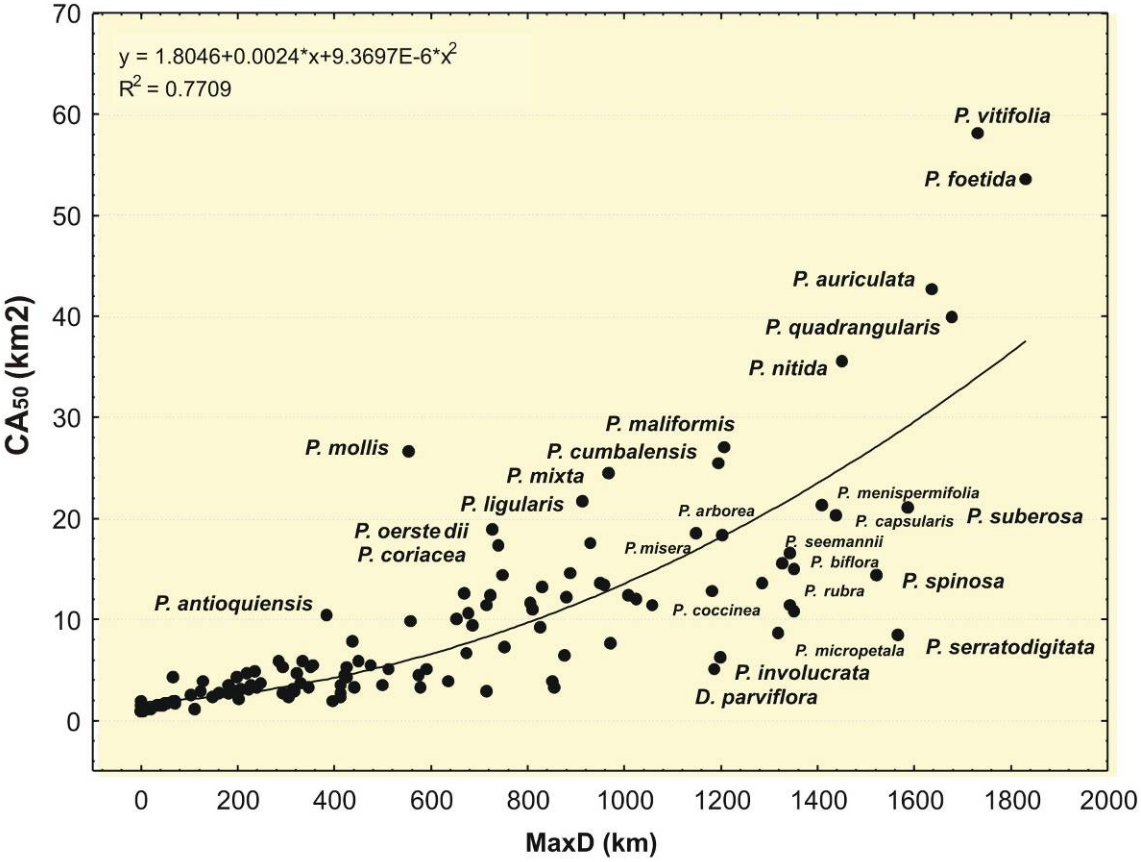

Figure 6. Extent of Passifloraceae species distribution in Colombia: circular area (CA_{50}) vs. maximum distance (MaxD).

Table 3. Total number of Passifloraceae present in Colombia. Number of observations, maximum distance (MaxD) and circular area (CA) for each species. Endemic species are highlighted by an asterisk (*). RC: species rare for Colombia; Roc: species rare in other countries; Rne: rare narrow endemic, Ne: narrow endemic; Re: rare endemic; Ce: common endemic. Presence in a richness spot is indicated by **Rs** and the identification number used in Figure 7.

Species	**Nb. observ.**	**MaxD (km)**	**CA (km2)**	**Rare species**	**Endemics and distribution**
Ancistrothyrsus antioquiensis L.K. Escobar (ined.)*	2	41	11,762	RC	Rne (Antioquia)
Ancistrothyrsus tessmannii Harms	1	0	7,814	RC / Roc	
Dilkea johannesii Barb. Rodr.	1	0	7,814	RC / Roc	
Dilkea parviflora Killip	22	1,185	40,688		
Dilkea retusa Mast.	5	952	106,159	RC	
Passiflora adenopoda Moc. & Sessé *ex* DC.	51	383	82,650		
Passiflora adulterina L.f. *	43	234	39,072		Ce
Passiflora alnifolia Kunth	121	1,244	170,761		
Passiflora alata Curtis	1	0	7,814	RC	
Passiflora ambigua Hemsl. *ex* Hook.	48	929	137,261		
Passiflora andina Killip	1	0	7,814	RC /Roc	Colombia and Ecuador
Passiflora andreana Mast.	3	45	12,214	RC	
Passiflora antioquiensis H. Karst. *	55	667	99,064		Ce
Passiflora apoda Harms	43	678	83,615		
Passiflora arbelaezii L. Uribe	48	746	113,491		
Passiflora arborea Spreng.	67	1,204	144,115		
Passiflora auriculata Kunth	128	1,635	334,952		
Passiflora azeroana L. Uribe *	10	574	34,734		Ce
Passiflora bicornis Mill.,	11	675	52,098		
Passiflora bicuspidata (H.Karst.) Mast. *	16	438	61,674		Ce
Passiflora biflora Lam.	40	1,326	122,047		
Passiflora bogotensis Benth. *	56	1,057	89,250		Ce
Passiflora bracteosa Planch. & Linden	7	122	23,180	RC /Roc	Colombia and Venezuela
Passiflora bucaramangensis Killip *	8	70	15,032	RC	Ne (Santander)
Passiflora callistema L.K. Escobar *	1	0	7,814	RC	Rne (Bolivar)
Passiflora candollei Tr. & Planch.	4	854	26,294	RC	

Passiflora capsularis L.	64	1,437	159,962		
Passiflora chelidonea Mast.	18	1,024	94,209		
Passiflora chocoensis G. Gerlach & T. Ulmer *	1	0	7,814	RC	Rne (Choco)
Passiflora cincinnata Mast.	1	0	7,814	RC	
Passiflora citrifolia (Juss.) Mast.	3	68	14,049	RC	
Passiflora coccinea Aubl.	21	1,285	107,128		
Passiflora colombiana L.K. Escobar *	2	42	11,910	RC	Rne
Passiflora coriacea Juss.	59	741	136,372		
Passiflora costaricensis Killip	1	0	7,814	RC	
Passiflora cremastantha Harms *	1	0	7,814	RC	Rne (Cauca)
Passiflora crispolanata L.Uribe *	11	246	29,720		Ce
Passiflora cuatrecasasii Killip *	9	181	21,312		Ne (**Rs** 2)
Passiflora cumbalensis (Karst.) Harms	156	1,196	199,941		
Passiflora cuneata Willd.	9	877	50,607		
Passiflora cuspidifolia Harms,	33	812	86,640		
Passiflora danielii Killip *	5	180	20,590	RC	Rne (Antioquia, **Rs** 2)
Passiflora dawei Killip *	4	208	23,702	RC	Rne (**Rs 3**)
Passiflora emarginata Humb. & Bonpl. *	46	654	78,393		Ce
Passiflora engleriana Harms *	2	110	8,902	RC	Rne (Antioquia, **Rs** 2)
Passiflora erytrophylla Mast. *	6	225	27,643		Ne (**Rs** 2,3)
Passiflora escobariana J.M. MacDougal	2	3	8,136	RC / Roc	(Antioquia, **Rs** 2)
Passiflora filipes Benth.	3	48	13,227	RC / Roc	México to Ecuador
Passiflora fimbriatistipula Harms *	18	198	33,664		Ne
Passiflora flexipes Triana & Planch. *	24	322	36,121		Ce
Passiflora foetida L.	143	1,830	420,440		
Passiflora formosa T. Ulmer *	1	0	7,814	RC	Rne (Boyacá)
Passiflora glandulosa Cav.	1	0	7,814	RC	
Passiflora gleasonii Killip	2	3	8,075	RC	
Passiflora gracillima Killip	29	684	74,546		
Passiflora grandis Killip *	2	14	9,161	RC	Rne
Passiflora gritensis H. Karst.	8	346	26,115		
Passiflora guatemalensis S. Watson	11	971	59,505		
Passiflora guazumaefolia Juss.	8	349	41,192		
Passiflora hahnii (Fourn.) Mast.	1	0	7,814	RC	
Passiflora haughtii Killip *	1	0	7,814	RC	Rne (Santander)
Passiflora hirtiflora Jorgensen & Holm-Nielsen	1	0	7,814	RC	

Passiflora holosericea L.	7	238	25,632		
Passiflora holtii Killip	1	0	7,814	RC / Roc	
Passiflora hyacinthiflora Planch. & Linden *	3	305	17,746	RC	Re
Passiflora involucrata (Mast) A.H. Gentry	8	1,197	48,827		
Passiflora jardinensis L.K. Escobar *	8	35	11,335	RC	Ne (Antioquia)
Passiflora kalbreyeri Mast. *	19	426	41,237		Ce
Passiflora killipiana Cuatrecasas	1	0	7,814	RC / Roc	Colombia to Peru
Passiflora lanata (Juss.) Poir. *	32	284	45,476		Ce
Passiflora laurifolia L.	11	1,350	84,672		
Passiflora lehmanni Mast. *	17	805	91,156		Ce
Passiflora leptomischa Harms *	21	449	46,331		Ce
Passiflora ligularis Juss.	101	914	170,123		
Passiflora lindeniana Planch. *ex* Triana & Planch.	2	395	15,628	RC / Roc	Colombia and Venezuela
Passiflora linearistipula L.K. Escobar *	4	8	8,695	RC	Rne (Caldas)
Passiflora lobata (Killip) Hutch. *ex* J.M. MacDougal	3	194	23,115	RC	
Passiflora longipes Juss. *	21	334	45,557		Ce
Passiflora lyra Planch. & Lind. *ex* Killip	4	69	14,716	RC / Roc	
Passiflora macrophylla Spruce *ex* Mast.	20	716	90,432		
Passiflora magdalenae Triana & Planch. *	21	129	31,127		Ne
Passiflora magnifica L.K. Escobar*	6	33	12,215	RC	Ne (Antioquia, **Rs** 2)
Passiflora maliformis L.	122	1,208	212,270		
Passiflora manicata (Juss.) Pers.	62	889	114,036		
Passiflora mariquitensis Mutis *ex* Uribe *	3	10	8,436	RC	Rne (Tolima)
Passiflora megacoriacea Porter-Utley (ined.)	1	0	7,814	RC	
Passiflora menispermacea Triana & Planch. *	2	18	9,610	RC	Rne (Tolima, **Rs** 4)
Passiflora menispermifolia Kunth	43	1,410	167,659		
Passiflora micropetala Mast.	11	1,318	68,015		
Passiflora misera Kunth	54	1,148	145,398		
Passiflora mixta L. f.	162	966	191,787		
Passiflora mollis Kunth	17	554	208,941		
Passiflora monadelpha Jorgensen & Holm-Nielsen	7	67	33,665	RC / Roc	Colombia and Ecuador
Passiflora morifolia Mast.	1	0	7,814	RC	
Passiflora multiformis Jacq.	4	147	17,652	RC	
Passiflora munchiquensis Hernandez (ined.)*	4	200	22,441	RC	Rne
Passiflora mutisii Killip *	1	0	7,814	RC	Rne (Tolima)
Passiflora nitida Kunth	72	1,452	279,511		

Passiflora occidentalis Hernandez (ined.)*	10	474	42,350		Ce
Passiflora oerstedii Mast.	41	728	148,975		
Passiflora pacifica L.K. Escobar *	9	510	39,585		Ce
Passiflora palenquensis Holm-Niels. & Lawesson	20	1,181	100,769		
Passiflora pamplonensis Planch.& Linden *ex* Tr. & Planch. *	1	0	7,814	RC	Rne (N. de Santander)
Passiflora pallida L.	6	898	50,078		
Passiflora panamensis Killip	15	295	41,614		
Passiflora parritae (Mast.) L.H. Bailey *	14	100	20,357	RC	Ne
Passiflora pennellii Killip *	6	313	24,413		Ce
Passiflora phaeocaula Killip	5	498	28,305	RC / Roc	
Passiflora picturata Ker	1	0	7,814	RC	
Passiflora pilosissima Killip *	2	270	15,628		Re
Passiflora pinnatistipula Cav.	21	750	57,114		
Passiflora pittieri Mast.	1	0	12,661	RC	
Passiflora platyloba Killip	4	201	16,471	RC	
Passiflora popayanensis Killip *	6	64	15,078	RC	Ne (Cauca)
Passiflora popenovii Killip	17	636	31,075		
Passiflora punctata L.	8	592	40,022		
Passiflora purdiei Killip *	1	0	7,814	RC	Rne
Passiflora putumayensis Killip	1	0	7,814	RC / Roc	
Passiflora pyrrhantha Harms	1	0	7,814	RC / Roc	
Passiflora quadrangularis L.	112	1,676	314,317		
Passiflora quadriglandulosa Rodschied	4	414	21,256	RC	
Passiflora quindiensis Killip *	8	225	24,711		Ne (Tolima, **Rs** 4)
Passiflora resticulata Mast. & André	4	414	18,938		
Passiflora rigidifolia Killip *	1	0	7,814	RC	Rne (Antioquia)
Passiflora riparia Mart. *ex* Mast.	3	716	23,442	RC	
Passiflora rubra L.	90	1,351	117,934		
Passiflora rugosa (Mast.) Triana & Planch	12	421	35,549		
Passiflora schlimiana Triana & Planch. *	7	181	27,852	Roc	Ne
Passiflora securiclata Mast	4	849	30,708	RC / Roc	Colombia and Venezuela
Passiflora seemannii Griseb.	40	1,341	129,777		
Passiflora semiciliosa Planch & Linden *	4	578	26,175	RC	Re
Passiflora serratodigitata L.	18	1,566	67,105		
Passiflora serrulata Jacq.	10	331	29,354		
Passiflora sexflora Juss.	14	353	43,143		

Passiflora sierrae L.K. Escobar *	2	46	12,194	RC	Rne (Magdalena)
Passiflora skiantha Huber	1	0	7,814	RC / Roc	Colombia and Peru
Passiflora smithii Killip	28	827	72,555		
Passiflora sodiroi Harms	1	0	7,814	RC / Roc	Colombia and Ecuador
Passiflora sphaerocarpa Triana & Planch. *	35	878	96,244		Ce
Passiflora spicata Mast.	1	0	7,814	RC / Roc	Colombia and Brazil
Passiflora spinosa (Poepp. & Endl.) Mast.	20	1,521	118,197		
Passiflora suberosa L.	66	1,497	158,860		
Passiflora subpeltata Ortega	35	1,344	89,527		
Passiflora tarminiana Coppens & Barney	28	832	103,373		
Passiflora tenerifensis L.K. Escobar *	4	71	15,195	RC	Rne (Valle del Cauca)
Passiflora tica Gómez-Laur. & L.D. Gómez	5	319	23,119	RC	
Passiflora tiliifolia L.	48	1,010	97,205		
Passiflora tolimana Harms *	12	426	33,711		Ce
Passiflora trianae Killip *	2	39	11,594	RC	Rne
Passiflora tribolophylla Harms *	1	0	7,814	RC	Rne
Passiflora tricuspis Mast.	1	0	7,814	RC	
Passiflora trinervia (Juss.) Poir.*	27	220	36,932		Ne (**Rs** 5)
Passiflora tripartita (Juss.) Poir.	56	1,210	145,398		
Passiflora trisulca Mast. *	8	441	25,258		Ce
Passiflora truxillensis Planch. & Linden *ex* Triana & Planch.	1	0	15,628	RC / Roc	Colombia and Venezuela
Passiflora tryphostemmatoides Harms	25	557	77,831		
Passiflora tuberosa Jacq.	1	0	7,814	RC	
Passiflora uribei L.K. Escobar *	3	54	12,960	RC	Rne
Passiflora ursina Killip & Cuatrec.	2	7	8,503	RC / Roc	Colombia and Ecuador
Passiflora variolata Poepp. & Endl.	6	412	27,059		
Passiflora venosa Rusby	1	0	7,814	RC / Roc	
Passiflora vespertilio L.	3	292	20,887	RC	
Passiflora vestita Killip	1	0	7,814	RC / Roc	Colombia and Ecuador
Passiflora vitifolia Kunth	359	1,729	456,229		
Passiflora x *rosea* (H. Karst.) Killip	7	161	20,988		

III.1.4.7. *Potential distribution of species and species assemblages*

For each of the 80 species with more than ten observations, the BioClim model provided a probabilistic prediction of its geographic distribution using climate data as the driver of species distribution. The results cannot be presented here for each individual species, but are available upon request from the authors. The potential distribution of richness was calculated by summing the 80 spatial predictions of species occurrence (Figure 7). The areas of highest predicted species richness (41 to 54 predicted sympatric species) are mostly located in the center of the country, on the slopes of the three cordilleras, between 1000 and 2,000 m of elevation. Collection has been intense in many of them, showing a high diversity, however the correspondence is not perfect between observed and modeled distribution. While the species-rich areas of Antioquia and Caldas, Quindío, Cundinamarca and eastern Boyacá, and even the poorly explored but promising Santander, are well represented on the map (areas 2, 5, 3, 4 and 1 respectively), only very small richness spots are drawn for Valle del Cauca (area 7), or no richness spot indicated for Cauca and southern Huila. Conversely, predicted richness spots 6, 8 and 9 (eastern Tolima-northern Huila- southern Cundinamarca, western Caquetá, Nariño) were not detected in the analysis of observed diversity, indicating potential collecting gaps. The model predicts a very poor representation of *Passiflora* in the lowlands of the Caribbean and Orinoquian and part of the Pacific, as well as in the Sierra Nevada de Santa Marta, an isolated mountain range on the Caribbean Coast, reputed for its high level of endemism. In both cases, this may be attributed to the poor exploration of these areas (low densities of observation) and to poor representation of their species (few observations per species) resulting in them not having sufficient observations to be used in the predictive modeling. This bias can be corrected by further collecting in these regions. Alternatively, materials of Colombian species collected in border regions of neighboring countries, belonging to the same biogeographic entities (*e.g.* the Venezuelan Llanos for the Orinoquian, Costa Rican and Ecuadorian Pacific, Brazilian, Ecuadorian and Peruvian Upper Amazonian) might be used to refine these models and increase the number of observations per species under analysis.

The biodiversity hotspot concept not only considers species richness and diversity but also endemism. In an analysis of New Zealand fern diversity, Lehmann et al. (2002) observed a

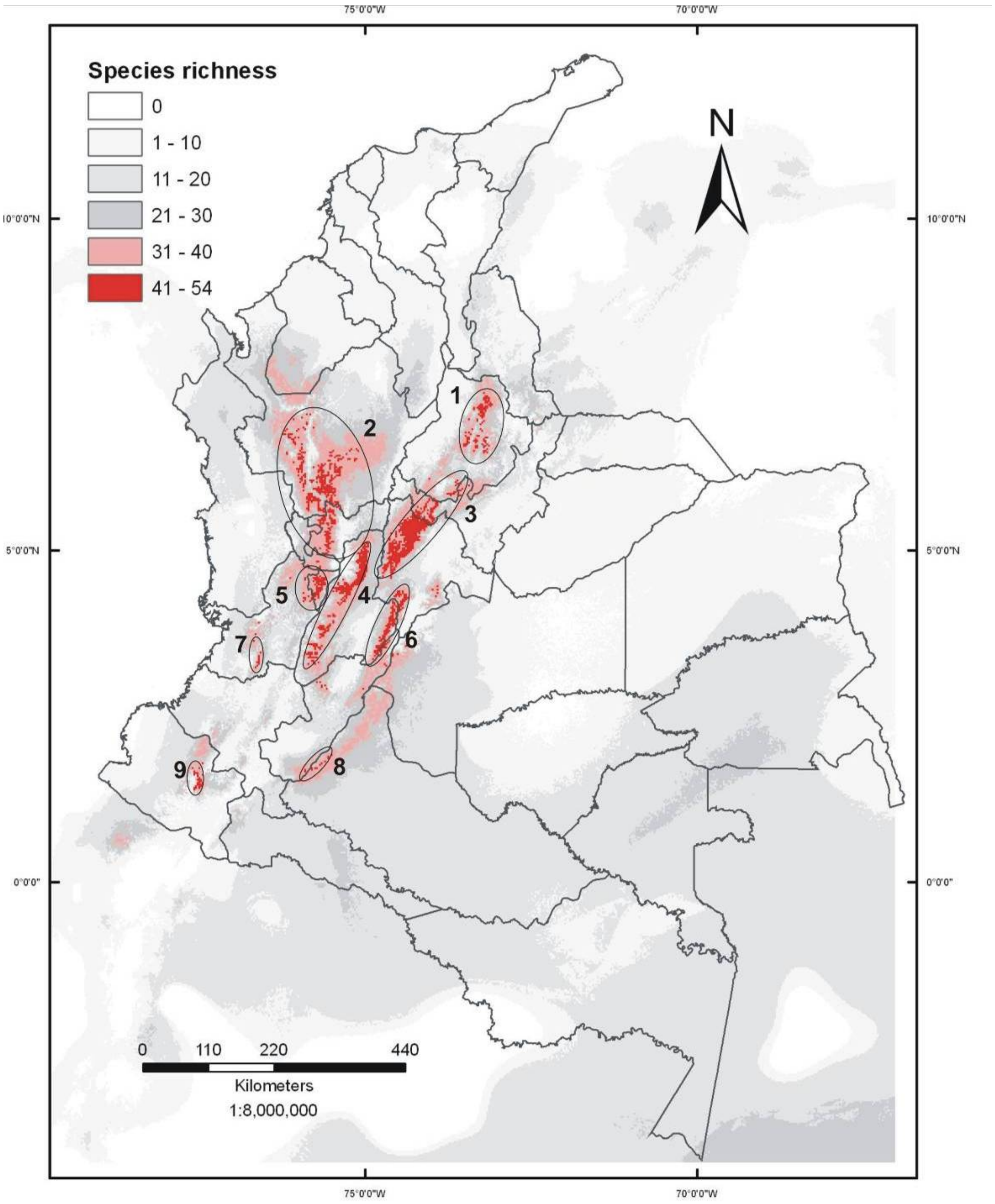

Figure 7. Modeled distribution of Colombian Passifloraceae diversity based on data from 80 species presenting more than 10 observations. Ellipses individualize high richness spots mentioned in the text.

poor correlation between both parameters. For Colombian Passifloraceae, we could not establish rigorously their correspondence, as the analysis was not designed for rare species, however we compared their distributions, distinguishing four categories among the 58 endemics: those with a relatively wide distribution (MaxD > 100 km, 19 species), the narrow endemics (MaxD under 100 km, three species), the rare endemics (less than six observations, three species), and the rare narrow endemics (both criteria, twenty species). Six of the 10 narrow endemics and seven of the 25 rare narrow endemics live in one of the nine hotspots defined by the diversity analysis. None of the three rare endemics are found in those sites. Of the 27 rare and/or narrow endemics living out of those hotspots, three are considered extinct (Ocampo et al., 2007), seven are only adapted to lowlands, which easily explains their absence in Andean hotspots; two species are endemic to the Sierra Nevada de Santa Marta, an area of endemism that could not be sufficiently taken into account for reasons explained previously. Finally, only 11 of the 27 living Andean rare/narrow endemic species, i.e. less than 50%, live in one of the hotspots. This proportion must be compared with more than 54 out of 80 in the case of the non-rare species whose distribution determined those hotspots. Thus, preserving these nine areas should have a less positive impact on the conservation of narrow endemics than on the general Passifloraceae diversity. Using an analysis of complementarity reserve selection developed by Rebelo (1994), 52 sites of 25km x 25km were selected to represent all 165 native species throughout the country. The best five sites, in Caldas, Risaralda, Norte de Santander, southern Antioquia and Boyacá, capture a total of 64 species. In just seven sites, 50% of all species could be conserved, though many of the endemic/rare species are not captured in these sites.

III.1.4.8. *Conservation of Passifloraceae and their habitat*

Figure 8 combines the estimated distribution of Passifloraceae diversity with that of protected areas in the Andes of Colombia, showing a general lack of correspondence. Most Andean protected areas are concentrated around the summits, obviously targeting páramo ecosystems. Very few small protected areas harbor a high diversity of Passifloraceae: the watershed forest reserves of Sierra del Peligro (Boyacá, 16.5 km²), Río Nare (Antioquia, 118.8 km²), Río San Francisco, Cuchillas Peñas Blancas, Cerro Quininí (Cundinamarca, 28.8, 16.3 and 18.0 km²), whose responsibility has recently been upgraded to the department level. The Parque Nacional Farallones (Valle del Cauca) is the only reserve of national importance to protect part of a small Passifloraceae hotspot, on the eastern fringes of the nature reserve. This poor coverage is not good news, neither for a family including 71% threatened species, nor for the habitats where these species have developed numerous interactions with many other organisms.

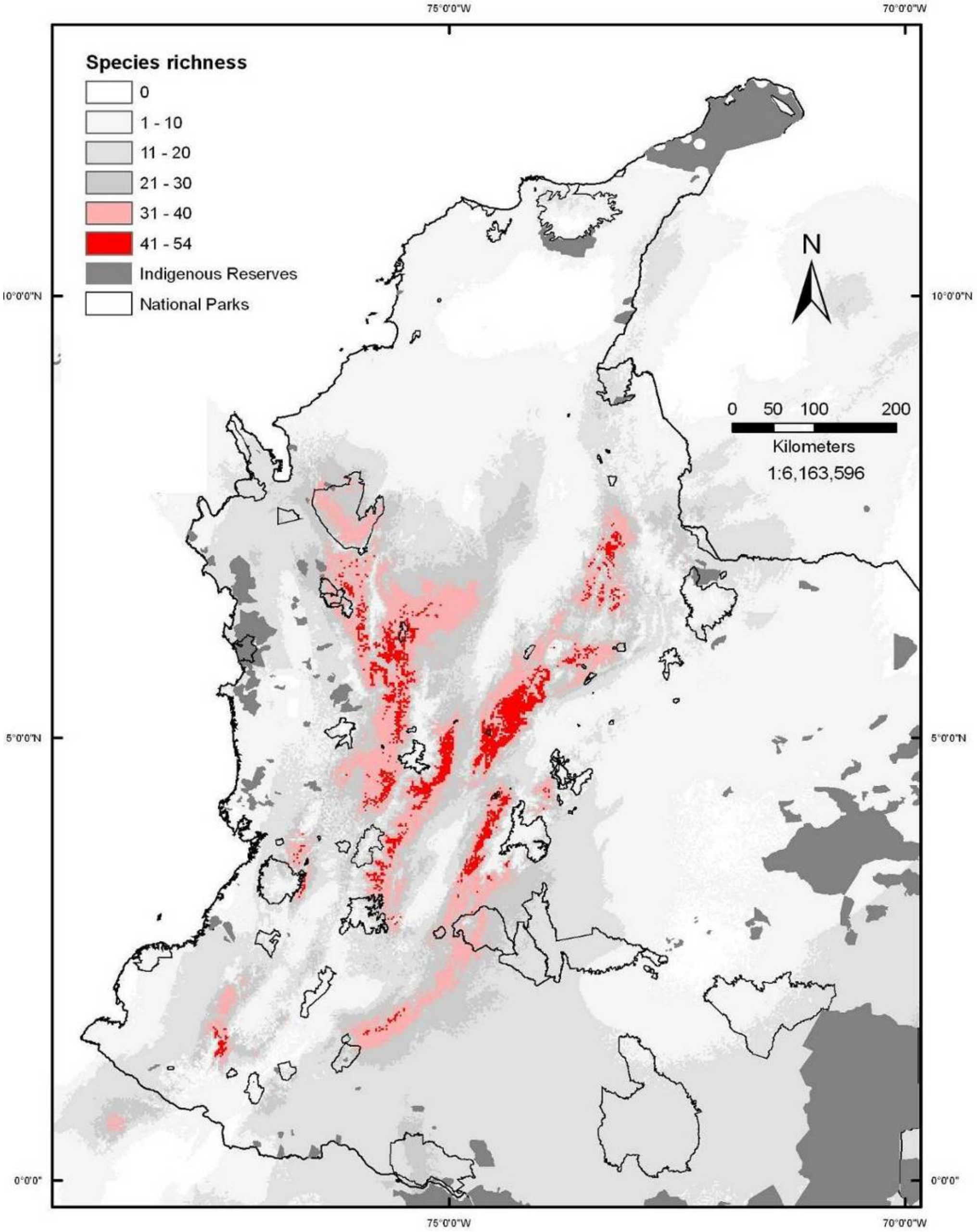

Figure 8. Distribution of protected areas in Colombia, showing poor correspondence with areas of high Passifloraceae diversity.

Figure 9 shows a striking general superposition of areas of high Passifloraceae diversity on certain Colombian coffee growing zone ecotopes (Cenicafé, 2005) whose conservation is of the utmost importance for the country. This is not surprising, as the corresponding elevation belts include or enclose those of major diversity (1000-2,500). It clearly shows that efforts for the conservation of Passifloraceae habitats and genetic resources must be integrated in the more general management of the coffee growing zone environment at the landscape level. The latter can be ensured by coordinating existing actions for watershed protection, management of private and low-level public reserves, as well as recreational areas for public education (rural and peripheral urban parks, arboreta, etc.), creation of environmental corridors, and improvement of agricultural practices, particularly in coffee farms (crop association, shade tree diversity, and guadua bamboo growing for building materials and water management at farm level).

III.1.4.9. *Passifloraceae as indicators of biodiversity*

According to Pearson (1994), an ideal indicator taxon should cumulate seven criteria: (i) a well-known and stable taxonomy, (ii) well known natural history, (iii) readily surveyed and manipulated, (iv) higher taxa broadly distributed geographically and over a breadth of habitats, (v) lower taxa specialized and sensitive to habitat changes, (vi) patterns of diversity in other taxa, and (vii) potential economic importance. Passifloraceae clearly fill the fifth and seventh criteria, taking into account that several common species are indicators of more or less perturbated habitats. Concerning the fourth criterion, our analyses have repeatedly underlined that Colombian Passifloraceae distribution is concentrated in the Andean region, so their use as indicators should be restricted to the corresponding elevation belts. Lianas growing in high trees are not always easily surveyed (third criterion), however their typical structures, showy flowers and interesting fruits make them easy to identify as a group, catching the attention of local populations and specialists (*e.g.* protected area staff), who can thus help in localizing the different species in particular places. The application of molecular techniques should produce important progress in the complex taxonomy of this group and further the understanding of its natural history. The sixth criterion is particularly important. The numerous interactions of Passifloraceae with other organisms (surrounding vegetation, pollinators, and herbivores) constitute a first indication that their diversity is necessarily related to that of other components of the ecosystem. Another indication came from a preliminary study, where we found an excellent correspondence between the distributions of diversity of *Passiflora* and *Vasconcellea* (mountain papayas), another plant group whose radiation is also clearly related to the rise of the Andes (Scheldeman et al., 2006). Similar results must be obtained with more plant taxa before considering unequivocally Passifloraceae as a reliable surrogate for floral diversity in Andean ecosystems. However, given the excellent correspondence between Passifloraceae diversity maps and coffee growing zone ecotope maps, we may already recommend them as useful indicators of habitat degradation or restoration in this environmentally and economically very important region.

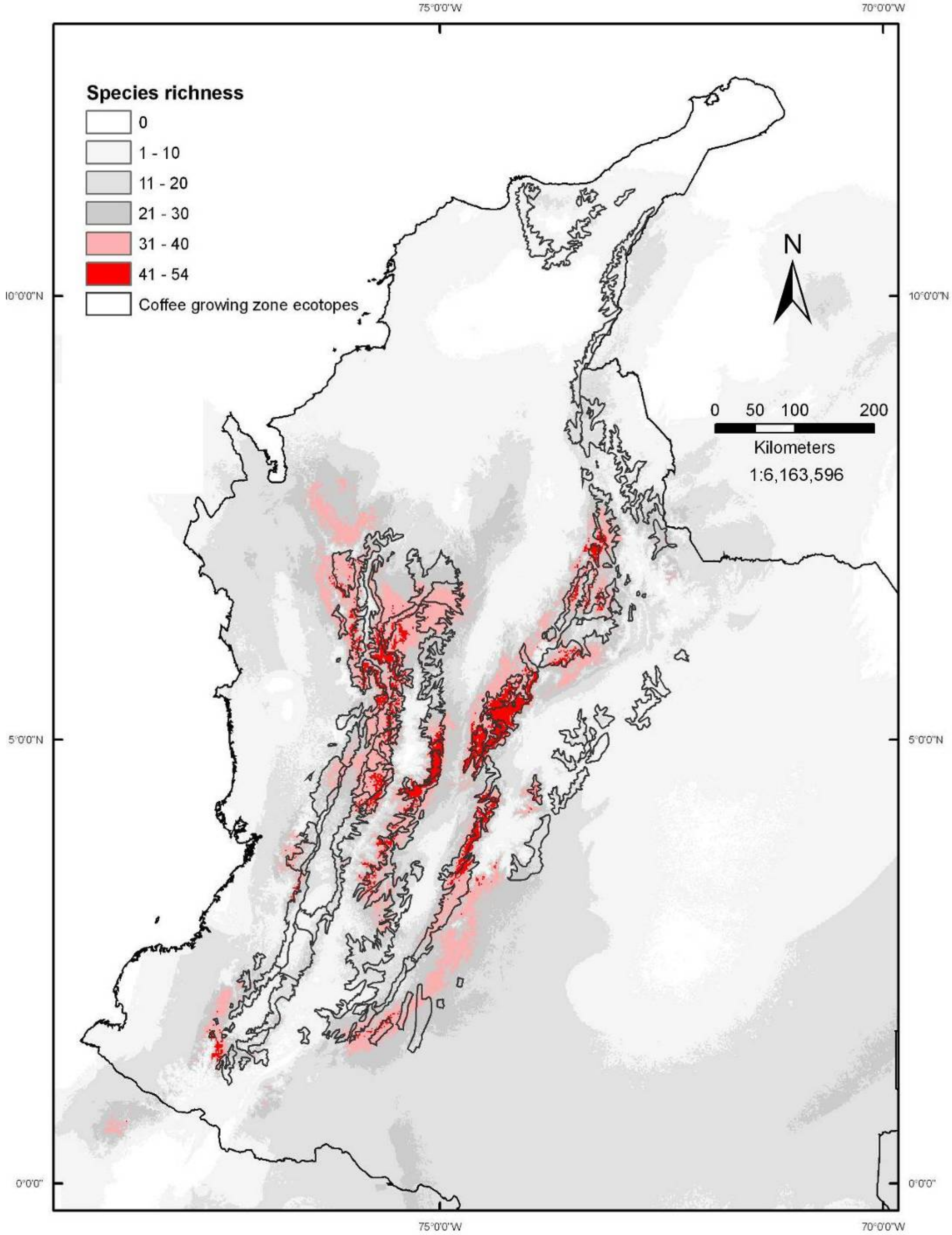

Figure 9. Correspondence between Passifloraceae high richness spots and coffee growing zone ecotopes.

III.1.5. Conclusions

Collections of Passifloraceae have not been uniform as a consequence of difficulty of access and/or chronic social conflict in many areas. It has been much denser in the central coffee growing zone, Antioquia, Valle del Cauca and Cundinamarca. The southern and northeastern Andes, and the Caribbean have been little explored. For the lowland forests of the Pacific, the Orinoquian and the Amazonian, data are so poor that they are misleading. Despite the resulting sampling bias, collecting parameters clearly point to the concentration of observed Passifloraceae diversity in the Andes, and more particularly the central coffee growing zone. This is further highlighted by the elevational pattern of diversity, showing three peaks, a small one for lowlands, and two higher ones at intermediate and high elevations (1000-2,000 and 2,500-3,000 m). A more thorough analysis shows that this trimodal pattern corresponds to different adaptive evolutions among genera and infrageneric divisions of *Passiflora*. This is also reflected in the analysis of the climatic preferences of these infrageneric groups.

The analysis of species distribution areas shows a trend for more extent dispersion of species occurring at low and intermediate elevations. On the contrary, narrow endemics are more frequent among highland species.

The modeled species richness map allowed to identify nine richness spots of variable size, three of which, located in the southern and southeastern Andes of Colombia, correspond to collection gaps, as they were not detected in the analysis of observed diversity. Another probable collection gap, not detected by diversity modeling, corresponds to the Sierra Nevada de Santa Marta, an isolated mountain range with both high diversity and endemism. The proportion of endemics living in high richness spots is lower than the proportion of all species used for modeling, confirming the lack of relation between diversity concentration and endemism reported in other studies. If this is further substantiated in different groups of organisms, it could limit the application of the biodiversity hotspot concept, as the best protected areas for diversity would not necessarily provide protection to a high proportion of narrow endemics.

Passifloraceae diversity is not currently conserved by the current network of Colombian protected areas. On the contrary, it is particularly concentrated on certain ecotopes of the coffee growing zone, i.e. highly disturbed habitats, so any conservation effort must be integrated in local management strategies at the landscape level. Passifloraceae may provide an interesting indicator to evaluate the outcome of such efforts.

III.1.6. Acknowledgements

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CHAPTER IV

A phenetic analysis of morphological diversity in the genus *Passiflora* L.

IV.1. A phenetic analysis of morphological diversity in the genus *Passiflora* L.

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IV.1.1. Abstract

Morphological variation was studied in 124 accessions from eight subgenera and 60 species among the most common cultivated and wild species of genus *Passiflora*, using the analysis of variance components and principal component analysis (PCA) on 43 quantitative traits, and *neighbor joining* cluster analysis on 84 qualitative traits. The coefficients of variation appear generally superior for subgenus *Decaloba*, indicating stronger differentiation, as compared with subgenera *Passiflora* and *Tacsonia*. Twenty-four quantitative descriptors showing high variation at the subgenus level, were selected for the PCA. The five principal components retained represent 84% of the total variation. The first one (32%) is closely associated with flower length (hypanthium, nectary chamber, androgynophore) and secondarily with the constriction of the floral cup above the nectary chamber. The second one (27%) is associated with flower width (length of bracts and length of corolla and corona elements) and bract shape. The third one (14%) is associated with peduncle branching, stem width and leaf length, which relates it clearly with variation between subgenus *Astrophea*, and secondarily subgenus *Tryphostemmatoides*, and all other subgenera. The projection of accessions in the resulting tridimensional space consistently separates subgenera. A selection of 32 qualitative traits and four categorized quantitative variables, whose segregation follows divisions among Killip's subgenera, allowed classifying our 60-species sample consistently, using a strictly phenetic approach. Most discriminating characters include size of stems and leaves, presence of tendrils, number and distribution of extrafloral nectaries, dimensions and general shape of bracts, width and length of flowers, corona complexity, ovary shape, and, although they could not be systematically analyzed, fruit size and color. Eight of the nine Killip's subgenera represented in our sample are supported by the morphological analysis, although subgenus *Tryphostemmatoides* is only supported in the quantitative analysis. In a second analysis, 74 qualitative descriptors were incorporated in the cluster analysis, which increased distances and improved bootstrap values, without affecting the general structure of the dendrogram, neither at the subgeneric nor at the interspecific level. Our results support seven of the eight Killip's subgenera of our sample, but no infrasubgeneric classifications. However, the new classification of subgenus *Decaloba* by Feuillet & MacDougal was partly supported. They converge on many points with previous phylogenetic results obtained with DNA sequences, although the latter group subgenera *Tacsonia* and *Distephana* with subgenus *Passiflora*.

Key words: *Passiflora* L, systematics, morphological descriptors, principal components, variation.

IV.1.2. Introduction

With more than 525 species, *Passiflora* L. is the most important genus of the Passifloraceae, a family including nearly 630 species. It is essentially neotropical, with only 22 species native to the Old World, in Southeast Asia, Australia and Oceania. Passionflowers are herbaceous or woody vines, usually climbing by tendrils, but a few are trees or shrubs. Other typical vegetative traits include alternate leaves, axillary stipules, and petiolar and/or laminar nectary glands. In addition, the genus exhibits several unique floral features, such as an androgynophore, a complex corona, constituted of one or several concentric rows of filaments, and a limen-operculum system limiting access to the nectary chamber, with impressive interspecific variation in size, shape and colors (see Figure 3 of Chapter I and Figure 1 of present chapter).

Many species exhibit interesting fruits, pharmacological properties (*e.g.* sedative effect) and/or ornamental potential. More than 80 *Passiflora* species produce an edible fruit, the most interesting ones belonging to subgenera *Passiflora* and *Tacsonia* (Coppens d'Eeckenbrugge, 2003). The two botanicals forms of *P. edulis* Sims, *flavicarpa* Degener (yellow maracuja) and *edulis* (purple maracuja) are by far the most important crops in the family, with a world production estimated at ca. 640.000 tons (http://www.passionfruitjuice.com). Other cultivated passion fruits are *P. tripartita* var. *mollissima* (Kunth) Holm-Nielsen & Jørgensen (curuba de Castilla), *P. tarminiana* Coppens & Barney (curuba India), *P. ligularis* Juss. (sweet granadilla), *P. maliformis* L. (granadilla de piedra), *P. quadrangularis* L. (giant granadilla), *P. popenovii* Killip (granadilla de Quijos), *P. alata* Curtis (fragrant granadilla) and *P. laurifolia* L. (golden apple). These eight species are mainly commercialized on South American local and national markets, principally in Colombia and Brazil, with incursions on the international market. Passion fruits are consumed fresh or processed into juices, sherbets, ice cream, and components of industrial pastry and candies. The most important commercial species are susceptible to a large number of pests and diseases, with considerable negative effects on production. The high potential of *Passiflora* for crop diversification and economic development induced research institutions in the Andean countries to prioritize their characterization and the evaluation of wild and cultivated populations (Debouck & Libreros, 1995), and develop strategies for conservation and improvement of these genetic resources.

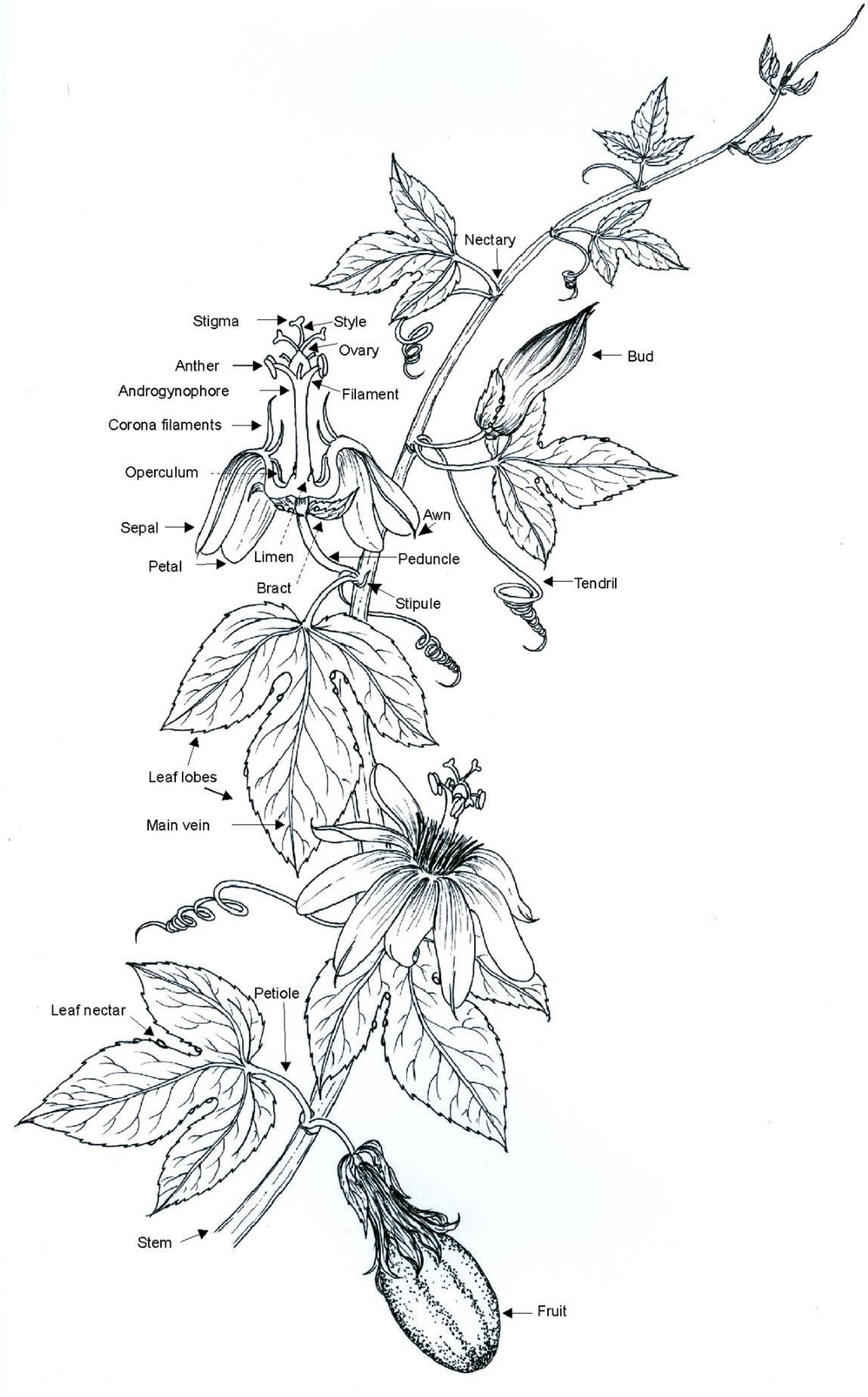

Figure 1. Schema of a flowering branch of *Passiflora vitifolia* Kunth (drawing by Jesus Salcedo).

The high diversity of combinations of characters related to the nectary glands, stipules, corona, operculum and limen (Figure 1 and 2), have been heavily relied upon for delimiting infrageneric divisions in *Passiflora* taxonomy, dividing it into subgenera, sections, and series. Although most species appear well delimited, there are many cases, in low level taxa (sections and series), where two or more species are very difficult to distinguish. The reference work is that of Killip (1938), who described 355 American species, plus 20 species in 1960, placing them in 22 subgenera (Annex 1). This classification was amended and completed with the renaming of several subgenera, the suppression of subgenus *Tacsoniopsis*, and the creation of subgenus *Porphyropathantus* (Escobar, 1988a,b, 1989; McDougal, 1994). In his description of the general Passifloraceae morphology, Killip (1938) underlined the particular contribution of certain organs to taxonomy. Among those of primary importance, he included the peduncle, the bracts (shape and position), the operculum, the presence or absence of petiolar glands and the grooved or reticulate seed surface, the two latter being almost perfectly correlated within subgenus *Decaloba*. He also mentioned habit (vines vs. trees), stipule shape and margin, leaf nervation (subgenus *Astrophea*), shape and arrangement of corona elements, petal absence, and fruit size. However, from the identification keys given by Killip (1938), no clear correlation emerges between main divisions and a particular character hierarchy. The presence of uncinate trichomes on the leaf epidermis was given particular importance by MacDougal (1994) in his revision of section *Pseudodysosmia* of subgenus *Decaloba*, which he defined as the “hooked trichome group”. In the same work, MacDougal mentions the taxonomic importance of the posture of apex in relation to the main shoot axis. However, a cernuous shoot tip is found in parts of subgenera *Decaloba*, *Astrophea*, and *Tacsonia* (Ulmer & MacDougal, 2004), which suggests instead that this trait is not determinant for delimiting subgenera.

Recently, Feuillet & MacDougal (2003; Annex 2) have proposed a new general classification, taking into account the Old World species and recognizing only four subgenera, *Astrophea* (unchanged; trees and shrubs, rarely lianas), *Decaloba* (vines with small flowers and fruits, the latter usually black), *Deidamioides* (vines, with two-flowered peduncles, not clearly defined as a morphological group) and *Passiflora* (vines to lianas, with large flowers and fruits). However, this classification has not been fully developed yet, the placement of most species must be deduced from earlier literature, and its morphological basis is not clear. In the book of Ulmer & MacDougal (2004), where about 200 species are described and assigned a place in the new classification, the revision of *Passiflora* morphology underlines taxonomic importance for shoot apex posture, extrafloral nectaries, bract size and shape, operculum, and seed coats, but only bract and seed traits are specifically mentioned as markers of subgenera, sections, and series. The new classification was presented as the “last premodern” classification, because it does not take into account the results obtained from molecular biology techniques. However, even on strictly morphogical grounds, it lacks the support of a systematic evaluation of morphological diversity in the genus and its subtending structure. The situation is further complicated as many new species have been described during the elaboration of this classification, most often by splitting well-known species on the basis of slight variations from their type, observed in small populations (*e.g. P. miniata* Vanderplank, *P. longicuspis* Vanderplank and *P. aimae* Anonay & Feuillet, from *P. coccinea* Aubl., and *P. formosa* Ulmer, from *P. lanata* Juss.).

On the other hand, the first molecular studies carried out on significant *Passiflora* species samples have consistently validated the three of the four major subdivisions proposed by Feuillet & MacDougal (2003). The results of Muschner et al. (2003; Annex 4a), on nuclear ribosomal internal transcribed spacers, (ITS-1 and ITS-2) and plastid *trn*L-*trn*F intergenic spacer, Yockteng (2003; Annex 4b), on chloroplast *mat*K Yockteng & Nadot (2004; Annex 4c), on chloroplast-expressed glutamine synthetase (ncpGS), and Hansen et al. (2006; Annex 4d), on sequences analysis of the chloroplast (*rpo*C1 and *trn*L-*trn*T), confirm the clear separation of three clades corresponding to the new contours of subgenera *Decaloba*, *Astrophea*, and *Passiflora*. These three major clades correspond to cytogenetic groups, as they appear characterized by chromosome numbers of $2n = 12$, 24, and 18, respectively. The results of Hansen et al. (2006) also support the small subgenus *Deidamioides*, whereas the two species that represent it in the study of Yockteng & Nadot (2004) are split in two widely divergent branches. In addition, the latter study indicated that four other small subgenera, *Dysosmia* (DC.) Killip, *Tryphostemmatoides* (Harms) Killip, *Polyanthea* (DC.) Killip, and *Tetrapathea* (DC.) Rchb., should also be recognized. More general problematic points, in these three genus-wide studies, are the monophyly of genus *Passiflora*, the position of subgenus *Astrophea*, and the low resolution at infrasubgeneric levels, particularly in the *Passiflora* clade, questioning the validity of supersections and series, where many ambiguities and inconsistencies still persist. In fact, such phylogenetic molecular studies cannot give us a definitive answer on the relationship between morphologically ill-defined species and species groups. Actually, if two or more species within a series are only distinguished by the exact number of filament whorls in the corona, the color of one of these whorls, or the number of nectary glands on the petiole, we must first question the discontinuity in the variation described, at both morphological and genetic levels, and assess objectively the morphological basis of the classification.

Despite the impressive morphological diversity described among *Passiflora* species, few studies have compared intra- and intersubgeneric, and intra- and interspecific variation with statistical tools. A first study was conducted by Villacís et al. (1998) on the most common species of subgenera *Tacsonia* and *Manicata*, on Colombian and Ecuadorian accessions. Floral traits were mostly represented in their set of 33 qualitative descriptors, and vegetative traits in the set of 28 quantitative descriptors. The former showed limited intraspecific variation and a consistent picture of interspecific relations, while the latter provided more information on intraspecific variation but a less consistent picture of the differences between species. The descriptor list was corrected, to take into account traits specific to subgenus *Tacsonia*, and augmented to 62 qualitative and 67 quantitative descriptors, giving a better balance between floral and vegetative traits. The sample was also amplified, to include more species and more origins, including similar materials from Venezuela, Colombia, Ecuador, Peru, and Bolivia (Coppens d'Eeckenbrugge et al., 2002). This study showed wide variation at both intra and interspecific levels, with a geographic component in the species best represented, and the overall picture was consistent with results obtained in the same subgenus with biochemical and molecular data (Segura et al., 2002, 2003, 2005). These convergent data led to the formal description of the cultigen *P. tarminiana* Coppens & Barney as a distinct species (Coppens d'Eeckenbrugge et al., 2001). The same descriptor list was used to study morphological variation in the three most common cultivated banana passion fruits and their hybrids, showing maternal effects in the hybrid phenotypes and confirmed the spontaneous introgression occurring between the wild *P. mixta* L. and the cultivated *P. tripartita* var. *mollissima* (Primot et al., 2005). With a descriptor list similar to the one used by Villacís et al. (1998), Medina et al. (2000) evaluated 25 accessions of the subgenera *Passiflora*, *Manicata*, *Tacsonia*, *Dysosmia*, and *Decaloba*. The qualitative descriptors allowed a clear separation between subgenera *Passiflora*, *Tacsonia* and *Decaloba*, with two groups in the latter. *P. foetida*

L. (subg. *Dysosmia*) and *P. manicata* (Juss.) clustered with subgenera *Passiflora* and *Tacsonia* respectively. The quantitative descriptors allowed distinction of subgenera *Tacsonia* and *Manicata*, but showed no structure among species of the three other subgenera. A very detailed descriptor list was also used by Porter-Utley (2003) to study section (Killip) or supersection (Feuillet & MacDougal) *Cieca* of subgenus *Decaloba*, and more particularly the species complex around *P. suberosa* L. and *P. coriacea* Juss. Seventy quantitative traits were measured, 33 to 39 of which could be categorized and gathered with qualitative traits for neighbor joining cluster analyses of the different subsamples. Morphological data appeared consistent with molecular data in confirming monophyly of section/supersection *Cieca*, recognizing *P. tridactylites* Hook. f. and *P. pallida* L. as distinct species, and detecting occasional introgression of the latter with its close relative *P. suberosa*. On the other hand, there was considerable incongruence between molecular (ITS sequences) and morphological phylogenies, which was mostly attributed to smaller sample and intraspecific variation in the molecular data. A Brazilian *Passiflora* collection including ten species was characterized by Crochemore et al. (2003) with 22 qualitative and quantitative descriptors. The results showed clear differentiation between the two botanical forms of *P. edulis*. More recently, De Oliveira et al. (2005) tested a new morphometric method, based on leaf structures in a sample of ten *Passiflora* species. The method was very accurate in correctly differentiating among species, but two species were not consistently classified, *P. foetida*, a problematic species in all classifications, and *P. miersii* Mast. Although its potential must be further assessed on wider samples, the method is very promising for species identification, as it can be applied on sterile specimens. On the other hand, this advantage becomes a limitation for any comparison with classical taxonomy works, where flower structures play an essential role, so this method must be seen as a powerful additional tool. In conclusion, despite the obvious interest of an objective classification in a plant family of such morphological richness and complexity, only a few teams have developed and applied the necessary methodology. Except for the studies targeting specifically subgenus *Tacsonia* or section/supersection *Cieca* of subgenus *Decaloba*, their success has been limited by the size and diversity of their species sample. This limitation is not specific to morphological characterization. However, it tends to be much more severe than in molecular characterization, because of the need of field germplasm collections gathering species with variable climatic adaptations in one or very few places where they can develop until flowering. In the case of wild *Passiflora* accessions, a possible solution is *in situ* characterization, which then must be taken into account to avoid or reduce environmental bias in the analysis.

The present study benefited from projects on diversity of Colombian Passifloraceae, including a component of collecting and establishing germplasm in field collections. As Colombia is the country with the highest *Passiflora* species diversity, both for wild and cultivated materials (Ocampo et al., 2007; Chapter II), a wide species sample could be studied, although practical limitations allowed describing accessions of only 51 species from eight subgenera, out of the 164 reported for the genus in the country. A few non-native species were added, extending the sample to 60 species. We revised the descriptor lists used by Medina et al. (2000) and Coppens d'Eeckenbrugge et al. (2002), aiming at a better description of variation in subgenera other than *Tacsonia* (particularly *Distephana*, *Decaloba*, *Astrophea* and *Tryphostemmatoides*). Our goal was twofold, to test the utility of the revised set of descriptors over a wide range of *Passiflora* species, and to study morphological divergence among subgenera, species and accessions.

IV.1.3. Materials and methods

IV.1.3.1. *Plant materials*

The morphological study was carried out in six experimental stations maintained by several institutions in Colombia (Andes region) (University of Caldas, the coffee grower federation research institute - Cenicafé, CIRAD/IPGRI, Passicol S.A). These germplasm collections were situated in La Italia (Caldas; 1,100 m), Tesorito (Caldas; 2,400 m), Paraguacito (Quindío; 1,250 m), El Moral (Valle del Cauca; 2,200 m), Tenerife (Valle del Cauca; 2,750 m) and El Tambo (Cauca; 1,800 m).

The germplasm sample consisted of 261 individuals, representing 124 accessions and 60 species belonging to the genus *Passiflora* and nine Killip's subgenera (Table 1 and Figure 2). The Colombian accessions were collected by Ocampo et al. (2007) in 2001-2004. Accessions from other countries were obtained from previously established collections. Geographic distribution was taken into account in the selection of accessions of a same species. Narrow endemics (e.g *P. trinervia* (Juss.) Poir.) are represented by one accession, and widespread species (*e.g. P. edulis* f. *flavicarpa*) by one accession per region.

Three plants were grown from seeds for each accession, at a distance of 3 m between rows and 3 to 5 m within rows, according to adult plant size. The taxonomic treatment of Killip (1938), with emends by Escobar (1988a,b, 1989, 1994) and MacDougal (1994) is followed in this text.

P. arborea **Spreng.**
ASTROPHEA

P. coriacea **Juss.**
DECALOBA

P. foetida **L.**
DYSOSMIA

P. vitifolia **Kunth**
DISTEPHANA

P. maliformis **L.**
PASSIFLORA

P. manicata **(Juss.) Pers.**
MANICATA

P. trinervia **(Juss.) Poir.**
PSILANTHUS

P. tarminiana **Coppens & Barney**
TACSONIA

P. arbelaezii **L. Uribe**
TRYPHOSTEMMATOIDES

Figure 2. Variation in shape and color among species from nine of Killip's subgenera.

IV.1.3.2. *Data collection*

The descriptor list (Annex 5) was developed, in various stages, mostly by experts of Bioversity International (formerly IPGRI), CIRAD and CORPOICA. It was adapted to take into account the wide diversity in our collections. It included 43 quantitative and 84 qualitative descriptors, presented synthetically in Table 2. They were assessed on three individuals per accession, and five measures were taken for quantitative characters for each individual. The color characters were recorded with the Royal Colour Chart (Royal Horticultural Society, 2002). Quantitative fruit traits were not taken into account, as they are too often submitted to convergent selection processes, both in the wild and in cultivated species.

IV.1.3.3. *Analyses of quantitative variation*

Shape descriptors were computed as ratios of crude ones. Quantitative data were submitted to an analysis of variance to compare variation among and within subgenera, species, accessions, and individuals. To identify characteristics that mostly contributed to the variation among subgenera, we selected traits for which more than half of the variance was caused by variation at this level. When shape descriptors showed similar discriminating power, they were preferred over crude descriptors, to avoid giving too much importance to size components of variation. The selected descriptor set was submitted to a principal component analysis (PCA), carried out with the *varimax normalized rotation* option using the STATISTICA 6.0 software (Hill & Lewicki, 2006), retaining those factors with an eigenvalue superior to one, and the individuals were projected on the first three PCA axes.

Table 1. List of accessions used in the present study. Taxonomy according to Killip (1938) and emends by Escobar (1988a,b, 1989) and MacDougal (1994).

Subgenus / section / serie / specie	Code	No. ind.	Country	Locality	Status
Subgenus *Astrophea* (DC.) Masters, 1871					
Section *Euastrophea* (Harms.) Killip					
Passiflora arborea Spreng.	arbCA	2	Colombia	Manizales (Caldas)	Wild, edible fruit
Passiflora emarginata Humb. & Bonpl.	emaCA	2	Colombia	Manizales (Caldas)	Wild, edible fruit
	emaVA	2	Colombia	Yotoco (Valle Del Cauca)	Wild
Passiflora sphaerocarpa Triana & Planch.	sphVA	2	Colombia	Cali (Valle Del Cauca)	Wild
Subgenus *Decaloba*(DC.) Rchb., 1828					
Section *Cieca* (Medic.) Mast					
Passiflora coriacea Juss.	corCA	2	Colombia	Palestina (Caldas)	Wild
	corVA	2	Colombia	Cartago (Valle Del Cauca)	Wild
	corVL	2	Colombia	Palmira (Valle Del Cauca)	Wild
	cotTO	2	Colombia	Ibagué (Tolima)	Wild
Passiflora suberosa L.	subAN	2	Colombia	Jerica (Antioquia)	Wild
	subCA	2	Colombia	Manizales (Caldas)	Wild
	subCAL	2	Colombia	Manizales (Caldas)	Wild
	subSA	2	Colombia	Barichara (Santander)	Wild
	subVA	3	Colombia	Palmira (Valle Del Cauca)	Wild
Section *Decaloba* (DC.) Mast					
Series *Auriculatae*					
Passiflora auriculata Kunth	aucCA	2	Colombia	Victoria (Caldas)	Wild
Series *Lutae*					
Passiflora filipes Benth.	filRI	2	Colombia	Pereira (Risaralda)	Wild
Series *Miserae*					
Passiflora misera Kunth	misVA	2	Colombia	Jamundí (Valle Del Cauca)	Wild
Passiflora trifasciata Lemaire	triEC	2	Ecuador	Misahuallí (Napo)	Wild
Series *Punctatae*					
Passiflora alnifolia Kunth	alnCA	2	Colombia	Manizales (Caldas)	Wild

	alnNA	2	Colombia	Chachagui (Nariño)	Wild
	alnSA	2	Colombia	Tona (Santander)	Wild
Passiflora bogotensis Benth.	bogCU	2	Colombia	Bogotá (Cundinamarca)	Wild
Passiflora biflora Lam.	bifCU	2	Colombia	Mariquita (Tolima)	Wild
	bifTO	2	Colombia	La Mesa (Cundinamarca)	Wild
Passiflora cuspidifolia Harms	cusBO	1	Colombia	Duitama (Boyacá)	Wild
Passiflora erythrophylla Mast.	eryBO	2	Colombia	Duitama (Boyacá)	Wild
Passiflora magdalenae Triana & Planch.	magCO	2	Colombia	Victoria (Caldas)	Wild
Series *Sexflorae*					
Passiflora sexflora Juss.	sexQU	2	Colombia	Calarca (Quindío)	Wild
Section *Xerogona* (Raf.) Killip					
Passiflora capsularis L.	capAN	2	Colombia	Jerico (Antioquia)	Wild
	capSA	2	Colombia	Barichara (Santander)	Wild
	capVA	2	Colombia	Cartago (Valle Del Cauca)	Wild
Passiflora rubra L.	rubCA	2	Colombia	Manizales (Caldas)	Wild
	rubQU	2	Colombia	Buenavista (Quindío)	Wild
Section *Pseudodysosmia* (Harms.) Killip					
Passiflora adenopoda Moc. & Sessé *ex* D.C	adeQU	2	Colombia	Buenavista (Quindío)	Wild, edible fruit
	adeTO	2	Colombia	Ibagué (Tolima)	Wild, edible fruit
Section *Hahniopathanthus* (Harms.) Killip					
Passiflora guatemalensis S. Wats.	guaCA	2	Colombia	Filadelfia (Caldas)	Wild
Subgenus *Dysosmia* (DC.) Killip, 1938					
Passiflora foetida var. *gossypiifolia* (Desv.) Mast.	fotCH	2	Colombia	Quibdó (Chocó)	Wild, edible fruit
Passiflora foetida var. *hispida* (DC.) Killip *ex* Gleason	fotTO	3	Colombia	Armero (Tolima)	Wild, edible fruit
Subgenus *Distephana* (Juss.) Killip, 1938					
Passiflora vitifolia Kunth	vitCA	2	Colombia	Victoria (Caldas)	Wild, edible fruit
	vitTO	2	Colombia	Ibagué (Tolima)	Cultivated, edible fruit
Subgenus *Manicata* (Harms) Escobar, 1988					
Passiflora manicata (Juss.) Pers.	manEC	1	Ecuador	Baños (Tungurahua)	Wild
	manSA	2	Colombia	Santander	Wild
	manSA	2	Colombia	Santander	Wild

	manSA	2	Colombia	Santander	Wild
	manVA	1	Colombia	El Cerrito (Valle Del Cauca)	Wild
Subgenus *Passiflora* [= *Granadilla* (Medic.) Mast. 1871]					
Series *Quadrangulares*					
Passiflora alata Curtis	alaBR	3	Brasil		Cultivated, edible fruit
	alaVA	3	Brasil		Cultivated, edible fruit
Passiflora quadrangularis L.	quaHU	3	Colombia	Paicol (Huila)	Cultivated, edible fruit
	quaVA	2	Colombia	Palmira (Valle Del Cauca)	Cultivated, edible fruit
Series *Digitatae*					
Passiflora serratodigitata L.	serrBR	2	Brasil		Wild, edible fruit
Series *Tiliaefoliae*					
Passiflora maliformis L.	malAN	2	Colombia	Fredonia (Antioquia)	Cultivated, edible fruit
	malCA	3	Colombia	Palestina (Caldas)	Wild, edible fruit
	malVA	2	Colombia	Buga (Valle Del Cauca)	Wild, edible fruit
	malQU	2	Colombia	Calarca (Quindio)	Wild, edible fruit
	malHU	2	Colombia	Rivera (Huila)	Cultivated, edible fruit
	malVA	3	Colombia	Tulua (Valle Del Cauca)	Wild, edible fruit
	malVA	1	Colombia	La Unión (Valle Del Cauca)	Wild, edible fruit
	malTO	2	Colombia	Ibagué (Tolima)	Wild, edible fruit
Passiflora ligularis Juss.	ligCA	3	Colombia	Anserma (Caldas)	Cultivated, edible fruit
	ligEC	1	Colombia	Cuenca (Azuay)	Cultivated, edible fruit
	ligQU	3	Colombia	Salento (Quindio)	Wild, edible fruit
	ligRI	1	Colombia	Santa Rosa (Risaralda)	Wild, edible fruit
	ligQU	2	Colombia	Genova (Quindio)	Cultivated, edible fruit
Passiflora serrulata Jacq.	serrMA	2	Colombia	Plato (Magdalena)	Wild, edible fruit
Passiflora tiliifolia L.	tilVA	2	Colombia	El Cerrito (Valle Del Cauca)	Wild, edible fruit
Series *Laurifoliae*					
Passiflora guazumaefolia Juss.	guzMA	2	Colombia	Plato (Magdalena)	Wild, edible fruit
Passiflora nitida Kunth	nitCH	1	Colombia	Quibdó (Chocó)	Cultivated, edible fruit
Passiflora popenovii Killip	popCA	2	Colombia	Timbío (Cauca)	Cultivated, edible fruit
	popNA	2	Colombia	Chachagui (Nariño)	Cultivated, edible fruit
Series S*erratifoliae*					

Passiflora bahiensis Klotzsch	bahBR	3	Brasil	Salvador (Bahia)	Cultivated, Edible fruit
Series *Incarnatae*					
Passiflora cincinnata Mast.	cinBR	3	Brasil		Cultivated, edible fruit
	cinBS	3	Brasil		Cultivated, edible fruit
Passiflora edulis f. *edulis* Sims	edeCA	3	Colombia	Salamina (Caldas)	Cultivated, edible fruit
	edeCAL	2	Colombia	Manizales (Caldas)	Cultivated, edible fruit
	edeCC	2	Colombia	Puracé (Cauca)	Cultivated, edible fruit
	edePE	1	Peru		Cultivated, edible fruit
	edeQU	1	Colombia	Genova (Quindío)	Cultivated, edible fruit
Passiflora edulis f. *flavicarapa* Degener	edf-BR	4	Brasil		Cultivated, edible fruit
	edfCA	3	Colombia	La Unión (Valle Del Cauca)	Cultivated, edible fruit
	edfHU	3	Colombia	Rivera (Huila)	Cultivated, edible fruit
	edfPE	3	Peru		Cultivated, edible fruit
	edfPR	3	Peru		Cultivated, edible fruit
	edfVA	3	Colombia	Anserma (Caldas)	Cultivated, edible fruit
Passiflora incarnata L.	incUS	1	U.S.A	Miami (Florida)	Cultivated, edible fruit
Series *Kermesinae*					
Passiflora lehmanni Mast.	lehQU	2	Colombia	Buenavista (Quindío)	Wild
Passiflora smithii Killip	smiTO	2	Colombia	Ibagué (Tolima)	Wild
Series *Lobatae*					
Passiflora caerulea L.	caeFR	3	France	Montpellier (Herault)	Cultivated, edible fruit
Passiflora subpeltata Ortega	supAN	3	Colombia	Santa Marta (Magdalena)	Wild
Passiflora gibertii N.E. Brown	gibBR	2	Brasil		Wild
Subgenus *Psilanthus* (DC.) Killip, 1938					
Passiflora trinervia (Juss.) Poir.	triCO	2	Colombia	Salento (Quindío)	Wild
Subgenus *Tacsonia* (Juss.) Tr. & Planch, 1873					
Section *Colombiana*					
Series *Leptomischae*					
Passiflora antioquiensis Karst.	ant-AN	2	Colombia	Sta. Rosa Osos (Antioquia)	Wild, edible fruit
	antCA	2	Colombia	Manizales (Caldas)	Wild, edible fruit
Passiflora flexipes Triana & Planch.	fleQU	2	Colombia	Salento (Quindío)	Wild, edible fruit
Passiflora tenerifensis L.K. Escobar	tenVA	2	Colombia	El Cerrito (Valle Del Cauca)	Wild, Edible fruit

	tenVA	1	Colombia	El Cerrito (Valle Del Cauca)	Wild, Edible fruit
Series *Colombianae*					
Passiflora adulterina L.f.	aduBO	2	Colombia	Duitama (Boyacá)	Wild
Passiflora lanata (Juss.) Poir.	lanBO	2	Colombia	Duitama (Boyacá)	Wild
Series *Quindiensae*					
Passiflora linearistipula L.K. Escobar	linCA	2	Colombia	Manizales (Caldas)	Wild
Section *Bracteogama*					
Passiflora cumbalensis var. *cumbalensis* (H. Karst.) Harms	cumEC	2	Ecuador	Tulcán (Carchi)	Wild, edible fruit
	cumNA	1	Colombia	Pasto (Nariño)	Wild, edible fruit
Passiflora luzmarina Jorgensen	luzEC	1	Ecuador	Loja (Loja)	Wild, edible fruit
	luzEC	1	Ecuador	Loja (Loja)	Cultivated, edible fruit
Passiflora tarminiana Coppens & Barney	tarAR	3	Argentina	Castellar	Cultivated, edible fruit
	tarBO	2	Colombia	Boyacá	Cultivated, edible fruit
	tarCC	2	Colombia	Silvia (Cauca)	Cultivated, edible fruit
	tarEC	4	Ecuador	Baños (Tungurahua)	Cultivated, edible fruit
	tarPE	1	Peru		Cultivated, edible fruit
	tarVA	3	Colombia	El Cerrito (Valle Del Cauca)	Cultivated, edible fruit
	tarVE	3	Venezuela	Tachira	Cultivated, edible fruit
Passiflora tripartita var. *mollissima* Holm-Nielsen & Jørgensen	tvmCU	4	Colombia	Cundinamarca	Cultivated, edible fruit
	tvmEC	1	Ecuador	Baños (Tungurahua)	Cultivated, edible fruit
	tvmNA	2	Colombia	Pasto (Nariño)	Cultivated, edible fruit
	tvmPE	1	Peru		Cultivated, edible fruit
	tvmVA	3	Colombia	El Cerrito (Valle Del Cauca)	Cultivated, edible fruit
	tvmVE	1	Venezuela	Tachira	Cultivated, edible fruit
Passiflora tripartita var. *tripartita* Holm-Nielsen & Jørgensen	tvtEC	2	Ecuador	Ambato (Tungurahua)	Wild, Edible fruit
Section *Parritana*					
Passiflora jardinensis L.K. Escobar	jarAN	2	Colombia	Jardin (Antioquia)	Wild
Passiflora paritae (Mast.) L.H Bailey	parTO	2	Colombia	Herveo (Tolima)	Wild, edible fruit
Section *Poggendorffia*					
Passiflora pinnatistipula Cav.	pinBO	1	Colombia	Boyacá	Wild, edible fruit
Passiflora x *rosea* (H.Karst.) Killip	xroBO	1	Ecuador	Tuta (Boyacá)	Wild, Edible fruit
Section *Tacsonia*					
Passiflora mathewsii (Mast.) Killip	matEC	1	Ecuador	Cuenca (Azuay)	Wild

Passiflora mixta L.f.	mixVA	2	Colombia	El Cerrito (Valle Del Cauca)	Wild, edible fruit
	mixVA	3	Colombia	El Cerrito (Valle Del Cauca)	Wild, edible fruit
	mixVA	3	Colombia	El Cerrito (Valle Del Cauca)	Wild, edible fruit
	mixVA	1	Colombia	El Cerrito (Valle Del Cauca)	Wild, edible fruit
	mixVA	1	Colombia	El Cerrito (Valle Del Cauca)	Wild, edible fruit
Subgenus *Trryphostemmatoides* (Harms) Killip, 1938					
Passiflora arbelaezii L. Uribe	arbCH	1	Colombia	Quibdó (Chocó)	Wild
Passiflora gracillima Killip	graQU	1	Colombia	Salento (Quindío)	Wild

IV.1.3.4 *Cluster analyses on qualitative data*

According to the PCA results, certain quantitative variables were selected on the basis of their contribution to the axes, categorized and added to the qualitative dataset, provided that the corresponding information was not yet included in a purely qualitative descriptor. The resulting dataset was treated in two steps. A first set of qualitative variables was selected on the basis of their contribution to differentiation between subgenera, discarding those that show frequent variation at lower levels. A second set included all qualitative descriptors. Both sets were submitted to a neighbor joining cluster analysis (Saitou & Nei, 1987), using the coefficient of dissimilarity of Sokal & Michener and calculating bootstrap values from 100 replicates, with the DARwin 5.2 software (Perrier et al., 2003). This phenetic approach was preferred because of the relatively poor information on morphological evolution in *Passiflora*.

Table 2. List of 127 descriptors used in the morphological characterization study.

Organ	Qualitative characters (84)	Code	Quantitative characters (43)	Code
Stem	Habit	STHA	Diameters	STDI
	Shape	STSH	Internode length	STIN
	Pubescence	STPU		
	Anthocyanin	STAN		
Tendril	Presence	TEPR		
	Shape	TESH		
	Pubescence	TEPU		
	Anthocyanin	TEAN		
Stipule	Presence	SPPR	Length	SPLE
	Permanence	SPPE	Width	SPWI
	Color	SPCO	Terminal arista length	SPTA
	Pubescence	SPPU		
	Shape	SPSH		
	Margin	SPMA		
	Anthocyanin	SPAN		
Petiole	Anthocyanin	PEAN	Length	PELE
	Pubescence	PEPU	Distance from base to first gland	PEDG
	Color	PECO	Nectary number	PENM
	Nectary shape	PENS		
	Nectary stipe	PESN		
Leaf	Heterophylly	LEPO	Margin serration density	LEMS
	Lobe number	LELN	Angle between lateral lobes	LEAB
	Margin	LEMA	Central lobe length	LELC
	Base shape	LEBS	Right lobe length	LERL
	Apex shape	LEAS	Central lobe width	LECL
	Presence of acumen	LEPA	Distance between leaf sinus and petiole insertion	LESS
	Pubescence – adaxial	LEAX	Nectary number on lamina	LELA
	Pubescente – abaxial	LEPB	Nectary number on leaf margin	LENN
	Anthocyanin – lamina	LEAL		
	Anthocyanine – nerves	LEAN		
	Color – adaxial	LECA		
	Heteroblasty	LEPH		
	Presence of laminar nectaries	LENL		

	Distribution of laminar nectaries	LEDN		
	Presence of marginal nectaries	LEPN		
	Distribution of margin nectaries	LELM		
	Nectary shape	LENS		
Peduncle	Pubescence	PDPU	Length	PDLE
	Anthocyanin	PDAN	Diameter	PDDI
	Bifurcation	PDBN	Pedicel length	PDPL
			Length to first bifurcation	PDLF
			Length to second bifurcation	PDBS
Bract	Union	BRUN	Length	BRLE
	Presence	BRPR	Width	BRWI
	Permanence	BRPE		
	Pubescence	BRPU		
	Position of pubescence	BRPP		
	Color	BRCO		
	Anthocyanin	BRAN		
	Shape	BRSH		
	Margin	BRMA		
	Apex shape	BRAS		
	Marginal nectaries	BRNM		
Flower	Corona type	FLCY	Orientation (in degrees to vertical)	FLOG
	Corolla type	FLCT	Petal length	FLPL
	Orientation	FLOR	Petal width	FLPW
	Pubescence on corolla	FLPU	Sepal length	FLSL
	Hypanthium pubescence	FLHP	Sepal width	FLSW
	Dominant petal color	FLCP	Diameter of nectary chamber	FLNC
	Chlorophylla on exterior of sepal	FLCS	Hypanthium diameter above nectary chamber	FLHD
	Keel-shaped sepals	FLKS	Hypanthium diameter -distal	FLHS
	Sepal awn	FLSA	Flower length	FLLE
	Presence of petals	FLPP	Hypanthium length	FLHL
	Union of sepals	FLUS	Length of nectary chamber	FLCN
	Color of filaments at base	FLCB	Number of corona series	FLNS
	Color of filaments at apex	FLCA	Filament length	FLFL
	Distribution of anthers	FLDA	Staminal filaments length	FLSF
	Ovary pubescence	FLOP	Ovary length	FLOL
	Color of ovary	FLCO	Style length	FLSL
	Color of style	FLCS	Gynophore length	FLGL
	Color distribution on styles	FLDS		
	Color of stigmas	FLCG	Androgynophore length	FLAL
	Color of androgynophore	FLCN	Operculum length	FLOP
	Color distribution on androgynophore	FLDN	Limen length	FLLL
	Pubescence of androgynophore	FLPN		
	Limen margin	FLML		
	Nectary chamber ring	FLNR		
	Hypantium type	FLHY		
	Internal color of hypanthium	FLCI		
	Chlorophylla on exterior of hypanthium	FLCE		
	Anthocyanin on exterior of hypanthium	FLAE		
	Nectaries on sepals	FLNS		
	Dominant sepal color	FLCP		
	Anthocyanin on exterior of sepals	FLAP		
Fruit	Type	FRTY		
	Shape	FRSH		

IV.1.4. Results and Discussion

IV.1.4.1. *Quantitative variation*

As expected, a very high variability was observed among the 124 accessions in the field. Table 3 gives the mean values and coefficients of variation for the whole sample and for the different subgenera. Coefficients of variation appear generally superior for subgenus *Decaloba*, as compared with subgenera *Passiflora* and *Tacsonia* that have comparable representation in number of species. This higher relative variation is much more obvious for inflorescences (18 out of 20 traits), and shape ratios (10 out of 13 ratios), of higher taxonomical importance, than for vegetative parts (9 of 21 descriptors), suggesting a higher interspecific differentiation in this subgenus.

Figure 3 shows the relative variance components for 57 quantitative descriptors. All the descriptors present a residual variance under 25% and then a high repeatability. Many descriptors appear to be efficient in discriminating among subgenera. Thus, the proportion of variance at this level exceeds 50% for 26 of them, including stem diameter, leaf margin indentation, leaf length, numbers of nectar glands on leaf margins and petiole, diameter of peduncle, length of first and second order peduncle segments, dimensions and shape of bracts, length of flower, hypanthium, sepals and petals, nectary chamber, crown longest series, androgynophore, stamens and ovary, relative constriction above nectary chamber, and bract/hypanthium length ratio. At the species level, 28 characters are more important. They are related to dimensions of stipule, lobation (angle between lateral nerves, shape of central lobe, length of lateral lobe, distance between leaf sinus and petiole insertion), number of laminar nectary glands, position of petiolar nectary glands, length of peduncle, diameter of hypanthium, length of gynophore, shape of petals and sepals, androgynophore/hypanthium length ratio (defining protrusion of gynoecium and androecium) and pedicel/peduncle ratio. At lower levels, variance between accessions and plants rarely contributes more than 20% of the total.

Table 3. Mean values and coefficients of variation for the whole sample and for the different subgenera.

Factor	Level	*Passiflora*	*Tacsonia*	*Decaloba*	*Astrophea*	*Manicata*	*Dysosmia*	*Distephana*	*Thryphostemmatoides*	*Psilanthus*	Total sample	Organ
Descriptors	*n*	504	340	310	50	35	25	20	10	10	1304	
STEDI	Mean	44.01	30.00	10.81	230.00	30.00	15.00	35.00	5.00	9.60	37.96	**Stem**
	CV	0.15	0.00	0.24	**0.25**	0.00	0.00	0.00	0.00	0.05	1.11	
STIN	Mean	321.40	285.54	98.50	54.67	321.63	40.04	61.30	22.91	50.80	235.09	
	CV	0.55	0.52	**1.05**	0.32	0.31	0.14	0.14	0.10	0.04	0.76	
SPLE	Mean	14.45	8.69	5.34	4.45	11.65	2.70	6.20	0.46	8.70	9.82	
	CV	**0.73**	0.55	0.47	0.16	0.12	0.26	0.17	0.61	0.08	0.83	
SPWI	Mean	5.98	7.48	2.46	2.86	18.64	5.35	1.00	0.25	1.00	5.59	
	CV	1.24	0.87	**1.88**	0.29	0.12	0.10	0.00	0.21	0.00	1.22	
SPTA	Mean	0.13	2.72	0.18	0.00	3.87	6.22	0.00	0.00	0.00	1.03	
	CV	**5.77**	0.94	3.40	-	0.19	0.04	-	-	-	1.96	
LEMS	Mean	4.26	6.81	0.21	0.00	8.63	5.00	6.10	0.00	0.00	3.89	**Leaf**
	CV	0.81	0.29	**3.50**	-	0.06	0.00	0.05	-	-	0.92	
LEAB	Mean	58.09	105.42	80.38	0.00	116.74	92.24	77.90	0.00	33.10	75.40	
	CV	**1.17**	0.40	0.39	-	0.07	0.03	0.10	-	0.08	0.75	
LELC	Mean	120.92	96.95	59.80	247.27	112.82	73.22	115.10	32.11	116.50	103.05	
	CV	0.26	0.21	**0.38**	0.26	0.24	0.04	0.09	0.38	0.01	0.46	
LERL	Mean	51.21	83.91	65.31	0.00	117.99	45.47	96.30	0.00	92.70	63.42	
	CV	**1.06**	0.41	0.35	-	0.27	0.04	0.13	-	0.03	0.72	
LECL	Mean	75.49	37.59	33.50	123.49	52.39	42.16	49.30	22.38	18.70	54.96	
	CV	**0.56**	0.39	0.53	0.31	0.23	0.05	0.11	0.15	0.08	0.69	
LESS	Mean	15.37	21.72	45.76	0.00	41.35	41.05	44.00	0.00	89.40	25.74	
	CV	**1.16**	0.55	0.38	-	0.22	0.08	0.02	-	0.01	0.83	
LELA	Mean	0.00	0.00	4.09	0.00	0.00	0.00	0.00	0.00	6.00	1.02	
	CV	-	-	**1.10**	-	-	-	-	-	0.00	2.79	
LENN	Mean	0.00	0.00	0.00	0.00	0.00	0.00	7.00	0.00	0.00	0.11	
	CV	-	-	-	-	-	-	**0.15**	-	-	8.10	
PELE	Mean	44.24	22.57	25.26	26.20	28.63	21.92	30.85	19.09	24.70	31.99	
	CV	0.58	0.34	**0.69**	0.36	0.21	0.16	0.18	0.14	0.05	0.66	
PEDG	Mean	23.91	9.25	15.25	26.38	7.89	0.00	0.50	19.09	0.00	16.65	
	CV	0.75	0.57	**1.18**	0.37	0.36	-	0.00	0.14	-	0.98	
PENM	Mean	2.90	6.09	0.81	2.00	9.20	0.00	2.00	2.00	0.00	3.27	
	CV	0.58	0.37	**1.22**	0.00	0.29	-	0.00	0.00	-	0.85	
BRLE	Mean	33.91	36.30	2.63	2.10	42.97	20.92	26.70	1.00	8.60	25.31	**Bract**
	CV	0.50	0.29	**1.68**	0.10	0.10	0.11	0.19	0.00	0.10	0.75	
BRWI	Mean	21.50	15.70	1.28	1.30	26.04	16.20	8.70	0.50	2.70	13.93	
	CV	0.47	0.36	**2.73**	0.00	0.09	0.27	0.18	0.00	0.18	0.81	
PDLE	Mean	44.50	86.71	19.74	17.88	65.70	49.39	46.85	23.86	99.30	49.56	**Flower**
	CV	0.45	**1.43**	0.63	0.35	0.25	0.16	0.13	0.10	0.01	1.41	
PDDI	Mean	2.66	2.50	1.51	2.92	2.50	1.50	2.50	0.80	1.11	2.30	
	CV	**0.12**	0.00	0.02	0.11	0.00	0.00	0.00	0.00	0.05	0.24	
PDPL	Mean	8.63	8.93	4.42	13.44	13.70	2.60	4.92	8.24	3.30	7.81	
	CV	0.41	0.40	**0.71**	0.42	0.12	0.00	0.07	0.05	0.15	0.54	
PDLF	Mean	0.00	0.00	0.00	23.30	0.00	0.00	0.00	26.50	0.00	1.10	
	CV	-	-	-	**0.21**	-	-	-	0.06	-	4.64	
PDBS	Mean	0.00	0.00	0.00	23.30	0.00	0.00	0.00	16.50	0.00	1.02	
	CV	-	-	-	**0.21**	-	-	-	0.10	-	4.68	
FLNS	Mean	5.00	1.40	2.00	1.00	5.00	4.20	2.00	2.00	1.00	3.10	
	CV	0.00	0.80	**1.10**	0.00	0.00	0.84	0.00	0.00	0.00	0.91	
FLOG	Mean	114.94	10.99	72.73	135.00	158.00	142.00	110.00	0.00	172.50	73.71	
	CV	0.45	**2.02**	0.96	0.20	0.14	0.23	0.42	-	0.03	0.94	
FLPL	Mean	34.58	44.28	7.98	24.08	42.27	18.90	56.25	13.54	11.20	30.28	
	CV	0.28	0.25	**0.76**	0.19	0.08	0.14	0.06	0.19	0.08	0.55	
FLPW	Mean	10.36	19.39	2.76	8.44	14.65	7.92	13.58	3.56	4.90	10.86	
	CV	0.43	0.23	**0.93**	0.35	0.09	0.13	0.20	0.27	0.06	0.66	
FLSL	Mean	36.15	46.91	14.62	24.47	44.36	19.47	59.60	14.51	39.10	33.51	
	CV	0.26	0.24	**0.38**	0.16	0.08	0.11	0.05	0.29	0.02	0.46	
FLSW	Mean	14.71	18.65	5.62	9.36	14.17	7.22	16.60	5.51	7.00	13.11	
	CV	0.34	0.28	**0.39**	0.27	0.13	0.12	0.07	0.34	0.13	0.50	
FLNC	Mean	13.32	15.07	8.55	7.59	15.85	8.32	13.90	7.10	10.00	12.33	
	CV	0.26	0.17	**0.34**	0.17	0.09	0.05	0.13	0.14	0.08	0.32	
FLHD	Mean	13.04	10.21	8.73	7.55	10.93	8.40	11.90	6.81	8.70	10.82	
	CV	0.30	0.23	**0.36**	0.17	0.07	0.05	0.15	0.14	0.06	0.34	
DHS	Mean	17.39	12.00	9.59	8.28	14.64	8.40	12.75	6.81	7.50	13.30	
	CV	0.29	0.21	**0.36**	0.21	0.11	0.05	0.06	0.14	0.07	0.39	
FLHS	Mean	27.00	103.36	11.52	23.24	42.44	12.88	55.75	8.30	162.00	44.56	
	CV	0.23	0.17	**0.31**	0.18	0.07	0.08	0.07	0.11	0.02	0.88	
FLLE	Mean	11.97	71.01	6.32	5.82	13.03	8.35	12.07	4.96	112.90	26.47	
	CV	0.31	0.28	**2.29**	0.25	0.24	0.10	0.09	0.16	0.02	1.16	
FLCN	Mean	5.56	10.17	3.64	4.92	8.58	2.48	6.10	3.80	29.30	6.48	
	CV	0.32	0.25	**0.34**	0.11	0.08	0.06	0.26	0.18	0.07	0.57	
FLFL	Mean	35.39	2.10	7.68	13.39	5.82	11.20	24.10	5.83	2.90	17.37	
	CV	0.44	**0.80**	0.40	0.19	0.23	0.33	0.05	0.11	0.25	1.02	
FLSF	Mean	11.08	14.86	4.26	6.36	12.19	4.60	14.20	2.46	8.30	10.13	
	CV	0.25	0.32	**0.34**	0.14	0.12	0.13	0.12	0.15	0.06	0.50	
FLOL	Mean	8.30	11.60	3.45	4.98	8.20	3.71	10.76	2.85	11.90	7.81	
	CV	0.30	0.17	**0.40**	0.14	0.10	0.20	0.06	0.07	0.06	0.47	
FLSL	Mean	11.11	13.61	4.62	6.76	12.14	6.44	13.20	3.63	5.10	9.92	
	CV	0.25	0.24	0.31	**0.33**	0.12	0.09	0.06	0.07	0.14	0.43	
FLGL	Mean	1.91	4.37	0.93	1.00	2.70	1.00	2.72	0.51	9.20	2.34	
	CV	0.58	**0.67**	0.26	0.00	0.19	0.02	0.09	0.06	0.11	0.94	
FLAL	Mean	11.36	82.69	6.25	12.40	29.11	8.46	42.08	4.86	150.50	30.69	
	CV	0.29	0.21	**0.36**	0.30	0.09	0.11	0.08	0.04	0.01	1.14	
FLOP	Mean	2.75	6.61	2.12	1.84	10.37	2.32	10.00	0.84	4.20	3.88	
	CV	0.46	0.24	**0.49**	0.17	0.08	0.07	0.06	0.06	0.10	0.67	
FLLL	Mean	1.65	1.53	0.87	0.60	1.25	1.40	3.55	0.65	0.00	1.38	
	CV	0.64	0.36	**0.70**	0.34	0.16	0.07	0.14	0.08	-	0.65	
PEDG/PELE	Mean	0.56	0.41	0.60	1.01	0.28	0.00	0.02	1.00	0.00	0.52	**Shape relation**
	CV	0.53	0.45	**0.67**	0.03	0.32	-	0.22	0.00	-	0.64	
LECL/LELC	Mean	0.59	0.39	0.58	0.50	0.47	0.58	0.43	0.76	0.16	0.52	
	CV	0.37	0.30	**0.44**	0.12	0.14	0.04	0.11	0.26	0.08	0.42	
BRWI/BRLE	Mean	0.64	0.43	0.18	0.62	0.61	0.78	0.34	0.50	0.32	0.47	
	CV	0.22	0.25	**1.41**	0.07	0.07	0.28	0.32	0.00	0.24	0.53	
FLPW/FLPL	Mean	0.30	0.44	0.24	0.34	0.35	0.42	0.24	0.26	0.44	0.33	
	CV	0.24	0.16	**0.82**	0.23	0.10	0.08	0.14	0.16	0.11	0.42	
FLSW/FLSL	Mean	0.41	0.41	0.42	0.38	0.32	0.37	0.28	0.38	0.18	0.40	
	CV	0.24	0.23	**0.38**	0.25	0.16	0.09	0.11	0.17	0.13	0.28	
FLNC/FLHD	Mean	1.04	1.53	0.99	1.01	1.46	0.99	1.17	1.05	1.16	1.17	
	CV	0.13	**0.23**	0.08	0.03	0.10	0.03	0.05	0.13	0.14	0.26	
FLLE/FLHL	Mean	2.33	1.54	5.85	4.25	3.42	1.56	4.64	1.70	1.44	3.07	
	CV	0.21	0.26	**0.71**	0.30	0.21	0.17	0.08	0.16	0.03	0.87	
FLCN/FLHL	Mean	0.47	0.15	1.89	0.89	0.69	0.30	0.50	0.77	0.26	0.74	
	CV	0.22	0.34	**0.78**	0.24	0.22	0.10	0.22	0.12	0.08	1.32	
FLAL/FLHL	Mean	1.01	1.23	3.36	2.21	2.35	1.03	3.50	1.00	1.33	1.75	
	CV	0.35	0.32	**0.79**	0.31	0.24	0.19	0.08	0.12	0.02	0.95	
PDDI/PDPL	Mean	0.08	0.08	0.11	0.18	0.04	0.03	0.05	0.03	0.01	0.09	
	CV	**0.77**	0.70	0.65	0.25	0.27	0.16	0.13	0.11	0.05	0.75	
PDPL/PDLE	Mean	0.23	0.29	0.40	0.76	0.22	0.05	0.11	0.35	0.03	0.30	
	CV	0.63	0.77	**1.36**	0.43	0.27	0.16	0.15	0.10	0.15	1.10	
BRLE/FLHL	Mean	2.89	0.54	0.92	0.38	3.52	2.55	2.25	0.21	0.08	1.67	
	CV	0.47	0.39	**1.28**	0.21	0.28	0.22	0.27	0.15	0.10	0.92	
FLGL/FLAL	Mean	0.18	0.06	0.17	0.09	0.09	0.12	0.06	0.11	0.06	0.14	
	CV	0.68	**1.49**	0.41	0.39	0.23	0.12	0.06	0.08	0.12	0.80	
LECL/LECL	Mean	0.58	0.39	0.59	0.76	0.50	0.58	0.47	0.16	0.43	0.52	
	CV	0.44	0.30	**0.37**	0.26	0.12	0.04	0.14	0.08	0.11	0.42	

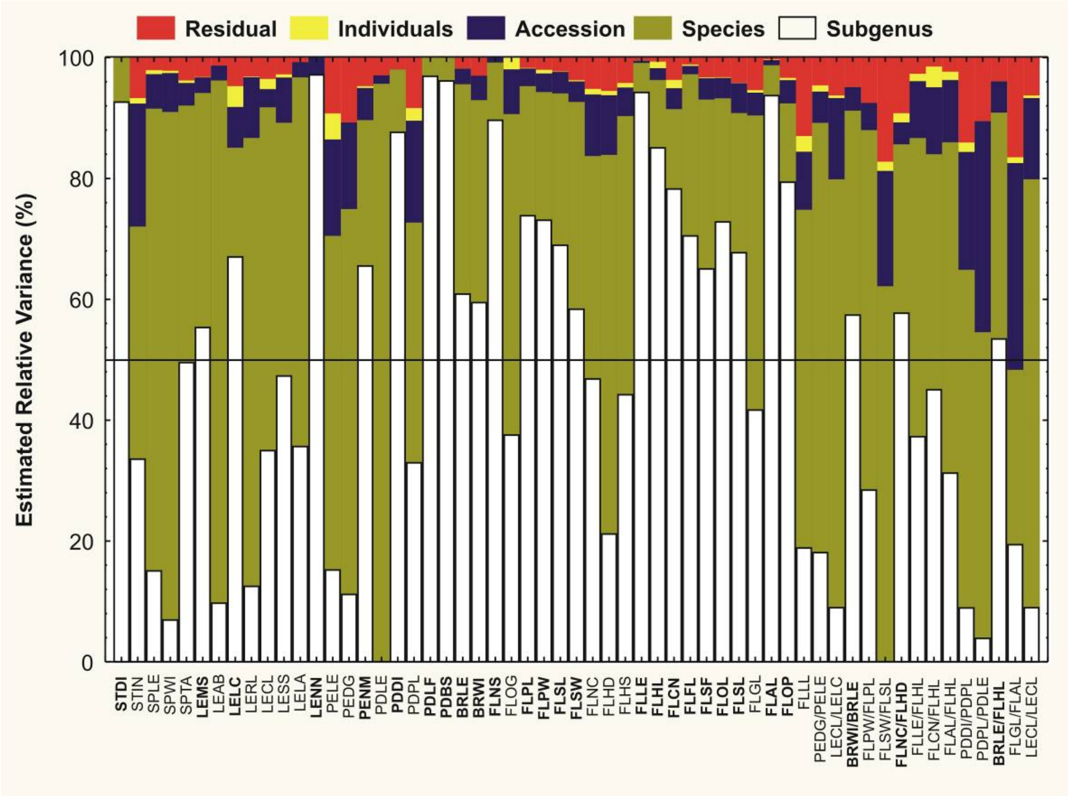

Figure 3. Relative variance components for 57 quantitative descriptors. Bold characters are used for traits displaying more than 50% of variance among subgenera.

IV.1.4.2. *Correlations and principal components analysis (PCA)*

A Pearson correlation (*r*) matrix shows high coefficients, between 0.71 and 0.97, among dimensions of certain floral components, such as petals and sepals, hypanthium, nectary chamber, operculum, androgynophore, stamens and ovary. The length of the corona is correlated with the upper hypanthium diameter (*r* = 0.75). Bract dimensions are moderately correlated with these traits (0.33 to 0.65, but 0.75 with ovary length). Stem diameter is correlated with peduncle branching (*r* = 0.73), which is due to the association of these traits in representatives of subgenus *Astrophea*.

From the 26 quantitative descriptors showing high variation at the subgenus level, 24 were selected for the PCA, discarding two of them to avoid redundancy between shape ratios and the original traits. Five principal components were retained, that represent 84% of total variation (Table 4). The first one (32%) is very clearly associated with flower length (hypanthium, nectary chamber, androgynophore) and secondarily with the constriction of the floral cup above the nectary chamber. The second one (27%) is associated with flower width (length of bracts and length of corolla and corona elements) and bract shape. The third one (14%) is associated with peduncle branching, stem width and leaf length, which relates it clearly with variation between subgenus *Astrophea*, and secondarily subgenus *Tryphostemmatoides*, and all other subgenera. The fourth one (5%) is associated with the number of nectaries on leaf margin, which essentially relates it to the differentiation of subgenus *Distephana*. The last one (5%) is correlated only with leaf serration.

Figure 4 presents the accessions in the three first axes, showing a clear grouping by subgenus. The representatives of subgenus *Tacsonia* are placed on the right along the first axis, in relation to their long and wide flowers. A few accessions, with shorter flowers (*P. luzmarina* Jørgensen and *P. pinnatistipula* Cav.), appear closer to the origin of this axis, together with *P. manicata* individuals. *P. trinervia*, of subgenus *Psilanthus*, is placed even further on the right, thanks to its very long floral tube, however it is clearly separated on the second axis by its much narrower flowers and minute setaceous bracts. On the left side, subgenera *Passiflora* and *Decaloba* are not differentiated by the flower length axis, but by the second, flower width related, axis. At the extremes of this second axis, we find the accessions of the large-flowered *P. alata* Curtis and *P. quadrangularis* (section *Quadrangulares* of subgenus *Passiflora*), on one side, and those of the small-flowered *P. arbelaezii* and *P. gracillima* Killip of subgenus *Tryphostemmatoides*, on the other side. As expected, the third axis clearly differentiates subgenera *Astrophea* and *Tryphostemmatoides*. On the whole, subgenera *Passiflora*, *Tacsonia*, *Decaloba*, *Psilanthus*, *Astrophea* and *Tryphostemmatoides* are clearly separated in the main tridimensional space. As expected, *P. manicata* (subgenus *Manicata*) takes an intermediate position between subgenera *Passiflora* and *Tacsonia*. This species not only combines morphological traits typical of both subgenera, but intermediate ecoclimatic requirements as well, as it may be found at lower elevations than *tacsos*, but higher elevations than representatives of subgenus *Passiflora*. The representatives of subgenus *Tacsonia* that come closest to *P. manicata* are *P. pinnatistipula* and *P. luzmarina*, two tacsos with relatively shorter floral tubes. The former is also differentiated by a filamentous corona, instead of the typical reduced *tacso* coronas. Another species taking a particular position is *P. foetida*, of Killip's subgenus *Dysosmia*, placed near both subgenera *Passiflora* and *Decaloba*, but closer to the former. Subgenus *Dysosmia* is considered a supersection of subgenus *Passiflora* in the Feuillet & MacDougal classification.

Table 4. Factor loadings from principal component analysis (*varimax normalized rotation*) on 24 quantitative descriptors.

	Principal components				
Descriptors	**1**	**2**	**3**	**4**	**5**
STDI	-0.088	0.215	**-0.892**	-0.023	0.041
LEMS	0.353	0.365	0.152	0.041	**0.759**
LELC	0.019	0.571	-0.686	0.009	-0.195
LENN	-0.017	0.040	0.011	**0.962**	0.014
PENM	0.648	0.407	0.013	-0.055	0.158
PDDI	0.135	**0.847**	-0.287	0.010	0.145
PDLF	-0.054	-0.136	**-0.943**	-0.007	-0.044
PDBS	-0.054	-0.113	**-0.973**	-0.006	-0.046
BRLR	0.296	**0.723**	0.186	-0.091	0.240
FLPL	0.501	**0.774**	-0.021	0.235	0.042
FLPW	**0.713**	0.595	-0.024	0.095	0.028
FLSL	0.577	**0.716**	0.036	0.243	-0.028
FLSW	0.520	**0.754**	0.034	0.074	-0.108
FLLE	**0.960**	0.179	0.045	0.017	0.090
FLHL	**0.904**	0.063	0.086	-0.100	0.119
FLCN	**0.824**	0.208	0.026	-0.080	-0.137
FLFL	-0.521	**0.723**	0.034	-0.007	-0.329
FLSF	0.529	0.651	0.082	0.097	0.171
FLOL	0.677	0.658	0.076	0.061	-0.049
FLSL	0.454	0.693	0.067	0.073	0.263
FLAL	**0.964**	0.064	0.047	0.033	0.099
FLOP	**0.711**	0.236	0.099	0.363	0.214
BRWI/BRLE	-0.160	**0.718**	-0.221	-0.131	0.241
FLNC/FLHD	**0.700**	0.056	0.042	0.043	0.368
Expl.Var	7.610	6.496	3.336	1.256	1.238
Prp.Totl	0.317	0.271	0.139	0.052	0.052

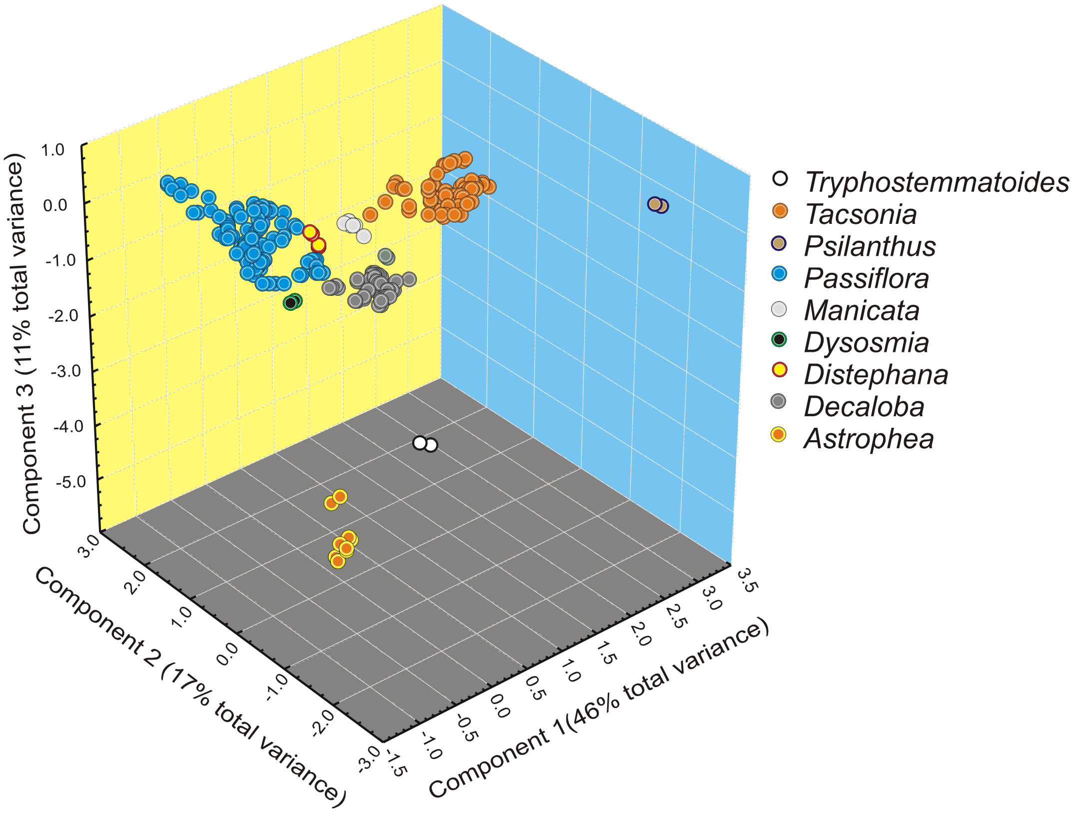

Figure 4. Tridimensional plot of the scores of *Passiflora* accessions for the first three components of quantitative variation. Colors refer to subgeneric classification.

IV.1.4.3. *Qualitative variation among and within subgenera*

Our first attempt to reduce the number of qualitative descriptors led us to retain 32 of them on the basis of their potential to discriminate among subgenera. The criterion was that the descriptor appears monomorphic or shows a highly dominant condition at least in one subgenus, while polymorphic among subgenera. Four quantitative descriptors were categorized and added because of their high correlations with the principal components of quantitative variation. Thus the first component was represented by androgynophore length, the second one by sepal length, the third one by stem diameter and leaf length. The fourth and fifth ones were not included to avoid redundancy with very similar qualitative descriptors. Table 5 synthesizes the observations for these descriptors. The species of subgenus *Astrophea* exhibit the highest number of unique/rare traits, including tree habit, wide stems of irregular section, very long leaves, absence of tendrils, short triangular stipules, dorsal scar-like nectaries (appressed against or near petiole), branched peduncles, bright-yellow sickle-sword-shaped corona filaments, and tricostate ovaries. Unique and rare traits of the two species of subgenus

Tryphostemmatoides include peduncle branching (shared with species of subgenus *Astrophea* and *P. sexflora* Juss. of subgenus *Decaloba*), the presence of tendrils at the axil of the peduncles, and the retuse leaf apex (unique in our sample, although this trait can be observed in individuals of *P. emarginata* Humb. & Bonpl.). *P. vitifolia* Kunth (subgenus *Distephana*) is differentiated by its tubular corona, formed by the partial fusion of its elements and conspicuous nectary glands on leaf sinus and bracts, *P. foetida* (subgenus *Dysosmia*) only by its pinnatisect bracts, and *P. trinervia* (subgenus *Psilanthus*) by the absence of a limen. Most of these traits are typical for each of these subgenera, ensuring that they will not bias the cluster analysis in terms of subgeneric classification. Subgenera *Decaloba*, *Passiflora*, *Tacsonia* and *Manicata* do not show unique traits, however they can be separated by clear segregations in non-exclusive traits. Thus, in subgenus *Decaloba*, the presence of nectary glands in the lamina is only shared with subgenus *Psilanthus*, the flat hypanthium with subgenus *Tryphostemmatoides*, the relatively small flower size with subgenera *Astrophea*, *Dysosmia*, and *Tryphostemmatoides*. On the other side, subgenera *Passiflora*, *Distephana*, *Manicata* and *Tacsonia* share wide flowers and the general presence of petiolar nectaries. The last three and subgenus *Psilanthus* also share large red or pink corollas and long tubular flowers (long androgynophores), typical of hummingbird-pollinated species. Floral tube length reaches extreme values in *Psilanthus* and *Tacsonia*, with the exceptions of *P. pinnatistipula* and *P. luzmarina*, in relation to their specific pollinator *Ensifera ensifera* Boissoneau, the sword-billed hummingbird. In addition they present reduced coronas of short filaments or tubercles, generally in one row only, while two-row coronas are most common in subgenera *Decaloba*, *Tryphostemmatoides*, *Astrophea*, and *Distephana*, and highly complex coronas (more than three rows) are typical in subgenera *Passiflora*, *Manicata* and *Dysosmia*. Bracts are foliaceous in subgenera *Passiflora* and *Tacsonia*. Fruit shape is generally globose to short ovate in subgenera *Astrophea*, *Decaloba*, *Tryphostemmatoides*, *Dysosmia*, *Passiflora* and *Distephana*, and oval to fusiform in subgenera *Tacsonia*, *Manicata*, and *Psilanthus*. Fruit color would also be interesting, with a particular frequency of blackish fruits in subgenus *Decaloba*, however this descriptor could not be observed in all species.

Table 5. Variation for 32 qualitative and four categorized quantitative descriptors in the different subgenera sampled.

Feuillet & MacDougal (2003)	***Astrophea***	***Decaloba***		***Passiflora***					***Deidamioides***
Killip (1938), Escobar (1988), MacDougal (1994)	***Astrophea***	***Decaloba***	***Psilanthus***	***Passiflora***	***Distephana***	***Dysosmia***	***Tacsonia***	***Manicata***	***Tryphostemmatoides***
Species/accession number	n= 3/4	n= 17/31	n= 1/1	n= 19/44	n= 1/2	n= 1/2	n= 16/36	n= 1/1	n= 2/2
Main pollinators	medium (honey) bees	small to large bees - wasps	sword-billed hummingbird	large (carpenter) bees	hummingbirds	bees	sword-billed hummingbird	hummingbirds	bees
Chromosome number	2*n* = 24	2*n* = 12, 22, 24, 36	2*n* = 12	2*n* = 18	2*n* = 18	2*n* = 18, 20, 22	2*n* = 18	2*n* = 18	2*n* = 12
Altitudinal range	1.000 - 2.200 m	60 - 2.700 m	2.600 - 3.200	20 - 2.400 m	50 - 1.200 m	30 - 1.200 m	2.100 - 3.700 m	1.900 - 2.500 m	50 - 2.000 m
Descriptors									
Habit	tree	vine	vine	vine	vine	vine	vine	vine	vine
Stem section	irregular	terete/angular	angular	terete/angular/winged	terete	terete	terete/angular	angular	terete
Secondery xylema	present	absent	absent	absent	absent	absent	absent	absent	absent
Tendril position	absent	axillary	axillary	axillary	axillary	axillary	axillary	axillary	axillary and peduncle
Stipule	short triangular	setaceous/linear/foliaceous-aristate	setaceous	setaceous/linear/foliaceous-aristate	linear	foliaceous-aristate	setaceous/linear/foliaceous-aristate	foliaceous-aristate	setaceous
Stipule nectaries (conspicuous)	absent	absent	absent	absent/present (*P. maliformis*)	present	present	absent	absent	absent
Leaf lobation	one	three	three	one/three/more	three	three	one/three	three	one
Leaf base	cuneate-rounded	cuneate-rounded/cordate/ peltate (*P. coriacea* and *P. guatemalensis*)	cordate	cuneate-rounded/cordate	cordate	cordate	cuneate-rounded/cordate	cordate	rounded
Leaf apex	obtuse/acute	rounded/obtuse/acute	acute/very acute	rounded to very acute	acute	acute	acute/very acute	obtuse to very acute	retuse
Leaf margin	entire	entire/serrate (*P. adenopoda*)	entire	entire/serrate	serrate	serrate	serrate	serrate	entire
Laminar nectaries	absent	present/absent (five species)b	present	absent	absent	absent	absent	absent	absent
Leaf margin nectaries (conspicuous)	absent	absent/sinus/ all margin (*P. adenopoda*)	absent	absent/sinus lateral lobe (*P. edulis* f. *edulis*)	sinus	absent	absent/sinus (*P. jardinensis*)	absent	leaf base
Petiolar nectaries	absent	absent/orbicular (*P. adenopoda*)/ cylindrical (*P. coriaceae* and *P. suberosa*) /auriculate (*P. auriculata*)	absent	all except auriculate	orbicular	absent	linear/orbicular	linear	absent
Dorsal nectaries	present	absent	absent	absent	absent	absent	absent	absent	absent
Peduncle branching	present	absent/present (*P. sexflora*)	absent	absent	absent	absent	absent	absent	present
Bract shape	linear	setaceous/linear/ foliaceous (*P. adenopoda* , *P. guatemalensis*) /absent (four species)*	linear	foliaceous	linear	pinnatisect	foliaceous	foliaceous	linear
Nectary on bract	absent	absent	absent	absent/present	present	absent	absent	absent	absent
Flower orientation	erect	erect/intermediate/pendular	pendular	erect/intermediate/pendular	erect	erect	erect/intermediate/pendular	erect	erect
Corolla shape	reflex	intermediate/campanulate	campanulate	intermediate/reflex	reflex	intermediate/reflex	campanulate/intermediate/reflex	reflex	reflex
Dominant corolla color	white	white	red (pink)	white/red	red	white	red (including pink or orange)	red	white
Corona type	filamentous	filamentous	filamentous	filamentous	filamentous	filamentous	tuberculous/	filamentous	filamentous
Corona filaments	sickle-sword-shaped free	linear free	linear free	linear free	linear fused at base	linear free	filamentous, linear free	linear free	linear free
Number of corona series	uniseriate	biseriate/ uniseriate (*P. guatemalensis* and *P. adenopoda*)/ triseriate (*P. filipes* and *P. magadalenae*)	uniseriate	pentaseriate	biseriate	3- to 5-seriate	uni- to 5-seriate	pentaseriate	biseriate
Corona color-clear (longest row)	white		white	white	red	white	white/purple	purple	white
Corona color-darkest (longest row)	yellow	white/purple/ yellow (*P. guatemalensis*)	white	purple white (*P. guazumaefolia*)	red	purple	purple white (*P. jardinensis*)	purple	white
Petals	present	present/ absent (*P. coriaceae* and *P. suberosa*)	present	present	present	present	present	present	present
Sepal awn	absent	absent/present	absent	present	present	present	present	present	absent
Nectar chamber ring	present	absent	absent	present	present	present	present	present	absent
Hypanthium	campanulate	flat	tubular	campalunate	tubular	campanulate	tubular	tubular	flat
Limen	present	present	absent	present	present	present	present	present	present
Ovary shape	tricostate	globose	globose	globose	globose	globose	globose	globose	globose
Fruit shape	globose	globose/ elongate (*P. rubra* and *P. capsularis*)	elongate	globose/ elongate (*P. quadrangularis*)	globose	globose	elongate/ globose (*P. pinnatistipula*)	elongate	globose
Categorized (from quantitatives traits)									
Stem diameter	≥ 120 mm	≤ 20 mm	≤ 20 mm	≥ 30 mm < 60 mm	≥ 30 mm < 60 mm	≤ 20 mm	≥ 30 mm < 60 mm	≥ 30 mm < 60 mm	≤ 20 mm
Leaf length	> 215 mm < 190 mm (*P. sphaerocarpa*)	< 190 mm	< 190 mm	< 190 mm	< 190 mm	< 190 mm	< 190 mm	< 190 mm	< 190 mm
Sepal length	≤ 30 mm	≤ 30 mm	> 30 mm	> 30 mm ≤ 30 mm (six species)^a	> 30 mm	≤ 30 mm	> 30 mm ≤ 30 mm (*P. luzmarina* and *P. mathewsii*)	> 30 mm	≤ 30 mm
Androgynophore length	< 23 mm	< 23 mm	> 25 mm	< 23 mm	> 25 mm	< 23 mm	> 25 mm	> 25 mm	< 23 mm

P. capsularis^b*, *P. coriacea**, *P. rubra*^{b}*, *P. suberosa*^{b}*, *P. sexflora*^{b}, *P. guatemelensis*^{b}, *P. bahiensis*^{a}, *P. edulis* f. *edulis*^{a}, *P. guazumaefolia*^{a}, *P. smithii*^{a}, *P. subpeltata*^{a}, *P. serrulata*^{a}.

Certain species show unusual trait combinations in their subgenus. This is particularly true in subgenus *Decaloba*. Thus, *P. adenopoda* Moc. & Sessé *ex* DC. shows foliaceous bracts, serrate leaf margins, with conspicuous nectary glands, orbicular petiolar glands, and an uniseriate corona. *P. guatemalensis* S. Watson also shows foliaceous bracts and glandless leaves, plus peltate leaves and a yellow uniseriate corona. *P. sexflora* shows multiple peduncles. *P. coriacea*, *P. suberosa*, *P. capsularis* L. and *P. rubra* L. lack bracts; in addition, the first two present petiolar nectaries, while the last two lack such glands in all their parts and produce an elongate fruit.

IV.1.4.4. *Cluster analysis on the reduced descriptor list*

Figure 5 presents the dendrogram obtained from these observations on the first set of descriptors. The four best-represented subgenera, *Passiflora*, *Tacsonia*, *Astrophea*, and *Decaloba*, are supported by the analysis. Their placement on the dendrogram shows a polarization of the latter according to several traits. On one side, we find subgenera *Passiflora*, *Distephana*, *Tacsonia*, and *Manicata*, i.e. species producing large flowers and fruits and very generally bearing petiolar nectaries, with a base chromosome number of n = 9. They also share foliaceous bracts, with the relative exception of *P. vitifolia*, whose long bracts appear linear. They are further divided between the carpenter bee-pollinated species (subgenus *Passiflora*) and the hummingbird-pollinated species of subgenus *Tacsonia*, *P. vitifolia*, and *P. manicata*. The consistency of this subclassification compensates for the low associated bootstrap values. The placement of *P. manicata* in the *Tacsonia* cluster supports the gathering of the Andean subgenera *Tacsonia* and *Manicata* in a same infrageneric taxon, as in the classification of Feuillet & MacDougal (2003). On the other hand, *P. vitifolia* is a good representative of the uniform subgenus *Distephana*, so its position does not support its downgrading to a supersection of subgenus *Passiflora*, also proposed by these authors. On the other side of the tree, we find subgenera whose species produce small to medium flowers and fruits, with relatively simple coronas of generally two rows of filaments (rarely one or three), where petiolar nectaries are rare, with a base chromosome number of 12 for tree species and 6 for the others. As could be expected from the number of their rare traits, the subgenus *Astrophea* species of our sample appear very uniform, and well separated in a very distant cluster. *P. trinervia* (subgenus *Psilanthus*) is placed on another long branch, inserted at the same position. A third, much larger, cluster is constituted by all the species of subgenera *Tryphostemmatoides* and *Decaloba*, but *P. adenopoda*. This species is placed on a well-separated branch, inserted in an intermediate position between the *Passiflora-Distephana-Tacsonia-Manicata* clusters and the *Astrophea-Decaloba-Tryphostemmatoides* clusters. Although the branch bearing the representatives of subgenus *Tryphostemmatoides*, *P. gracillima* and *P. arbelaezii*, is relatively long, it is clearly inserted within subgenus *Decaloba*, suggesting that the qualitative morphological differentiation of subgenus *Tryphostemmatoides* is fragile, which is consistent with the very low number of traits supporting it (Table 5), but contrasting with the PCA results on quantitative traits. The position of *P. adenopoda* may look surprising, as it is not consistent with either classification (*Decaloba* section *Pseudosysosmia* for Killip, supersection *Bryonioides* for Feuillet & MacDougal), however, this species showed several unusual features as compared to *Decaloba* as a group. *P. foetida* (subgenus *Dysosmia*), takes a very similar position, that is clearly more consistent with its classification in subgenus *Dysosmia* by Killip (1938) than with its inclusion in subgenus *Passiflora* by Feuillet & MacDougal (2003). Interestingly, these two problematic species materialize the separation between the two cytogenetic groups in our tree. Indeed, chromosome counts for *P. adenopoda* give $2n = 12$ (MacDougal, 1994), as in most species of subgenus *Decaloba*, while those for *P. foetida* vary between $2n = 18$, 20, and 22 (Yockteng & Nadot, 2004; De Melo et al., 2001). According to de Melo et al. (2001) and De Melo & Guerra (2003), *P. foetida* appears cytologically quite isolated, but closer to the $n = 9$ group, its smaller chromosomes and areticulate interphase nuclei being similar to species with $n = 6$, while its chromosome number, higher karyotype symmetry, CMA staining properties, and the number of 45S rDNA sites make it similar to species of subgenus *Passiflora*.

The first set of qualitative data also allows distinguishing some structure within clusters corresponding to subgenera. Thus, within the *Passiflora* cluster, one main branch corresponds to *P. edulis* f. *edulis* and medium-flowered species as *P. bahiensis* Kl. and *P. guazumaefolia* Juss., one to large-flowered species of series *Incarnatae*, i.e. *P. edulis* f. *flavicarpa*, *P. incarnata*, and *P. cincinnata* Mast., one to series *Quadrangulares* and the most typical representatives of series *Tiliifoliae*, one to typical representatives of series *Laurifoliae*, one to accessions of *P. maliformis*, and one to species of series *Kermesinae*. Series *Lobatae* is shared between the *Incarnatae* subcluster (including *P. caerulea* L. and *P. gibertii* Brown) and the *Kermesinae* subcluster (*P. subpeltata* Ortega), which shows the fragility of these subclusters, as *P. gibertii* and *P. subpeltata* are morphologically very similar. Within the *Tacsonia-Manicata* cluster, there are three main branches. A first one includes the common and widely dispersed *P. mixta*, *P. tripartita*, *P. tarminiana*, *P. cumbalensis* and endemic species related to one of them, as *P. mathewsii* (Mast.) Killip and *P. luzmarina*. A second one includes species of Section *Colombiana*, plus two accessions of *P. tripartita* var. *mollissima*, and the last one includes the relatively short-tubed species *P. pinnatistipula* and *P. manicata*. Within the *Decaloba-Tryphostemmatoides* cluster, one branch corresponds to section *Cieca* (*P. coriacea* and *P. suberosa*) and one to section *Xerogona* (*P. capsularis* and *P. rubra*). *P. guatemalensis*, the only representative of section *Hahniopathantus*, is placed apart. Section *Decaloba* is split between three distinct branches, one for the closely related *P. alnifolia* Kunth and *P. bogotensis* Benth., one for *P. auriculata* Kunth, and one for all its other representatives.

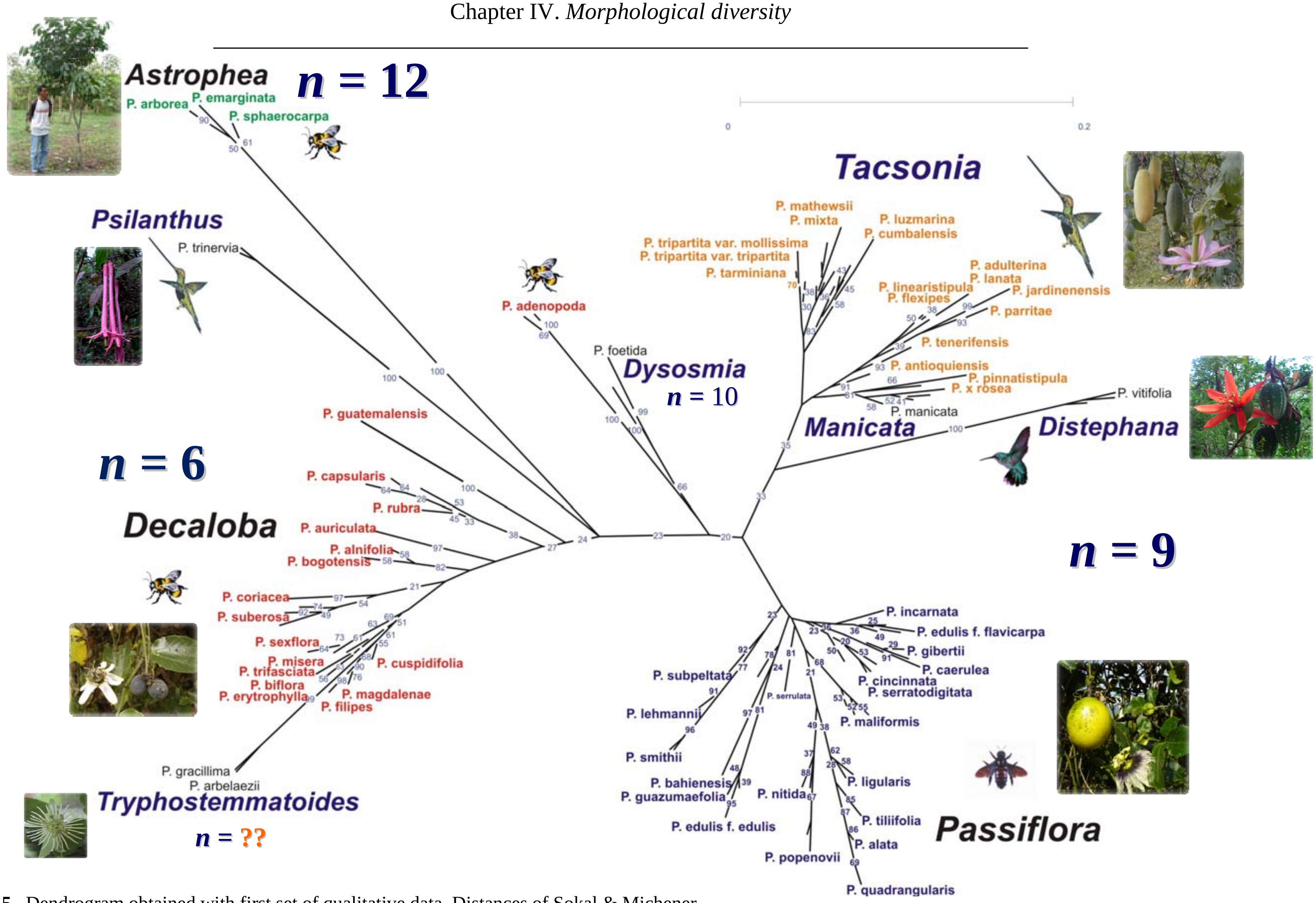

Figure 5. Dendrogram obtained with first set of qualitative data**.** Distances of Sokal & Michener.

IV.1.4.5. *Cluster analysis on the global descriptor dataset*

In a second analysis, all qualitative descriptors (74) were incorporated in the cluster analysis, except those related to pubescence and anthocyanins because of a likely higher sensitivity to environmental conditions, and the difficulty to control redundancy of information (*e.g*. pubescence of different organs is often, but not always, correlated). Removing these descriptors did not affect the structure of the dendrogram, neither at the subgeneric nor at the interspecific level, however it increased distances and improved bootstrap values. The general structure of the tree based on most descriptors (Figure 6) is highly similar to the one obtained with the reduced descriptor set. Branches support is improved, as bootstrap values increase to more than 50% between subgenera, indicating that descriptors showing high polymorphism within subgenera, and sometimes even at the intraspecific level, still contribute to differentiation among subgenera. Distances and bootstrap values between species, and even accessions of a same species, are much higher, reflecting high polymorphism at the lowest levels. However, this does not affect the tree general consistency, as subdivisions among species can be even more easily interpreted. Below the species level, individuals are most often grouped by accessions, but these accessions do not cluster according to their geographic origin.

IV.1.4.6. The "*Passiflora* cluster"

Within subgenus *Passiflora*, all species are consistently separated from each other. Several subclusters are constituted by species of obvious morphological affinity, but these fail to reflect Killip's series. Every time a series is represented by three species, one of them diverges. A first example is the subcluster associating the two forms of *P. edulis* and *P. incarnata* (series *Incarnatae*), but not *P. cincinnata*. A second one is the *P. popenovii* and *P. nitida* subcluster (series *Laurifoliae*), which does not include the less typical representative *P. guazumaefolia*, with small to medium flowers and a white hirsute corona, placed closer to another relatively small-flowered species, *P. bahiensis*. Third is the subcluster associating *P. tiliifolia* and *P. ligularis* (series *Tiliifoliae*), which does not include *P. maliformis*. The latter is highly variable and forms a cluster of its own, only including the very similar *P. serrulata,* which essentially differs by its serrated and bi-/trilobed leaves and smaller flowers and fruits. Fourth, the series *Lobatae* is split between the loose subcluster of *P. subpeltata* and *P. gibertii* and a diverging *P. caerulea* branch. In two cases, there is no discordance, but only two species are represented, i.e. *P. quadrangularis* and *P. alata* (series *Quadrangulares*), and *P. lehmannii* and *P. smithii* (series *Kermesinae*). The subdivisions observed within the *Passiflora* cluster reinforce the general impression that the creation of series have essentially resulted from the too obvious morphological similarity within small groups of species of subgenus *Passiflora*, which have provided the core of the taxonomist's series or sections. This is the case for *Tiliifoliae*, where *P. tiliifolia*, *P. ligularis*, *P. palenquensis*, *P. platyloba* are so closely related that their descriptions are often accompanied by a detailed comparison. Another case is that of series *Quadrangulares*, with *P. alata*, *P. quadrangularis* and *P. trialata*, and series *Kermesinae*, with *P. lehmanni*, *P. smithii* and *P. trisulca*, all species that are differentiated by very few traits, such as nectary shape. The most difficult case is that of *Laurifoliae*, where many species can only be distinguished with considerable difficulties, as very few traits of unknown genetic determinism (exact position of nectaries on petiole, number and relative length of corona whorls), are used to differentiate them. When, in a second step, other, better-differentiated species, are aggregated to these uniform groups, problems and inconsistencies arise, and the solutions depend on which traits are prioritized among the dazzling quantity of polymorphic traits. Another option is to widen the infrageneric groups. Thus, in their classification, Feuillet & MacDougal (2003) have gathered series *Laurifoliae*, *Quadrangulares*, and *Tiliifoliae* in a supersection *Laurifolia*. This view is not supported by our results either. Indeed, in our tree, the link between *P. popenovii*, *P. nitida* Kunth, *P. quadrangularis*, *P. ligularis,* and *P. tiliifolia,* is not supported, and the accessions of *P. maliformis* (also classified in supersection-*Laurifolia* /series-*Laurifoliae* by Feuillet & MacDougal) are placed in a distinct subcluster. In conclusion, our analysis of the *Passiflora* cluster can be conciliated neither with the infrasubgeneric classification of Killip, nor with that of Feuillet & MacDougal. Its essentially radial structure points to the risk of overclassification instead, which is probably the reason why Killip did not use the section level in this subgenus.

IV.1.4.7. The "*Tacsonia* cluster"

The structure of the branch corresponding to subgenera *Manicata* and *Tacsonia* shows the close relationship between the most common species of the latter, *P. mixta*, *P. tripartita*, *P. tarminiana*, and *P. cumbalensis*, forming a cluster onto which are grafted the less common *P. mathewsii* (very similar to *P. mixta*) and *P. luzmarina* (very similar to *P. cumbalensis*). The second subcluster, constituted by Colombian endemics, indicates greater genetic distances. It gathers species from sections *Parritana*

(*P. parritae* (Mast.) L.H. Bailey and *P. jardinensis* L.K. Escobar) and *Colombiana* of Escobar. The latter is represented by series *Colombianae* (*P. lanata* and *P. adulterina* L. f.), *Quindiensae* (*P. lineariistipula*) and *Leptomischae* (*P. antioquiensis* H. Karst.., *P. flexipes* Triana & Planch. and *P. tenerifensis* L.K. Escobar). Escobar's classification is not supported by our analysis. Among the common species, there appears no division between sections *Tacsonia* and *Bracteogama*. Previous morphological and isozyme studies (Villacís et al., 1998, Segura et al., 2002, 2005), as well as hybridization experiments (Schöniger, 1986), have clearly shown closer similarity of *P. tripartita* (section *Bracteogama*) with *P. mixta* (section *Tacsonia*) than with *P. cumbalensis* (section *Bracteogama*). In the second subcluster, there appears to be a slight differentiation of species with "normal" peduncle from those with extremely long peduncles (series *Leptomischae* of section *Colombiana*). In the former group, all remaining sections and series are mixed. Only the two species of series *Colombianae*, *P. lanata* and *P. adulterina*, show a very close morphological similarity, with distances remaining well under the order of intraspecific variation. These distances would have been only slightly higher if pubescence had better been taken into account. In this respect, it must be noted that the two specimens of *P. lanata* were typical for all characters, and they exhibited a lanate ovary. Killip (1938) and Uribe (1955a) mention a glabrous ovary for this species, a trait not mentioned in the original description by Jussieu (1805). Escobar describes the plant as pubescent, except for leaf upper face, with lanate flowers and fruits, which implies necessarily that the ovary is lanate too. In herbarium material, we have found both glabrous and lanate ovaries for this species. The confuse situation between *P. lanata*, *P. adulterina*, *P. cuatrecasasii* Killip, and the recently proposed *P. formosa* (whose author mentions a lanate ovary as an important distinctive feature - in fact the only qualitative one - in the comparison with *P. lanata*), justifies a multivariate analysis to separate intra- and interspecific variation in what could be a species complex or simply a lower number of variable species.

IV.1.4.8. The "*Decaloba* cluster"

Differentiation appears higher in subgenus *Decaloba* than in subgenera *Passiflora* and *Tacsonia*, with the formation of six subclusters. The largest one is formed by accessions of section *Decaloba*, including *P. alnifolia*, *P. bogotensis*, *P. biflora* Lam., *P. cuspidifolia* Harms, *P. erythrophylla* Mast., *P. magdalenae* Triana & Planch. (series *Punctatae*), *P. filipes* Benth (series *Lutae*, although very similar to *P. magdalenae*), *P. misera* Kunth and *P. trifasciata* Lemaire (series *Miserae*). The substructure of this large cluster does not support Killip’s subdivisions. Instead, it agrees with the grouping of all these species in a uniform section *Decaloba* of supersection *Decaloba*, as proposed by Feuillet & MacDougal. *P. auriculata* is placed at the base of this large cluster, at a respectable distance, which may justify its classification in a distinct series (Killip’s *Auriculatae*) or supersection (Feuillet & MacDougal supersection *Auriculata*). *P. sexflora* (section *Decaloba* series *Sexflorae*) is even more isolated from the other species of section *Decaloba*. Its placement in our tree questions its inclusion within Killip’s section *Decaloba*, as well as in the section *Decaloba* sensu Feuillet & MacDougal. *P. guatemalensis*, is also individualized, which is consistent with its classification in a distinct section *Hahniopathanthus* in both classifications. The sixth branch of the *Decaloba* cluster is subdivided in two consistent branches, one gathering *P. suberosa* and *P. coriacea*, and the other uniting *P. rubra* and *P. capsularis* (section *Xerogona* in both classifications). *P. suberosa* and *P. coriacea* are classified in a same section *Cieca* in both classifications, however this section is placed in supersection *Decaloba* in the proposal of Feuillet & MacDougal, which is not supported by our results. As could be expected in such common and widely distributed species, the accessions of *P. suberosa*, *P. capsularis* and *P. rubra* present a high polymorphism. However, the two last species could not be separated on the basis of their morphology. Their accessions cluster two by two according to the population of origin, sometimes with relatively wide intrapopulational variation, but not following interspecific boundaries. Indeed, all authors insist on the difficulty to distinguish them. Killip (1938) and Holm-Nielsen et al. (1988) state that this is practically impossible on sterile specimens. Their descriptions give particular importance to fruit shape and ovary pubescence, although they do not agree on the distribution of ovary pubescence between the two species. Ulmer & MacDougal (2004) insist on the color of the corona base. Our identification was based on these three criteria, prioritizing fruit shape and corona color (see Figure 7), but then we had to admit three different levels in ovary pubescence (glabrous, puberulent, hirsute) in *P. capsularis*. Changing the priority of criteria would just give a different but also inconsistent identification. Thus it appears that these traits can combine in different ways, so they are not reliably discriminant, and the analysis for all other traits, including or not pubescence, only confirms that the status of these two species should be revised, downgrading them to botanical varieties, unless elements of reproductive biology contradict this view. But even this is improbable, as self-incompatibility and self-compatibility coexist within *P. capsularis* (Ulmer and MacDougal, 2004).

IV.1.4.9. The "*Astrophea* cluster"

Subgenus *Astrophea* appears very uniform, which could be expected as only one section, *Euastrophea*, is represented in our small sample of this subgenus. The accessions share most of their qualitative traits, and the divergence of one population of *P. emarginata* can only be attributed to differences in leaf shape descriptors. This accession also differs slightly in the pubescence of the ovary, but this trait did not interfere as it was not used in the cluster analysis. The sample was too limited to draw any conclusion on intra-and interspecific boundaries between the species represented.

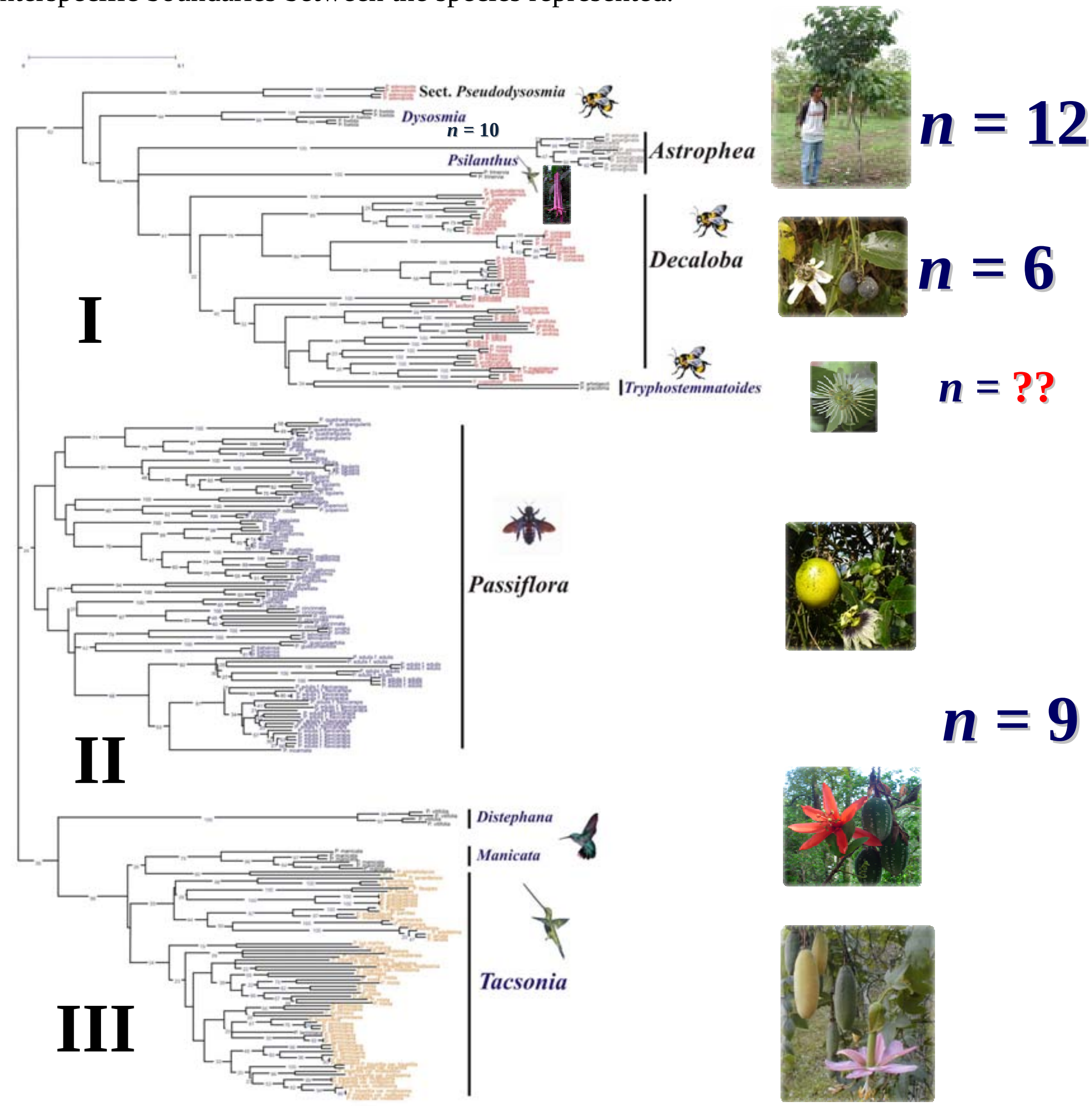

Figure 6. Dendrogram obtained on complete set of qualitative data. Distances of Sokal & Michener.

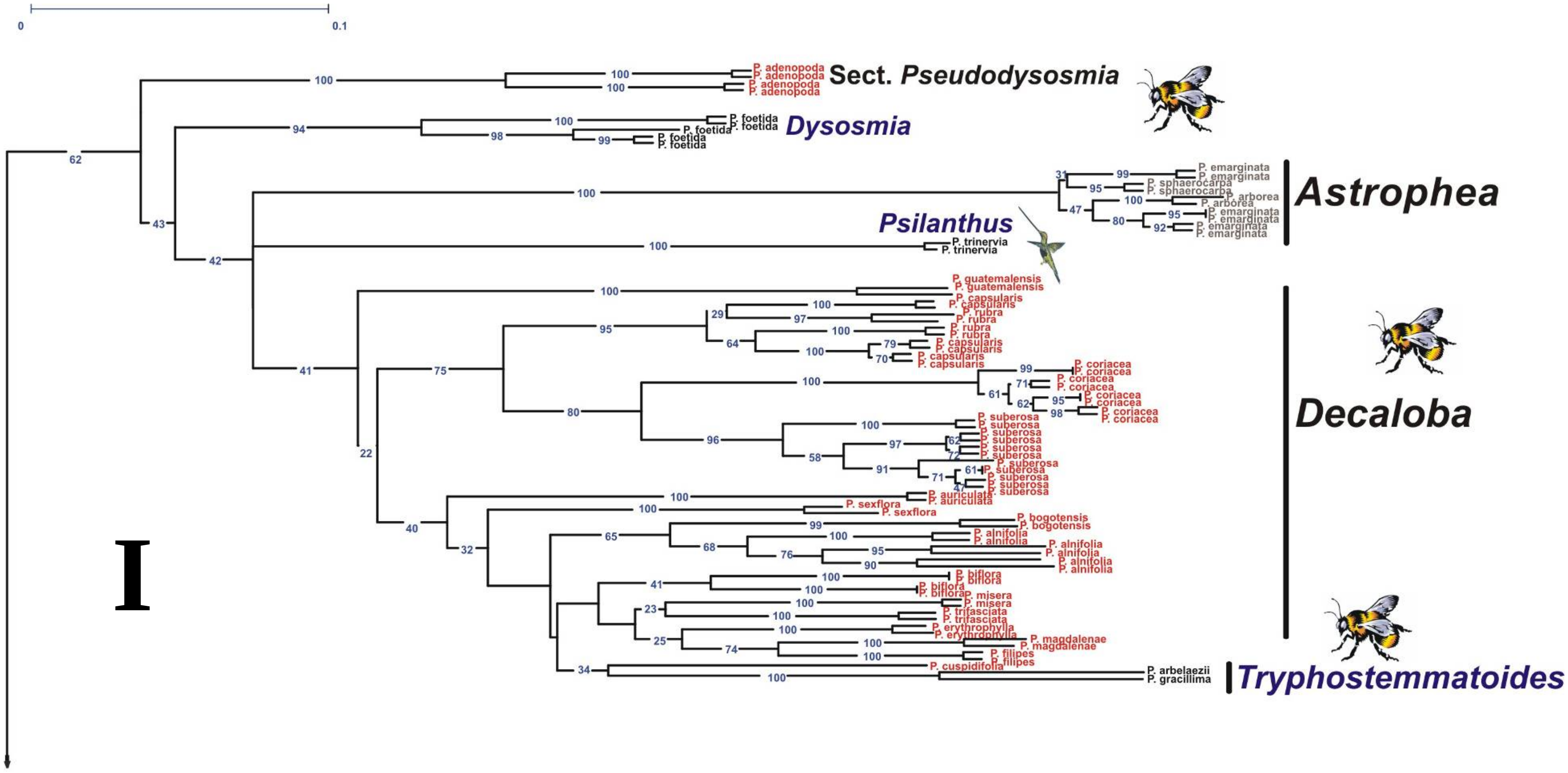

Figure 6a. First part of the dendrogram obtained on the complete set of qualitative data.

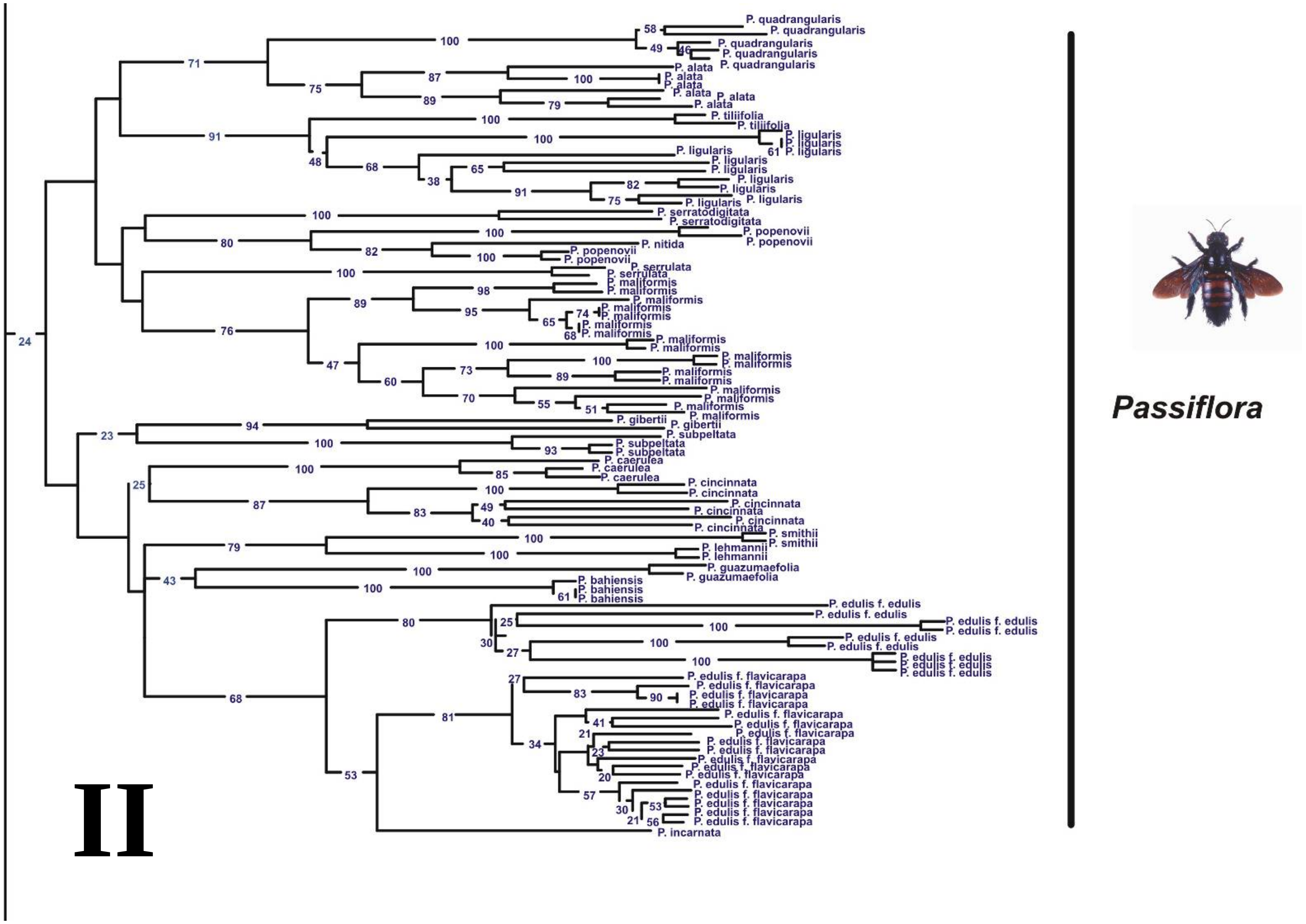

Figure 6b. Second part of the dendrogram obtained on the complete set of qualitative data.

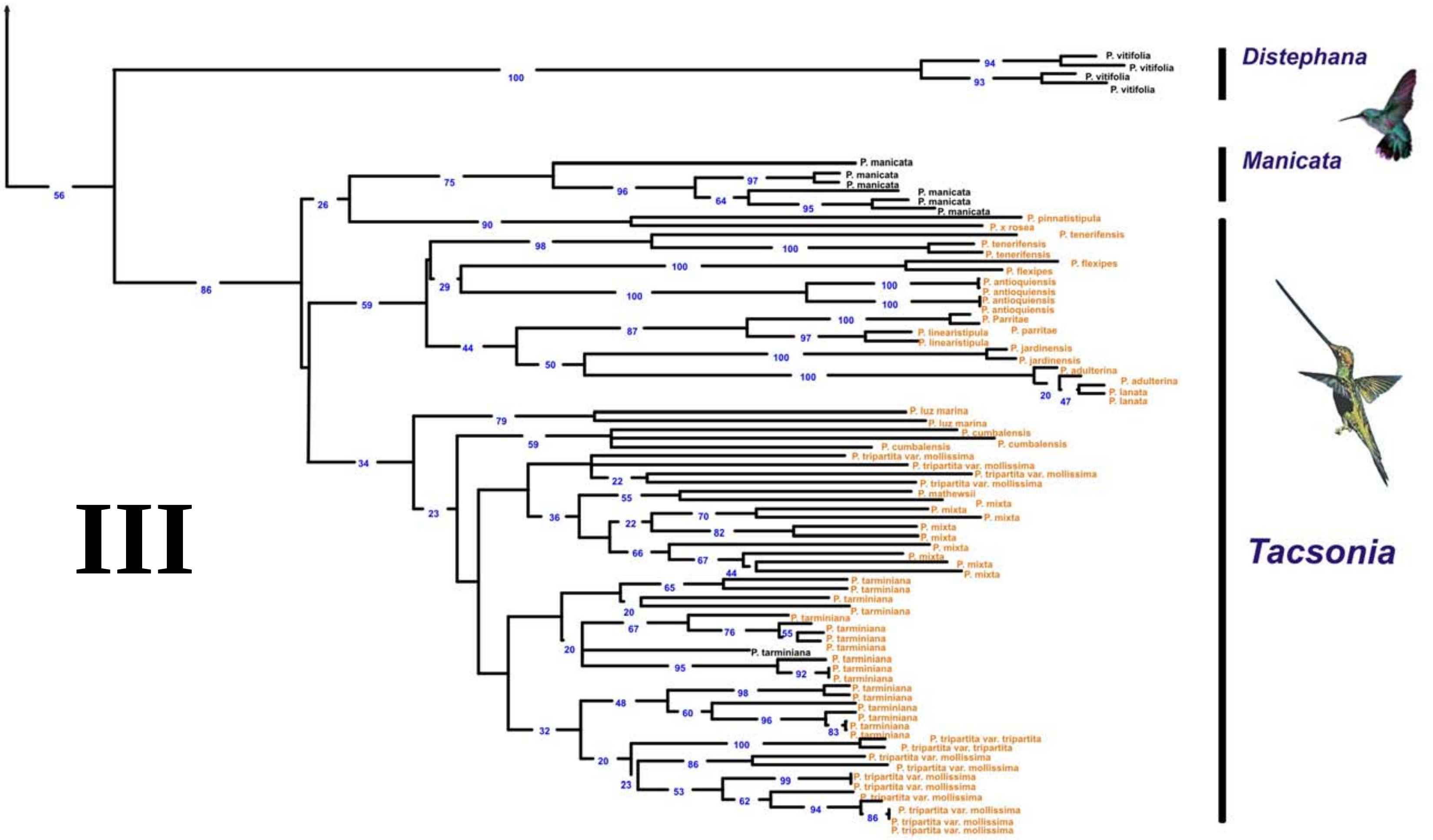

Figure 6c. Third part of the dendrogram obtained on the complete set of qualitative data.

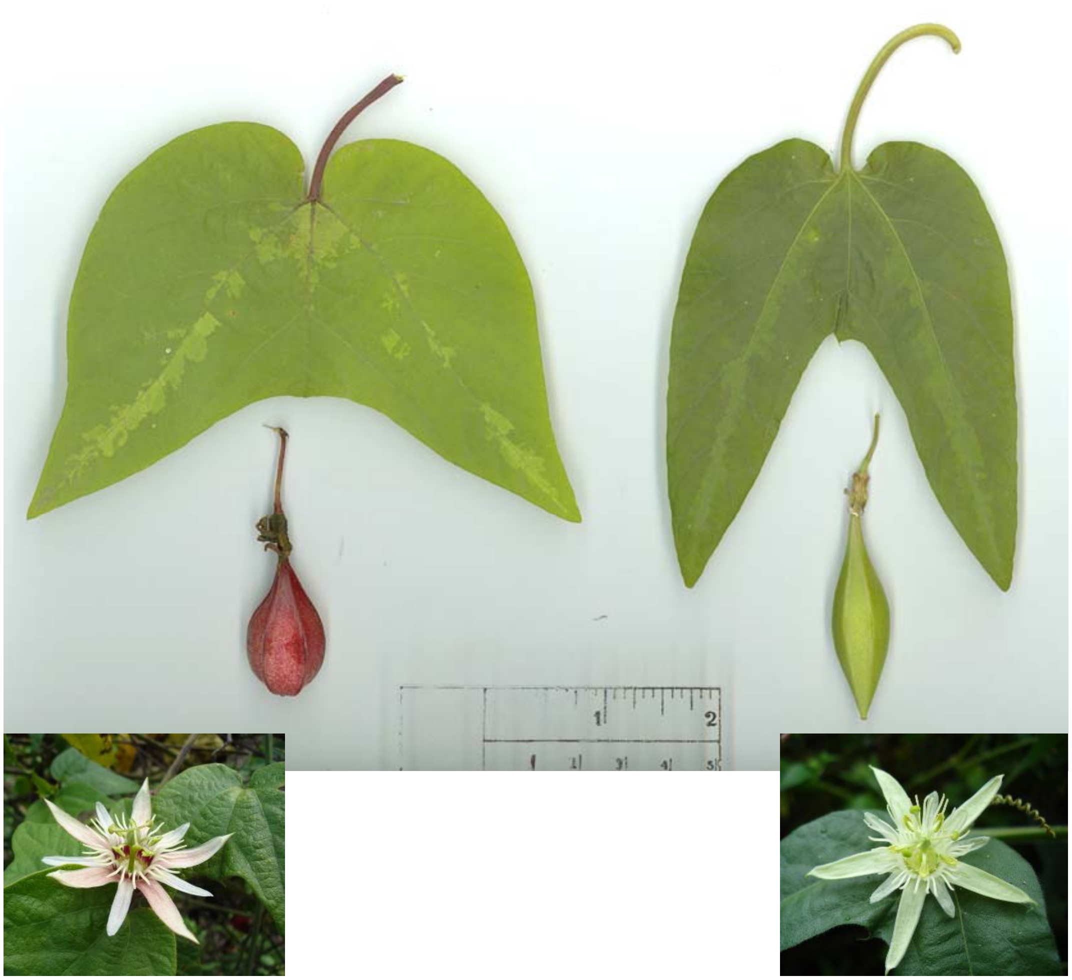

Figure 7. Morphological affinity between typical representatives of *P. rubra* (**a**) and *P. capsularis* (**b**). Accessions from Colombia (**a**, Calarcá, Quindío – **b**, Cartago, Valle del Cauca).

IV.1.4.10. *Morphological and molecular diversity*

To appreciate the reliability of the morphological approach to *Passiflora* diversity, we have compared some of the interspecific associations or divergences with similar results obtained in phenetic studies with biochemical and molecular markers on samples including some of our species. Indeed, a first series of genetic studies were carried out on smaller species samples, mostly from Colombia too. In the trees obtained with RAPD and cpDNA RFLP markers by Fajardo et al. (1998) and Sánchez et al. (1999), the species of subgenus *Tacsonia* only constitute one subcluster within a large cluster gathering them with species of subgenus *Passiflora*. Subgenus *Decaloba* is represented by *P. coriacea* and *P. adenopoda*, both species strongly diverging from this *Passiflora*-

Tacsonia cluster, but also between themselves, which appears consistent with our results. In the RAPD study, subgenera *Distephana* and *Astrophea* are represented respectively by *P. vitifolia* and *P. spinosa* (Poepp. & Endl.) Mast., and both species are placed at considerable distance from the *Passiflora-Tacsonia* cluster, their divergence being intermediate between that of *P. adenopoda* and that of *P. coriacea*. Within the *Tacsonia* subcluster, the distances between the species, *P. tripartita* var. *mollissima*, *P. cumbalensis*, *P. pinnatistipula*, and *P. antioquiensis*, follow the same order as in the corresponding morphological cluster. This is still true when the comparison is extended to subgenus *Manicata*, considering the results obtained by Segura et al. (2002, 2003) with AFLP markers (*P. tenerifensis* and *P. parritae* also included), and with isozymes, although *P. antioquiensis* is placed closer to the most common tacsos than *P. pinnatistipula* in the isozyme study. Another convergence between morphological and AFLP markers is the clear separation of *P. maliformis* from the typical species of series *Tiliifoliae* of subgenus *Passiflora* (Ocampo et al., 2004).

Genetic relationships between subgenera and between particular species can also be deduced from subsequent phylogenetic studies carried out on wider species samples by Muschner et al. (2003) with ITS, *trnL-trnF* and rps4 sequences, by Yockteng (2003) with chloroplastic *mat*K sequences, Yockteng & Nadot (2004) with sequences of the nuclear chloroplast-expressed glutamine synthetase gene (ncpGS), and Hansen et al. (2006) with *trnL/trnT* sequences. All these studies support the existence of three major clades, one corresponding to subgenus *Astrophea*, one formed around subgenus *Decaloba*, and one formed around subgenus *Passiflora*. When included in these studies (i.e. all studies except that of Muschner et al., 2003), species of subgenus *Tacsonia* form a subclade within the *Passiflora* clade. *P. vitifolia*, and other representatives of subgenus *Distephana* in the Yockteng's studies, are also included in this large *Passiflora* clade, although they are not grouped consistently in the matK tree (Yockteng, 2003). The relative position of the three major clades differs among studies. Subgenus *Astrophea* takes an intermediate position in the ITS tree, it is closer to the *Passiflora* clade in the other trees of Muschner et al. (*trnL-trnF* and *rps*4), but closer to the *Decaloba* clade in the *trnL-trnT* tree of Hansen et al., while the *Decaloba* clade appears closer to the *Passiflora* clade in the sample of Yockteng (ncpGS and *mat*K trees). *P. foetida* is clearly placed within the *Passiflora* clade according to rps4 and *trnL-trnF* sequences, but more distant, although basal to this clade, in the trees obtained with ITS, ncpGS, and *mat*K sequences. *P. adenopoda* is basal to the *Decaloba* clade in the ncpGS tree, as well as in the ITS study of Krosnick & Freudenstein (2005). *P. morifolia* Mast., another species of section *Pseudodysosmia*, is also basal to the *Decaloba* clade, on a branch between *Decaloba* and *Astrophea*, in the ITS and *trnL-trnF* trees. In the ncpGS tree of Yockteng & Nadot (2004) and the ITS study of Krosnick & Freudenstein (2005), subgenus *Tryphostemmatoides*, represented by *P. tryphostemmatoides* Harms and by *P. arbelaezii* L. Uribe respectively, is placed close to subgenus *Astrophea*. Strangely, in the study of Yockteng & Nadot (ncpGS tree), *P. sanguinolenta* Mast., a representative of subgenus *Psilanthus*, is placed in a *Passiflora* subclade dominated by representatives of series *Tiliifoliae*.

Within the *Decaloba* clade, we can recognize the higher level of divergence between subclusters, the association we have observed between representatives of series *Punctatae* and *Miserae* in the widest subclade (*trnL-trnF* tree of Muschner et al., 2003), the relative separation of *P. sexflora* from this group, and the even more distant position of *P. coriacea* and of the couple formed by *P. capsularis* and *P. rubra* (ITS, *trnL-trnF*, and ncpGS sequences). However, the two last species are closely associated with *P. sexflora* in the ncpGS tree.

As in our morphological study, the *Passiflora* clade identified in phylogenetic studies generally shows loose relations between species. The interpretation of the poorly supported subclades is very uneasy, with the partial exception of the ncpGS tree presented by Yockteng & Nadot (2004), where branches are better defined, although not easier to interpret, given, for example, the dispersion of species belonging to the series *Incarnatae* and *Laurifoliae*. Among the close associations documented by our morphological study, we can only recognize those of *P. quadrangularis* with *P. alata* and *P. incarnata* with *P. edulis* (ITS and ncpGS trees).

As a first major point of conclusion on this comparison between morphological and molecular diversity, we can underline that the major morphological divisions observed in our study find support in the genetic studies. The cytological groups are always validated, with the clear separation of subgenera *Astrophea* (*n* = 12), *Tryphostemmatoides* and *Decaloba* (*n* = 6) between themselves and from subgenera *Passiflora*, *Tacsonia*, and *Distephana* (*n* = 9). Concerning subgenus

Tryphostemmatoides, the consistency between morphological and genetic studies is clear only when considering our quantitative analysis, where it is associated with subgenus *Astrophea* mostly on peduncle traits (third principal component). This trait is represented also in the qualitative descriptors, however its effect is blurred by the high number of traits shared with subgenus *Decaloba*. While the comparison is difficult for subgenus *Tryphostemmatoides*, it is impossible for subgenus *Psilanthus*, because of insufficient data and the unlikely placement of *P. sanguinolenta* in the *Passiflora* clade in the ncpGS study. The two species, *P. adenopoda* and *P. foetida*, that take an intermediate position in the general “morpho-cytological” pattern, or their close relatives, are consistently placed in intermediate positions, in most phylogenetic studies, *P. adenopoda* or *P. morifolia* (section *Pseudodysosmia* of subgenus *Decaloba*) appearing basal to a general *Decaloba* clade and *P. foetida* (subgenus *Dysosmia*) basal to the general *Passiflora* clade.

The comparison becomes more difficult at lower, infrasubgeneric, levels. Subgenus *Decaloba* appears better structured than the other numerous subgenera, and shows similarities in morphological and molecular diversity patterns, with the grouping of Killip’s sections *Punctatae* and *Miserae*, and the differentiation of species of sections *Xerogona*, *Cieca*, and series *Auriculata* and, less clearly, *Sexflorae*. The placement of *P. adenopoda* in the different trees questions the inclusion of section *Pseudodysosmia*, while the structure observed among representatives of several sections provides support to some simplification, but not for as many fusions as those operated in the new morphological classification of Feuillet & MacDougal. In any case, more species should be gathered in a same phenetic study before revising objectively the morphological classification.

Within the $n = 9$ group, molecular data and morphological diverge partially, as studies of DNA sequences allow the distinction of a *Tacsonia*-*Manicata* group and fail to separate clearly subgenus *Distephana*, placing both of them within a *Passiflora* clade, while morphological analysis supports these three subgenera at the same level of differentiation. The fact that species of subgenera *Distephana*, *Tacsonia* and *Manicata* have developed ornithophyly is obviously related to their strong morphological differentiation, which does not minor the importance of their separation from subgenus *Passiflora*. Whether their probable evolution from a “*Passiflora*-like” common ancestor justifies their inclusion in the bee-pollinated *Passiflora* subgenus, as proposed in the new classification, is just the same classical question about considering birds as dinosaurs. In the end, it seems a problem of putting more emphasis on the adaptative forces commanding evolution or more emphasis on the genetic structure that subtend them. Concerning subgenus *Passiflora* sensu Killip, no clear structure appears at the interspecific level that could result in clear subdivisions into series. The study of sequence variation for the ncpGS gene provides the only tree with reasonably well supported structure at this level, however several obvious abnormalities question the robustness of the information. Our morphological observations only confirm closer associations between the most typical representatives of some series, however the number of contradictions with the classification and the lack of a clear hierarchy in the branch structure point to the difficulty of the work and the risk of under- or overclassification, leading to chose between a limited number of poorly supported series or a great number of poorly represented series. Similarly, the structure of the *Tacsonia-Manicata* branch does not support clearly sections and series in subgenus *Tacsonia*, however it allows differentiation between two groups of *tacsos*, one corresponding to common species that probably have their center of diversity in Ecuador, as is obvious for *P. cumbalensis*, *P. luzmarina* and *P. matthewsii*, and very likely for *P. mixta*, *P. tripartita* and *P. tarminiana* (Segura et al., 2005), and another cluster only including species endemic to Colombia, with a slight but clear differentiation related to extreme variation for peduncle length.

IV.1.5. Conclusions

In the absence of a clear set of morphological criteria for discriminating at the different hierarchic levels of the infrageneric classification of *Passiflora*, we have used a quite exhaustive list of 43 quantitative and 84 qualitative descriptors. A shorter list of 32 qualitative traits, selected after analyzing variation among Killip’s subgenera, allowed to classify our 60-species sample consistently, using a strictly phenetic approach. Most discriminant characters include size of stems and leaves, presence of tendrils, number and distribution of extrafloral nectaries, dimensions and general shape of bracts, width and length of flowers, corona complexity, and, although they could not be systematically analyzed, fruit size and color. Eight of the nine Killip’s subgenera represented in our sample are supported by the morphological analysis, although subgenus *Tryphostemmatoides* is only supported in the quantitative analysis. By contrast, the simplification proposed by Feuillet & MacDougal is not clearly supported in our analyses, except for the possible inclusion of *P. manicata* in subgenus *Tacsonia*, as this species is intermediate with subgenus *Passiflora* for quantitative traits but very similar to *tacsos* for most qualitative traits. Furthermore, the placement of *P. adenopoda* and its close relatives, in our analyses as well as in molecular ones, questions their treatment as a division of subgenus *Decaloba*. More generally, as compared to molecular results, our phenetic approach provides a better resolved vision of relations among passifloras. Beyond the differentiation between cytological groups (n = 6, 12 or n = 9; de Melo et al., 2001) underlined in most analyses, appear other features of considerable importance for their evolution. The division between the two cytological groups is particularly paralleled by a division on the presence and position of extrafloral nectaries and the complexity of the corona, showing the importance of coevolution. In the same line, Yockteng (2003) underlined the differentiation appearing in the spectrum of cyanogenic components developed against herbivores in the two cytological groups. Even clearer appears the coevolution with pollinators, causing the main line of floral divergence between subgenera *Passiflora*, pollinated by large bees, *Tacsonia*, pollinated only by the sword-billed hummingbird, and *Distephana*, pollinated by other hummingbirds. In the n = 6/12 group, where small to medium size insects dominate as pollinators, the morphological divergence of *P. trinervia* (subgenus *Psilanthus*), showing exactly the same adaptation to Andean highlands and pollination by the same bird species as subgenus *Tacsonia*, is not less significant. This convergence is logically expressed in the evolution of the corona. However, the minute corona of *P. trinervia*, and other typical representatives of subgenus *Psilanthus*, probably results from the transformation of the two-ranked corona common in subgenera *Astrophea* and *Decaloba*, while the reduced corona of most *tacsos* has evolved from the complex corona observed in all species of subgenus *Passiflora* at the same time as their specialized hypanthium. Remnants of these complex coronas can still be observed in species with a less developed hypanthium, as *P. manicata* and *P. antioquiensis*, with one or two external whorls, plus a few other series of thinner filaments under the floral tube throat, and even in typical long-tubed *tacso* flowers. Thus, a more or less developed second whorl is not rare in *P. mixta*, while loose whorls of very thin white filaments can be observed far in the hypanthium of *P. tripartita* var. *mollissima*. The evolution has probably been different for subgenus *Distephana*, and its differentiation within the $n = 9$ group earlier in the history of *Passiflora*, as its species show no such signs of an ancestral complex corona. Instead, they are constituted by two or three rows, which can be compared with numbers observed in subgenera *Decaloba* and *Astrophea*. The fusion of the elements into a prolongation of the floral tube is paralleled in certain representatives of subgenus *Decaloba*, such as *P. tulae* Urban (Murucuja), forming another striking case of convergence between species from very different evolutive backgrounds.

IV.1.6. Acknowledgements

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CHAPTER V

Chloroplast and mitochondrial DNA variation in the genus *Passiflora* L. (Passifloraceae) as revealed by PCR-RFLP

V.1. Chloroplast and mitochondrial DNA variation in the genus *Passiflora* L. (Passifloraceae) as revealed by PCR-RFLP

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V.1.1. Abstract

The chloroplast and mitochondrial DNA diversity of 213 accessions belonging to 151 *Passiflora* species of 15 subgenera recognized by Killip (1938) was studied by PCR-RFLP analysis of two non-coding cpDNA regions (*psb*C- *trn*S and *trn*S - *trnf*M) and two non-coding mtDNA region (*nad*4-1/2 and *nad*1-B/C). This sample set was supplemented with six accessions from three African Passifloraceae genera *Adenia*, *Barteria,* and *Smeathmannia,* as outgroup species. The PCR-amplified cpDNA regions were digested with six endonucleases. A total of 614 fragments were scored, of which 93% were found to be polymorphic in the sample. Two-hundred-eighty haplotypes were found for the chloroplast and 372 for the mitochondria. A higher level of interspecific variation was detected in the mtDNA regions than in the cpDNA regions. The first two axes of the principal co-ordinates analysis accounted for 59% of the total variation on cpDNA data. They allowed visualizing a strong structure, as the genera *Adenia*, *Barteria*, and the *Passiflora* subgenera *Astrophea*, *Calopathanthus*, *Dysosmia*, *Distephana*, *Manicata*, *Passiflora*, *Tacsonia*, *Tacsonioides* and *Tryphostemmatoides*, and *P. deidamioides* occupy the left half of the principal plane, while the species of subgenera *Apodogyne*, *Decaloba*, *Murucuja*, *Pseudomurucuja* and *Psilanthus* form a very well separated group, placed in a quite extreme position on the right, only the accessions of *Smeathmannia* and *P. lancetillensis* (subgenus *Deidamioides*) taking intermediate positions. The phenogram obtained by the neighbor-joining method on cpDNA data is more coherent with the major divisions of the taxonomy proposed recently by Feuillet & MacDougal than the corresponding mtDNA tree. The cpDNA tree shows three major, well supported clusters within *Passiflora*. The first one, named the "*Passiflora* group", includes subgenera *Calopathanthus*, *Deidamioides*, *Distephana*, *Dysosmia*, *Dysosmioides*, *Manicata*, *Passiflora*, *Tacsonia*, and *Tacsonioides*, with a very loose substructure and considerable intraspecific variation. The second one includes subgenus *Astrophea*, and the third one, named the "*Decaloba* group", comprises most species of subgenera *Apodogyne*, *Decaloba, Murucuja, Pseudomurucuja* and *Psilanthus*. *P. gracillima* (subg.enus *Tryphostemmatoides*) appears in basal position, forming a fourth cluster of its own. The position of *P. lancetillensis* (subgenus *Deidamioides*) is undefined, as it is placed on a long branch between the outgroup and the "*Decaloba* group", the outgroup itself taking an undefined position among the three major *Passiflora* clusters. The phenogram obtained with mtDNA data separates four main clusters. As for cpDNA, a first large, well supported, cluster corresponds to the "*Decaloba* group", where accessions are grouped by species, with the only exception of *P. adenopoda.* The numerous accessions of section *Decaloba* series *Punctatae* and *Miserae* tend to form a subcluster, while Killip's subgenera *Apodogyne*, *Murucuja*, *Pseudomurucuja* and *Psilanthus* cannot be recognized. The other major clusters are different from those evidenced by cpDNA data, as subgenera *Astrophea* and *Tryphostemmatoides* appear integrated within the "*Passiflora* group", while subgenus *Tacsonia* forms a uniform distinct cluster, close to another one comprising species of series *Kermesinae*, *Simplicifoliae*, *Lobatae*, and *Menispermifoliae*. The analyses of chloroplastic and mitochondrial fragments gave very different pictures on the genetic structure of genus *Passiflora*. Differences appear at all levels, in the position of the outgroup, the relative position of four subgenera, and the relationships between species. The divergence in the information obtained from chloroplast and mitochondrial genomes are attributed to differences in their rate of evolution and mode of transmission and to reticulate evolution in the genus.

Key words: *Passiflora,* PCR-RFLP, chloroplast and mitochondrial DNA, variation, evolution.

V.1.2. Introduction

The family *Passifloraceae* is divided into two tribes, *Pariopsieae* and *Passifloreae,* and includes more than 650 species (Escobar, 1988; Ulmer & MacDougal, 2004) distributed throughout the tropics. The base number of chromosome varies among x = 6 and x = 9 (De Melo & Guerra, 2003). With approximately 525 species, including several cultivated ones, *Passiflora* is numerically and economically the most important genus of the family. Passionflowers are generally vines, although some representatives are shrubs or trees. *P. edulis* Sims (yellow maracuja) is by far the best-known and economically most important species of the family.

In the last extensive revision of the genus, Killip (1938) classified 355 *Passiflora* species into 22 subgenera (Annex 1). For long, while the list of species was considerably extended, his views were only amended or supplemented. In Colombia, Escobar (1988a,b, 1989, 1990 inedited, 1994) reviewed subgenera *Astrophea*, *Distephana*, *Manicata*, *Rathea* and *Tacsonia*, merging subgenera *Tacsoniopsis* and *Tacsonia*, subdividing them into sections and series, and proposing one additional subgenus, *Porphyropathanthus*. Recently, Feuillet & MacDougal (2003; Annex 2) have proposed a new infrageneric classification of *Passiflora* recognizing only four subgenera, further divided into 16 supersections. Three of their subgenera are strictly American: *Astrophea*, *Deidamioides*, and *Passiflora*, with 57, 17 and 234 species respectively, with an essentially tropical distribution. *Decaloba*, with its 204 species, is mainly distributed in America, but it is also represented in Southeast Asia and Australia (Ulmer & MacDougal, 2004). In this new proposal, the genus *Tetrastylis* is placed as a section of subgenus *Deidamioides*, and the subgenus *Tetrapathea* from New Zealand is excluded from the genus *Passiflora* (Hutchinson, 1967; Green, 1972; Yockteng & Nadot, 2004).

Both classifications of Killip (1938) and Feuillet & MacDougal (2003) are based on the extreme morphological richness and complexity of *Passiflora*, whose species present numerous particular traits, including a wide variation in leaf shape, even within species and within individuals (heterophylly and heteroblasty), the presence of extrafloral nectaries in different parts (on leaf petiole, lamina or margins, on bracts, on sepals), floral traits showing a high level of coevolution with particular pollinators, particularly in corolla color, the variable development of the hypanthium and that of the corona. However, no clear hierarchy emerges in the relative contributions of these traits to taxonomy of the genus. Ocampo & Coppens d'Eeckenbrugge (*in preparation*; cfr. Chapter IV), have used a list of 127 morphological descriptors in a phenetic approach of morphological differentiation among 60 *Passiflora* species from nine of the Killip's subgenera. The quantitative descriptors clearly separated subgenera *Astrophea*, *Decaloba*, *Passiflora*, *Psilanthus*, *Tacsonia*, and *Tryphostemmatoides.* Subgenus *Dysosmia* appeared intermediate between *Passiflora* and *Decaloba*, while the representatives of subgenera *Manicata* and *Distephana* showed affinity with subgenera *Tacsonia* and *Passiflora* respectively. Qualitative trait analysis showed a major distinction between species with $2n = 12$ or 24 chromosomes, and species with $2n = 18$ chromosomes, and discriminated more clearly among Killip's subgenera *Astrophea*, *Psilanthus*, *Decaloba*, in the former cytological group, and *Distephana*, *Dysosmia*, *Passiflora* and *Tacsonia*, in the second cytological group. Subgenera *Manicata* and *Tryphostemmatoides* could not be distinguished from subgenera *Tacsonia* and *Decaloba* respectively. While these main divisions could be easily interpreted following Killip's subgenera, this was not true at lower levels. No clear subdivisions were observed within subgenus *Passiflora* and only a slight geographical structure was detected in subgenus *Tacsonia*. Differentiation was higher in subgenus *Decaloba*, where subclusters partly supported the simplification proposed by Feuillet & MacDougal. The most obvious contradiction with both classifications was the placement of *P. adenopoda* (subgenus *Decaloba* section *Pseudodysosmia*) in an intermediate position, between subgenera *Passiflora* and *Decaloba*.

In many plant groups, molecular genetics have provided powerful new tools to understand the structure and evolution of species diversity. The first studies of genetic variation in *Passiflora* were based on RAPD, RFLP, AFLP and isozyme markers, and initiated in a breeding perspective, focusing on cultivated species and their wild relatives in subgenera *Passiflora* and *Tacsonia* (Fajardo et al., 1998; Sánchez et al., 1999, Segura et al., 2002; Segura et al., 2003a; Ocampo et al., 2004; Segura et al., 2005). As discussed in the preceding chapter, their results are consistent with our morphological analyses, but their narrow samples limited the reach of comparisons. The application of molecular tools to phylogenetic analysis of wider samples is more recent.

The first genus-wide molecular analysis of *Passiflora*, using the nuclear ribosomal internal transcribed spacers, (ITS-1 and ITS-2), plastid *trn*L-F intergenic spacer and the *rps4* plastid gene, was reported by Muschner et al. (2003; Annex 4a). Eleven subgenera were represented by 61 species. The ITS alignment appeared highly variable, with shorter sequences in subgenera with 2*n* = 18 or 2*n* = 20 chromosomes than in subgenera with 2*n* = 12 or 24 chromosomes. The three phylograms consistently showed three major clades, corresponding with three of the subgenera proposed by Feuillet & MacDougal (2003), i.e. the '*Passiflora* clade', composed of 2*n* = 18/20 species, the '*Decaloba* clade' composed of 2*n* = 12 species, and one composed of 2*n* = 24 species (i.e. subgenus *Astrophea*). The representatives of subgenus *Deidamioides* contributed to the *Decaloba* clade in the ITS phylogram, while they appeared independent from the three major clades in the *trn*L-*trn*F and *rps4* phylograms. The substructure of the two most numerous clades, '*Passiflora*' and '*Decaloba*', were not consistent with either taxonomical classification. Within the '*Passiflora* clade', bootstrap values are low and there is no clear structure that could correspond to sections or series, although a few associations are recognized between closely related species, such as *P. alata* and *P. quadrangularis*, *P. edulis* and *P. incarnata*, in the ITS tree. These associations are not expressed in the *trnL-trnF* tree, where even the two species of the uniform subgenus *Distephana* do not appear related. The '*Decaloba* clade' shows a stronger substructure, with an association between species of sections *Decaloba*, *Miserae* and *Punctatae* of subgenus *Decaloba*, an smaller subclusters representing sections *Cieca* and *Xerogona*, while *P. morifolia* (section *Pseudodysosmia*) takes a relatively basal position in both phenograms. However, in the *trnL-trnF* tree, *P. rubra* strongly diverges from the *Decaloba* clade, which is not the case for *P. capsularis,* a species that is so similar that our morphological analysis led us to consider the two as synonyms (see Chapter IV). An even stronger inconsistency concerns the placement of the outgroups in both phenograms. *Adenia keramanthus* is positionned as sister to the '*Passiflora* clade', with a support value of 97%, while *Mitostemma* *brevifilis* is placed as sister to the ‘*Decaloba*’ and *Astrophea* clades in the ITS tree, both species diverging from *Passiflora* species in the *trnL-trnF* tree. In addition, *Mitostemma brevifilis* also appears in an unexpected position at the base of the ‘*Passiflora*’ and *Astrophea* clades in the *rps4* tree. Muschner et al. (2003) concluded that the monophyly of the genus *Passiflora* was not supported by any statistical or phylogenetic method, “and in several trees there was even support of a non-monophyletic *Passiflora*”.

One year after Muschner et al. (2003), Yockteng & Nadot (2004; Annex 4c) published a phylogenetic study of a 91 species-sample representing 17 of the 23 subgenera recognized by Killip (1938) and Escobar (1988a), based on the sequences of the chloroplast-expressed glutamine synthtase gene (ncpGS). Their phenogram showed the same three major clades, with significant differences in length of introns. These results provided support to three of the four subgenera defined by Feuillet & MacDougal (2003), but indicated that three additional subgenera, *Polyanthea* (DC.) Killip, *Dysosmia* (DC.) Killip, and *Tetrapathea* (DC.) Rchb., should also be recognized. The *Astrophea* clade is sister to the other species, except *P. cirrhiflora*. *P. tryphostemmatoides* (subgenus *Tryphostemmatoides*) appears closely related to it. Within the *Passiflora* clade, appears a *Tacsonia* subclade that also includes *P. manicata* (subgenus *Manicata*) and *P. racemosa* (subgenus *Calopathantus*). Two other subclades are more difficult to interpret. One of them includes a small third-order cluster constituted by species of subgenus *Distephana*, joined surprisingly by *P. cincinnata* (subgenus *Passiflora* series *Incarnatae*). Several third-order subclusters appear dominated by particular morphological groups, but too many exceptions hamper a consistent interpretation. The dispersion of species of the uniform series *Laurifoliae* provides the best example of this situation. The inclusion of *P. sanguinolenta* (subgenus *Psilanthus*) is the strangest abnormality in the *Passiflora* clade. Like in the study of Muschner et al. (2003), the *Decaloba* clade shows a stronger substructure, with similar associations, and relatively basal position of the species of section *Pseudodysosmia*. Very surprisingly, this *Pseudosysosmia* cluster included *P. alnifolia*, thus isolated from its closest relatives. An even more surprising placement is that of *P. candida* (subgenus *Astrophea*) close to *P. auriculata*. The same large sample was studied for sequences of the chloroplastic gene *mat*K (Yockteng, 2003; Annex 4b).

The results were generally consistent in defining the same three clades, despite some divergence in their relative positions. *Tryphostemmatoides* appeared fully included in the *Astrophea* clade. Resolution was poor at the section and series level, however second order subdivisions were also consistent with ITS and ncpGS results in the '*Decaloba* clade', and a *Tacsonia-Manicata-Calopathanthus* subclade was individualized within the '*Passiflora* clade'. *P. candida* was placed more logically in the *Astrophea* clade, which discards the hypothesis of a misidentification invoked in the interpretation of the ncpGS study.

Krosnick & Freudenstein (2005) showed that the 22 species of Old World *Passiflora* form a monophyletic group and supported their placement by Feuillet & MacDougal in supersection *Disemma,* within subgenus *Decaloba,* using plastid (*trnL-F*) and nuclear (ITS) DNA sequences. More recently, Hansen et al. (2006; Annex 4d) analyzing chloroplast sequences *rpoC1* and *trnL*/*trnT* from 136 species of genus *Passiflora*, also obtained the three major clades, with problems of resolution and consistency at section and series level, and a few striking cases of inconsistent positioning. The most spectacular example came from *P. microstipula*, a species with $2n = 18$ chromosomes, two accessions being placed in the *Passiflora* clade, close to the very different *P. nitida*, and a third one at the base of the *Decaloba* clade. As stated by the authors, the most likely explanation is an extreme case of chloroplast capture. Hansen et al. (2006) sustain that their data unequivocally support the subgeneric classification of Feuillet & MacDougal, however the position and composition of subgenus *Deidamioides* is not clearly defined, and the phylogram presented places *Dilkea* and *Tetrapathea* as sister group to a *Decaloba-Deidamioides* clade, which throws additional doubts on *Passiflora* monophyly.

This revision of the phylogenetic studies consistently shows the existence of three major clades in the genus *Passiflora,* with a stronger structure in the *Decaloba* clade than in the *Passiflora* clade. When *tacsos* (species of subgenus *Tacsonia*) are included in the sample, they are placed in a particular subclade of the latter. Beyond this general pattern, several points of conflict are obvious too. First are the inconsistencies in the relative placement of the three major clades. Such variation affects more markedly the placement of several morphologically atypical species. Also, there are cases of highly improbable placement concerning a few species. The variable placement of the outgroup species is even more problematic, generating doubts on the monophyly of the genus. A comparison of all phenograms also shows that chloroplastic sequence data tend to produce trees with less consistent and less supported structure than the nuclear ncpGS and ITS trees.

In the last decade, the genetic information present in the plant chloroplastic genome has been particularly used for phylogenetic purposes (Clegg et al., 1994; Vekemans et al., 1998), because of its non-Mendelian mode of inheritance and low rate of evolution as compared to that of the nuclear genome, which makes it very useful in studying the variation at levels higher than the species, considering that the probability of detecting intraspecific variation is low. This trend has been furthered accentuated by the development of efficient techniques to study this variation, among them PCR-RFLP or CAPS (cleaved amplified polymorphic sequence), which employs universal primers for amplification of specific noncoding DNA, followed by their restriction. This technique soon appeared to be more efficient than traditional RFLP to reveal polymorphism. Its successful application to a number of crop and forest species for which extensive nucleotide information is now available (Mes et al., 1997; Lakshmi et al., 2000; Parani et al., 2000; Duval et al., 2003; Van Droogenbroeck et al., 2004; Kyndt et al., 2005), has changed the common perception of the variability of chloroplast genome. Reviewing cases of cpDNA variation at the intraspecific level, and even within individuals, Harris & Ingram (1991) have underlined that hybridization, introgression and lineage sorting all may influence a taxon's position in cpDNA phylogenies. They have also underlined that the occurrence of widespread biparental plastid transmission in the Angiosperms makes the implicit assumption that hybridization can be ignored not always tenable. The mitochondrial genome has been less used because of its high degree of intramolecular recombination and low rate of base substitution. In *Passiflora*, biparental plastid transmission was first suspected by Corriveau & Coleman (1988), following epifluorescence microscopy observations on *P. edulis*. Do et al. (1992) showed that RFLP markers of cpDNA were mostly inherited maternally in crosses between yellow and purple maracuja when the former (*P. edulis* f. *flavicarpa*) was used as female parent, and biparental in the reciprocal cross, suggesting asymmetric post-fertilization exclusion processes. Transmission was paternal in the hybrid '*P. coccinea* x *P. edulis* f. *flavicarpa*'. More recently, Mráček (2005) observed biparental transmission between *P. menispermifolia* and *P. oerstedii* and heteroplasmy in resulting hybrids. Muschner et al. (2006) established paternal transmission of cpDNA in four interspecific hybrids of subgenera *Passiflora* and *Dysosmia* and maternal transmission in an interspecific hybrid of subgenus *Decaloba*. All mtDNA were maternally transmitted in these five hybrids. Hansen et al. (2007) studied 17 crosses and found paternal or biparental inheritance of cpDNA, except in their intraspecific crosses, where it was predominantly maternal. Hansen et al. (2007) evoked the possible effect of genetic divergence between the parents, however it should be noted that the progeny studied was from *P. costaricensis*, the only species of subgenus *Decaloba* in their study. Hence, an alternative and simpler explanation, consistent with the results of Muschner et al. (2006), could be differences in cpDNA transmission between subgenera.

The study presented here was planned before the publication of phylogenetic studies in *Passiflora*. The implementation of projects including extensive collecting of *Passiflora* germplasm in Colombia, the country with the widest *Passiflora* diversity (Chapter II), provided a unique opportunity to study a very wide sample of the genus, taking into account possible variation at the infraspecific level. The species sample was significantly widened thanks to the contribution of the French National collection. The PCR-RFLP technique was chosen because of its relative simplicity, rapidity, and cost efficiency. At that time, sequence analyses would have been more expensive, not allowing the study of the genomes of both organelles on so many individuals. Two cpDNA spacer regions, (*psb*C-*trn*S and *trn*S-*trnf*M), and two mtDNA introns (*nad*4-1/2 and *nad*1-B/C) were analyzed for variation at both intra-and intergeneric levels in the 151 *Passiflora* species of our sample and four species of the Old World genera *Adenia*, *Barteria* and *Smeathmannia*. The objective was to study the general structure of genetic diversity in the genus, with particular attention to the cultivated species and their close relatives.

V.1.3. Materials and methods

V.1.3.1. *Taxon sampling*

The germplasm sample consisted of 213 individuals from 151 species, representing 15 of the subgenera recognized by Killip (1938), Escobar (1988) and MacDougal (1994), and eight outgroup accessions of *Adenia*, and *Barteria*, and *Smeathmannia*, from Africa (Table 1). This sample included several representatives of the principal cultivated species. Most of the materials were collected in Colombia, from the wild, home gardens, and farms (see Chapter II). Voucher specimens were deposited at COL and VALLE herbaria. Other samples were obtained from the living National Collection in Blois (France), mainly collected in French Guiana and Brazil, and maintained by Christian Houel. Specimen identification was based on the morphological descriptions of Killip (1938), Holm-Nielsen et al. (1988), Escobar (1988a,b, 1994) and MacDougal (1992, 1994), and the comparison with herbarium material (mostly COL, HUA, MEDEL, COAH, K, MA, MO, NY, P, PSO). Infrageneric taxonomy follows the same references, unless specified otherwise.

Table 1. List of species used in this study according to classification by Killip (1938), Escobar (1988a,b) and MacDougal (1994).

Infrageneric clasification	**Collection data**	**Status**
Passifloraceae Juss. *ex* Kunth.		
Tribe *Paropsieae* D.C., 1828		
Genus *Barteria* Hooker, J.D., 1860		
B. fistulosa Mast.	Cameroon, Kandara (Central Province)	Wild
B. fistulosa Mast.	Cameroon, Ebodjé (Southwest Province)	Wild
B. nigritiana Hook. f.	Cameroon, Ebodjé (Southwest Province)	Wild
B. nigritiana Hook. f.	Gabon	Wild
B. solida F. J. Breteler	Cameroon, Dikome Balue (Southwest Province)	Wild
Genus *Smeathmannia* Solander *ex* R. Brown, 1821		
S. pubescens Sol. *ex* R. Br.	Cameroon, Ebodje (Southwest Province)	Wild
S. pubescens Sol. *ex* R. Br.	Cameroon, Mamalles (Southwest Province)	Wild
Tribe *Passifloreae* D.C., 1828		
Genus *Adenia* Forsskal, 1775		
Adenia glauca Schinz	National Collection - Blois - France	Wild
Genus *Passiflora* L., 1753		
Subgenus *Astrophea* (DC.) Mast., 1871		
Section *Dolichostemma*		

P. mariquitensis Mutis *ex* L. Uribe	Colombia, Tolima, Mariquita	Wild
Section *Euastrophea*		
P. arborea Spreng.	Colombia, Caldas, Manizales	Wild
P. emarginata Humb. & Bonpl.	Colombia, Caldas, Manizales	Wild
P. emarginata Humb. & Bonpl.	Colombia, Valle del Cauca, Yotoco	Wild
P. sphaerocarpa Triana & Planch.	Colombia, Valle del Cauca, Cali	Wild
P. sphaerocarpa Triana & Planch.	Colombia, Tolima, Ibagué	Wild
P. macrophylla Spruce *ex* Mast.	Ecuador, National Collection - Blois - France	Wild
Section *Pseudoastrophea*		
P. citrifolia (Juss.) Mast.	Guiana French, Belgian National Botanic Garden - Meise	Wild
P. citrifolia (Juss.) Mast.	National Collection - Blois - France	Wild
P. haematostigma Mart. *ex* Mast.	Guiana French, National Collection - Blois - France	Wild
P. kawensis Feuillet	National Collection - Blois - France	Wild
Subgenus *Calopathanthus* (Harms) Killip, 1938		
P. racemosa Brot.	National Collection - Blois - France	Wild
Subgenus *Decaloba* (DC.) Rchb.		
Section Cieca		
P. apoda Harms	Colombia, Caldas, Manizales	Wild
P. coriacea Juss.	Colombia, Caldas, Palestina	Wild
P. coriacea Juss.	Colombia, Tolima, Ibagué	Wild
P. coriacea Juss.	Colombia, Valle del Cauca, Palmira	Wild
P. exoperculata Mast.	Ecuador, Tunguragua, Ceballos	Wild
P. gracilis J. Jacq. *ex* Link	USA, National Collection - Blois - France	Wild
P. holosericea L.	National Collection - Blois - France	Wild
P. monadelpha P. Jorg. & Holm-Niels.	Colombia, Valle del Cauca, El Cerrito	Wild
P. mutiflora L.	National Collection - Blois - France	Wild
P. suberosa L.	Colombia, Antioquia, Jerico	Wild
P. suberosa L.	Colombia, Caldas, Manizales	Wild
Section *Decaloba*		
Series *Apetalae*		
P. apetala Killip	National Collection - Blois - France	Wild
Series *Auriculatae*		
P. auriculata Kunth	Colombia, Caldas, Victoria	Wild
P. auriculata Kunth	Guiana French, National Collection - Blois - France	Wild
P. jatunsachensis Schwerdtfeger	National Collection - Blois - France	Wild
Series *Luteae*		
P. filipes Benth.	Colombia, Risaralda, Pereira	Wild
Series *Miserae*		
P. amalocarpa Barb. Rodr.	National Collection - Blois - France	Wild
P. misera Kunth	Colombia, Valle del Cauca, Jamundi	Wild
P. misera Kunth	National Collection - Blois - France	Wild
P. trifasciata Lem	Colombia, Quindio, Buenavista - (introduced)	Wild
P. tricuspis Mast.	Bolivia, Santa Cruz	Wild
P. tricuspis Mast.	Brasil, National Collection - Blois - France	Wild
Series *Punctatae*		
P. alnifolia Kunth	Colombia, Valle del Cauca, El Cerrito	Wild
P. alnifolia Kunth	Colombia, Caldas, Manizales	Wild
P. alnifolia Kunth	Colombia, Nariño, Pasto	Wild
P. biflora Lam.	Colombia, Caldas, Victoria	Wild
P. biflora Lam.	Colombia, Tolima, Mariquita	Wild
P. boenderi MacDougal	National Collection - Blois - France	Wild
P. bogotensis Benth.	Colombia, Cundinamarca, Bogotá	Wild
P. colinvauxii Wiggins	Ecuador, National Collection - Blois - France	Wild

P. cuneata Wild.	Colombia, Boyacá, Duitama	Wild
P. cuneata Wild.	National Collection - Blois - France	Wild
P. cupraea L.	National Collection - Blois - France	Wild
P. erytrophylla Mast.	Colombia, Boyacá, Duitama	Wild
P. gilbertiana MacDougal	National Collection - Blois - France	Wild
P. occidentalis	Colombia, Valle del Cauca, Buenaventura	Wild
P. pohii Mast.	National Collection - Blois - France	Wild
P. magdalenae Triana & Planch.	Colombia, Caldas, Victoria	Wild
P. magdalenae Triana & Planch.	Colombia, Cundinamarca, San Juan de Rio Seco	Wild
P. micropetala Mast.	National Collection - Blois - France	Wild
P. vespertilio L.	Guiana French, National Collection - Blois - France	Wild
P. yucatanensis Killip	Mexico, National Collection - Blois - France	Wild
Series *Sexflorae*		
P. allantophylla Mast.	National Collection - Blois - France	Wild
Section *Eudecaloba*		
P. aurantia G. Forst.	Australia, National Collection - Blois - France	Wild
P. herbertiana Ker-Gawl.	National Collection - Blois - France	Wild
Section *Hahniopathanthus*		
P. guatemalensis S. Watson	Colombia, Caldas, Filadelfia	Wild
Section *Organenses*		
P. ornithoura Mast.	National Collection - Blois - France	Wild
Section *Pseudodysosmia*		
P. adenopoda Moc. & Sessé *ex* DC.	Colombia, Caldas, Manizales	Wild
P. adenopoda Moc. & Sessé *ex* DC.	National Collection - Blois - France	Wild
P. karwinskii Mast.	National Collection - Blois - France	Wild
P. lobata (Killip) Hutchinson *ex* MacDougal	National Collection - Blois - France	Wild
Section *Pseudogranadilla*		
P. bicornis Mill.	National Collection - Blois - France	Wild
P. bicornis Mill.	National Collection - Blois - France	Wild
P. indecora Kunth	National Collection - Blois - France	Wild
P. telesiphe Knapp & Mallet	National Collection - Blois - France	Wild
Section *Xerogona*		
P. rubra L.	Colombia, Quindio, Calarca	Wild
Subgenus *Deidamioides* (Harms) Killip, 1938		
P. deidamioides Harms	National Collection - Blois - France	Wild
P. lancetillensis MacDougal & Meerman	National Collection - Blois - France	Wild
Subgenus *Distephana* (Juss,) Killip, 1938		
P. aimae Annonay & Feuillet	Guiana French, National Collection - Blois - France	Wild
P. coccinea Aubl.	Guiana French, Belgian National Botanic Garden - Meise	Wild
P. quadriglandulosa Rodschied	National Collection - Blois - France	Wild
P. speciosa Gardn.	National Collection - Blois - France	Wild
P. variolata Poep & Endl.	National Collection - Blois - France	Wild
P. vitifolia (Harv.) Harms	Colombia, Chocó, Quibdo	Home garden
P. vitifolia (Harv.) Harms	Colombia, Tolima, Ibagué	Wild
Subgenus *Disosmioides* Killip, 1938		
P. campanulata Mast.	Brasil, National Collection - Blois - France	Wild
P. setulosa Killip	National Collection - Blois - France	Wild
Subgenus *Dysosmia* DC., 1938		
P. foetida var. *moritziana* (Planch.) Killip *ex* Pull	Guiana French, National Collection - Blois - France	Wild
P. foetida var. *gossypiifolia* (Desv.) Mast.	Colombia, Chocó, Quibdo	Wild
P. arida (Mast. & Rose) Killip	National Collection - Blois - France	Wild
Subgenus *Manicata* (Harms) Escobar, 1988		
P. macropoda Killip	National Collection - Blois - France	Wild

P. manicata (Juss.) Pers.	Colombia, Quindio, Salento	Wild
P. manicata (Juss.) Pers.	Ecuador, Tunguragua, Ambato	Wild
P. trisecta Mast.	National Collection - Blois - France	Wild
Subgenus *Murucuja* (Medic.) Mast., 1871		
P. murucuja L.	National Collection - Blois - France	Wild
P. tulae Urban	National Collection - Blois - France	Wild
Subgenus *Pseudomurucuja* (Harms.) Killip		
P. perfoliata L.	National Collection - Blois - France	Wild
Subgenus *Psilanthus* (DC.) Killip, 1938		
P. trinervia (Juss.) Poir.	Colombia, Quindio, Salento	Wild
Subgenus *Passiflora*		
Series *Digitatae* Killip		
P. serrato-digitata L.	National Collection - Blois - France	Wild
Series *Incarnatae*		
P. cincinnata Mast.	Brasil	Wild
P. edulis f. *edulis* Sims	Colombia, Cauca, Timbio	Home garden
P. edulis f. *edulis* Sims	Colombia, Antioquia, Fredonia	Wild
P. edulis f. *edulis* Sims	Colombia, Cundinamarca, San Juan de Río Seco	Home garden
P. edulis f. *flavicarpa* Degener	Brasil, Araguari	Cultivated
P. edulis f. *flavicarpa* Degener	Colombia, Amazonas, Leticia	Home garden
P. edulis f. *flavicarpa* Degener	Ecuador, Guayas, Guayaquil	Cultivated
P. edulis f. *flavicarpa* Degener	Perú, Santa Vilma	Cultivated
P. edulis f. *flavicarpa* Degener	Colombia, Chocó, Quibdo	Cultivated
P. edulis f. *flavicarpa* Degener	Colombia, Valle del Cauca, La Unión	Cultivated
P. edulis f. *flavicarpa* Degener	Brasil, National Collection - Blois - France	Wild
P. incarnata L.	USA, Florida, Miami	Home garden
P. incarnata L.	USA, National Collection - Blois - France	Wild
Series *Kermesinae*		
P. edmundoi Sacco	Brasil, National Collection - Blois - France	Wild
P. kermesina Link & Otto	National Collection - Blois - France	Wild
P. lehmanni Mast	Colombia, Quindio, Calarca	Wild
P. lehmanni Mast	Colombia, Caldas, Manizales	Wild
P. loefgrenii Vitta	Brasil, National Collection - Blois - France	Wild
P. miersii Mast.	National Collection - Blois - France	Wild
P. smithii Killip	Colombia, Tolima, Fresno	Wild
P. smithii Killip	Colombia, Tolima, Ibagué	Wild
P. trisulca Mast.	National Collection - Blois - France	Wild
Series *Laurifoliae*		
P. acuminata DC.	National Collection - Blois - France	Wild
P. ambigua Hermsl.	Colombia, Belgian National Botanic Garden - Meise	Wild
P. carinata	National Collection - Blois - France	Wild
P. crenata Feuillet & Cremers	National Collection - Blois - France	Wild
P. fernandezii L. K. Escobar	Bolivia, National Collection - Blois - France	Wild
P. gabrielliana Vanderplank	Guiana French, National Collection - Blois - France	Wild
P. laurifolia L.	Guiana French, National Collection - Blois - France	Wild
P. nigradenia Rusby	National Collection - Blois - France	Wild
P. nitida Kunth	National Collection - Blois - France	Wild
P. nitida Kunth	Colombia, Chocó, Quibdo	Home garden
P. odontophylla Harms *ex* Glaz.	Brasil, National Collection - Blois - France	Wild
P. popenovii Killip	Colombia, Cauca, El Tambo	Home garden
P. popenovii Killip	Colombia, Nariño, Chachagui	Home garden
P. riparia Mart. *ex* Mast.	National Collection - Blois - France	Wild
P. rufostipulata Feuillet	Guiana French, Belgian National Botanic Garden - Meise	Wild
Series *Lobatae*		

P. amethystina Mikan	National Collection - Blois - France	Wild
P. caerulea L.	France, Herault, Montpellier - (introduced)	Home garden
P. caerulea L.	Brasil, National Collection - Blois - France	Wild
P. eichleriana Mast.	National Collection - Blois - France	Wild
P. elegans Mast.	National Collection - Blois - France	Wild
P. garckei Mast.	Guiana French, Belgian National Botanic Garden - Meise	Wild
P. garckei Mast.	Guiana French, National Collection - Blois - France	Wild
P. gibertii N. E. Brown	National Collection - Blois - France	Wild
P. gritensis Karts.	National Collection - Blois - France	Wild
P. mooreana Hook.	National Collection - Blois - France	Wild
P. pallens Poepp. *ex* Mast.	National Collection - Blois - France	Wild
P. sprucei Mast.	National Collection - Blois - France	Wild
P. stipulata Aubl.	National Collection - Blois - France	Wild
P. subpeltata Ortega	National Collection - Blois - France	Wild
P. tucumanensis Hook.	National Collection - Blois - France	Wild
P. urubicensis Cervi	National Collection - Blois - France	Wild
Series *Marginatae*		
P. marginata Mast.	National Collection - Blois - France	Wild
Series *Menispermifolia*		
P. crassifolia Killip	National Collection - Blois - France	Wild
P. menispermifolia Kunth	Colombia, Tolima, Ibagué	Wild
P. menispermifolia Kunth	National Collection - Blois - France	Wild
P. nephrodes Mast.	Bolivia, National Collection - Blois - France	Wild
P. reitzii Sacco	National Collection - Blois - France	Wild
Series *Quadrangulares*		
P. alata Curtis	Brasil	Cultivated
P. alata Curtis	Brasil, National Collection - Blois - France	Wild
P. quadrangularis L.	Colombia, Huila, Paicol	Cultivated
Series *Serratifoliae*		
P. bahiensis Klotzsch	Brasil, Bahia, Salvador	Wild
*P. serratifolia*L.	National Collection - Blois - France	Wild
Series *Simplicifoliae*		
P. dispar Killip	National Collection - Blois - France	Wild
P. galbana Mast.	Guiana French, National Collection - Blois - France	Wild
P. mapiriensis Harms	Guiana French, National Collection - Blois - France	Wild
P. oerstedii Mast.	Colombia, Tolima, Ibagué	Wild
P. oerstedii Mast.	Colombia, Cauca, Popayán	Wild
P. oerstedii var. *choconiana* (S. Watson) Killip	National Collection - Blois - France	Wild
P. subrotunda Mast.	National Collection - Blois - France	Wild
Series *Tiliifoliae*		
P. ligularis Juss.	Colombia, Nariño, Ipiales	Cultivated
P. ligularis Juss.	Colombia, Risaralda, Marsella	Cultivated
P. ligularis Juss.	Colombia, Caldas, Manizales	Wild
P. ligularis Juss.	Colombia, Quindio, Calarca	Home garden
P. maliformis L.	Colombia, Santander, Barichara	Home garden
P. maliformis L.	Colombia, Antioquia, Fredonia	Home garden
P. maliformis L.	Colombia, Huila, La Plata	Cultivated
P. multiformis Jacq.	Colombia, Norte de Santander, Ocaña	Home garden
P. palenquensis Holm-Niels. & Lawesson	Colombia, Chocó, Quibdo	Cultivated
P. seemannii Griseb	National Collection - Blois - France	Wild
P. serrulata Jacq.	Colombia, Magdalena, Plato	Wild
P. tiliifolia L.	Colombia, Quindio, Filandia	Wild
P. tiliifolia L.	Colombia, Valle del Cauca, El Cerrito	Wild
Subgenus *Tacsonia* (Juss.) Tr. & Planch, 1873		

Section *Colombiana*		
Series *Colombiana*		
P. adulterina L. f.	Colombia, Boyacá, Duitama	Wild
P. adulterina L. f.	Colombia, National Collection - Blois - France	Wild
P. lanata (Juss.)	Colombia, Boyacá, Duitama	Wild
Series *Leptomischae*		
P. ampullacea (Mast.) Harms	National Collection - Blois - France	Wild
P. antioquiensis Karst.	Colombia, Caldas, Villamaria	Wild
P. antioquiensis Karst.	Colombia, Antioquia, Santa Rosa de Osos	Wild
P. antioquiensis Karst.	Colombia, Caldas, Manizales	Wild
P. flexipes Triana & Planch	Colombia, Quindio, Salento	Wild
P. tenerifensis L. K. Escobar	Colombia, Valle del Cauca, El Cerrito	Wild
Series *Quindensae*		
P. linearistipula L. K. Escobar	Colombia, Caldas, Manizales	Wild
Section *Bracteogamma*		
P. cumbalensis var. *cumbalensis* (Karst.) Harms	Ecuador	Wild
P. cumbalensis var. *goudotiana* (Tr. & Planch.) L.K. Escobar	Colombia, Boyacá, Duitama	Wild
P. luzmarina Jorgensen	Ecuador, Loja, Loja	Wild
P. tarminiana Coppens & Barney	Colombia, Caldas, Villamaria	Home garden
P. tarminiana Coppens & Barney	Perú, Huancavelica	Home garden
P. tarminiana Coppens & Barney	Venezuela, Táchira	Home garden
P. tarminiana Coppens & Barney	Venezuela, Tachira	Home garden
P. tarminiana Coppens & Barney	Colombia, Cauca, Slivia	Wild
P. tripartita var. mollissima (Kunth) Holm-Niel & Jorg	Colombia, Boyacá, Nuevo Colón	Cultivated
P. tripartita var. mollissima (Kunth) Holm-Niel & Jorg	Colombia, Cundinamarca, Tequendama	Wild
P. tripartita var. mollissima (Kunth) Holm-Niel & Jorg	Venezuela, Táchira, Villa Paez, Betania	Home garden
Section *Parritana* Escobar		
P. parritae (Mast.) L. H. Bailey	Colombia, Tolima, Herveo	Wild
Section *Poggendorffia*		
P. pinnatistipula Cav.	Ecuador, Tunguragua, Ambato	Wild
Section *Tacsonia*		
P. matthewssii (Mast.) Killip	Ecuador	Wild
P. mixta L. f.	Colombia, Valle del Cauca, El Cerrito	Wild
P. mixta L. f.	Colombia, Cauca, Totoró	Wild
Subgenus *Tacsonioides* (DC.) Killip, 1938		
P. mendoncaei Harms	National Collection - Blois - France	Wild
P. reflexiflora Cav.	National Collection - Blois - France	Wild
P. umbilicata (Griseb.) Harms	National Collection - Blois - France	Wild
Subgenus *Tryphostemmatoides* (Harms) Killip, 1938		
P. gracillima Killip	Colombia, Salento, Quindío	Wild

V.1.3.2. *DNA Extraction and PCR-RFLP analyses*

Total genomic DNA was extracted from frozen leaves following the protocol of Doyle & Doyle (1987) with minor modifications and purified on anion exchange micro-columns (Qiagen). All samples were qualified on a 0.8% agarose gel, in 1x TBE buffer and electrophoresed at 110 V during 1 hour and visualized under UV light.

Two cpDNA regions, intergeneric spacer (*psb*C- *trn*S and *trn*S - *trnf*M), and two mtDNA introns (*nad*4-1/2 and *nad*1-B/C), were amplified using PCR and the universal primer pairs indicated by Demesure et al. (1995) and evaluated in the subgenus *Passiflora* by Vargas (2000). The PCR products were subsequently digested with six endonucleases selected by Varón (2000) (*Hae* III, *Hha* I, *Hinf* I, *Hpa* II, *Taq* I, and *Rsa* I - *BioLabs*$^{\copyright}$; Table 2). The PCR reaction mix contained 25 ng of template DNA, 10 mM Tris-HCl, 50 mM KCL, 1.5 mM MgCl2, 0.15 μM of each primer, 2.5 μM of each dNTP and 10 units of *Taq* polymerase, in a total volume of 50 μl. PCR-amplification was performed at 95°C for 4 min for initial denaturation, followed by 35 cycles at 94°C for 30 s, 57°C for 1 min, 72°C for 3 min, and was terminated by 10 min at 72°C. To confirm successful amplification and to determine the size of amplified fragments, 8 μl of PCR products were separated by electrophoresis in a 1% agarose gel, in 1 x TBE buffer. The DNA fragments were visualized by UV fluorescence after staining with ethidium bromide. The approximate product size was calculated by comparison of the migration distance of the PCR product with a DNA marker (1-kb ladder).

Ten microliters of each PCR product was restricted in a volume of 20 μl containing 5 units of restriction enzyme for 3 hours at 37°C, according to the manufacturer's procedures. Restriction fragments were separated on 1.2% agarose gels containing ethidium bromide in 1x Trisborate EDTA (TBE), run at 110 V for 3 hours, and visualized under UV light. Figure 1 shows the general schema of the PCR-RFLP markers.

Table 2. DNA sequence and type of primer pairs used in the present study by Demesure et al. (1995).

Primers	**Code**	**Sequence (5'- 3')**	**Organelle - DNA type**
*psb*C [psII 44 kd protein]	PC1 – PC2	GGTCGTGACCAAGAAACCAC	Chloroplast
*trn*S [tRNA-Ser (UGA)]		GGTTCGAATCCCTCTCTCTC	
*trn*S [tRNA – Ser (UGA)]	TS1 – TS2	GAGAGAGAGGCATTCGAACC	Chloroplast
*trn*fM [tRNA- fMet (CAU)]		CATAACCTTGAGGTCACGGG	
*nad*4 exon 1	N41 – N42	CAGTGGGTTGGTCTGGTATG	Mitochondrial
*nad*4 exon 2		TCATATGGGCTACTGAGGAG	
*nad*1 exon B	N1B – N1C	GCATTACGATCTGCAGCTCA	Mitochondrial
*nad*1 exon C		GGAGCTCGATTAGTTTCTGC	

V.1.3.3. *Data analysis*

Most restriction patterns were impossible to interpret in terms of mutations, because of the high number of bands. Instead, these were scored for presence (1) or absence (0) and used to identify chloroplast and mitochondria haplotypes, generating a binary data matrix for the subsequent phenetic analyses. The Sokal & Michener (1958) coefficient of genetic similarity was calculated for each pair of haplotypes. The similarity matrix was employed in a principal co-ordinate analysis (PCO) and the construction of a phenogram by the neighbor-joining method (Saitou & Nei, 1987), calculating bootstrap values from 1000 replicates. These analyses were performed using the DARwin 5.0 software (Perrier et al., 2003).

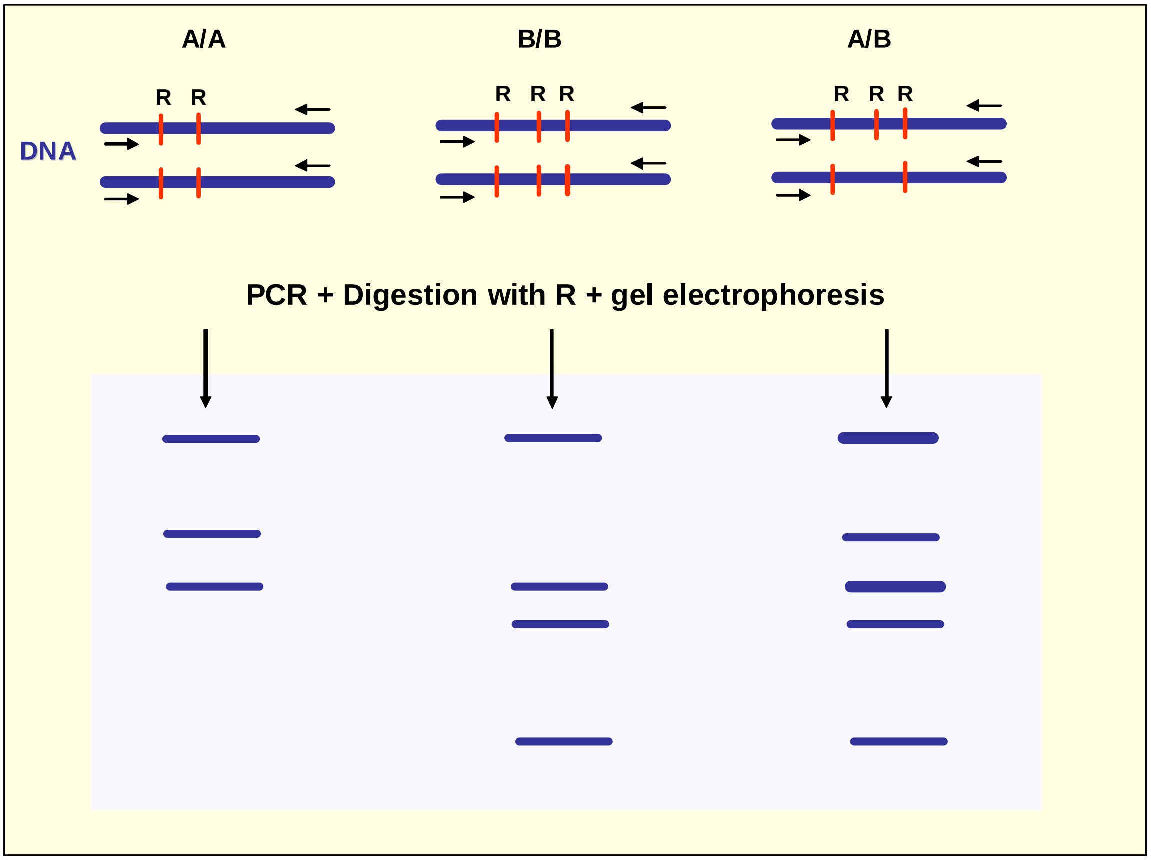


Figure 1. General schema of the PCR-RFLP markers (CAPS).

V.1.4. Results

V.1.4.1. *PCR amplification*

All four primer pairs used in the present study successfully amplified the corresponding cpDNA and mtDNA regions in 151 species of genus *Passiflora* and four species of *Adenia*, *Barteria* and *Smeathmannia*, producing fragment whose length varied from 820 to 2,040 bp (Table 3). Polymorphism for chloroplast fragment (PC1-PC2) distinguishes *P. tripartita* var. *mollissima*, *P. antioquiensis*, *P. pinnatistipula* and *P. murucuja* from all other species. Four different fragment lengths were observed for TS1-TS2, two for subgenus *Decaloba*, with a difference between Australian and American species, one for three species of subgenus *Passiflora* series *Laurifoliae* (*P. popenovii*, *P.nitida* and *P. laurifolia*), and one for all the other species. Eight fragment lengths are observed for the mitochondrial N1B-N1C, discriminating *P. coriacae*, *P. multiflora*, *P. perfoliata* and all the species of subgenus *Tacsonia*. For the N41-N42 region, only one fragment was detected with a weak degree of amplification.

Table 3. Numbers of haplotypes and fragments for each combination primer/ enzyme.

Primers	**Size of amplification products (bp)**	**Degree amplification**	***Hinf* I**	***Rsa* I**	***Hpa* II**	***Hae* III**	***Hha* I**	***Taq* I**
			Total number haplotypes / fragments					
PC1 – PC2	1875-1896-1930-2000	strong	13 / 17	2 / 4*	19 / 18	29 / 34	27 / 34	15 / 16
TS1 – TS2	820-1200-1250-1345-1400-1470-1500-1550-1650-1693-1735-1780-1810	strong	60 / 28	34 / 26	32 / 46	10 / 11	13 / 16	30 /22
N41 – N42	2036	weak	27 /22	34 / 32	48 / 59	36 / 31	50 / 47	22 / 29*
N1B – N1C	1500-1580-1605-1690-1885-1910-2000-2040	good	26 / 29	17 / 21	27 / 22	20 / 22	16 / 16	12 / 31

* not interpretable.

V.1.4.2. *Restriction analysis*

All twenty-four fragment/enzyme combinations revealed polymorphism, but restriction profiles could not be read in two cases [(N41-N42/*Taq*I) and (PC1PC2/*Rsa*I)]. A total of 614 fragments were scored, of which 93% were found to be polymorphic in the sample (Table 3). All the polymorphism was due to insertion-deletion (indel) mutations. Because of the high number of fragments in relation to the sample size (213 individuals), banding patterns could not be interpreted in terms of particular mutations. Figure 2 presents examples of the interspecific variation for cp/mtDNA.

The PCR-RFLP analysis of the chloroplast regions showed polymorphism with all enzymes, resulting in 268 interpretable polymorphic fragments for the 11 fragment/enzyme combinations. The 11 mitochondrial fragment/enzyme combinations exhibited a high polymorphism too, with 307 interpretable fragments, but the resolution of the fragments was less clear. The combination N41-N42/*Hpa*II was by far the most polymorphic one, with 59 fragments differentiating among genera and subgenera.

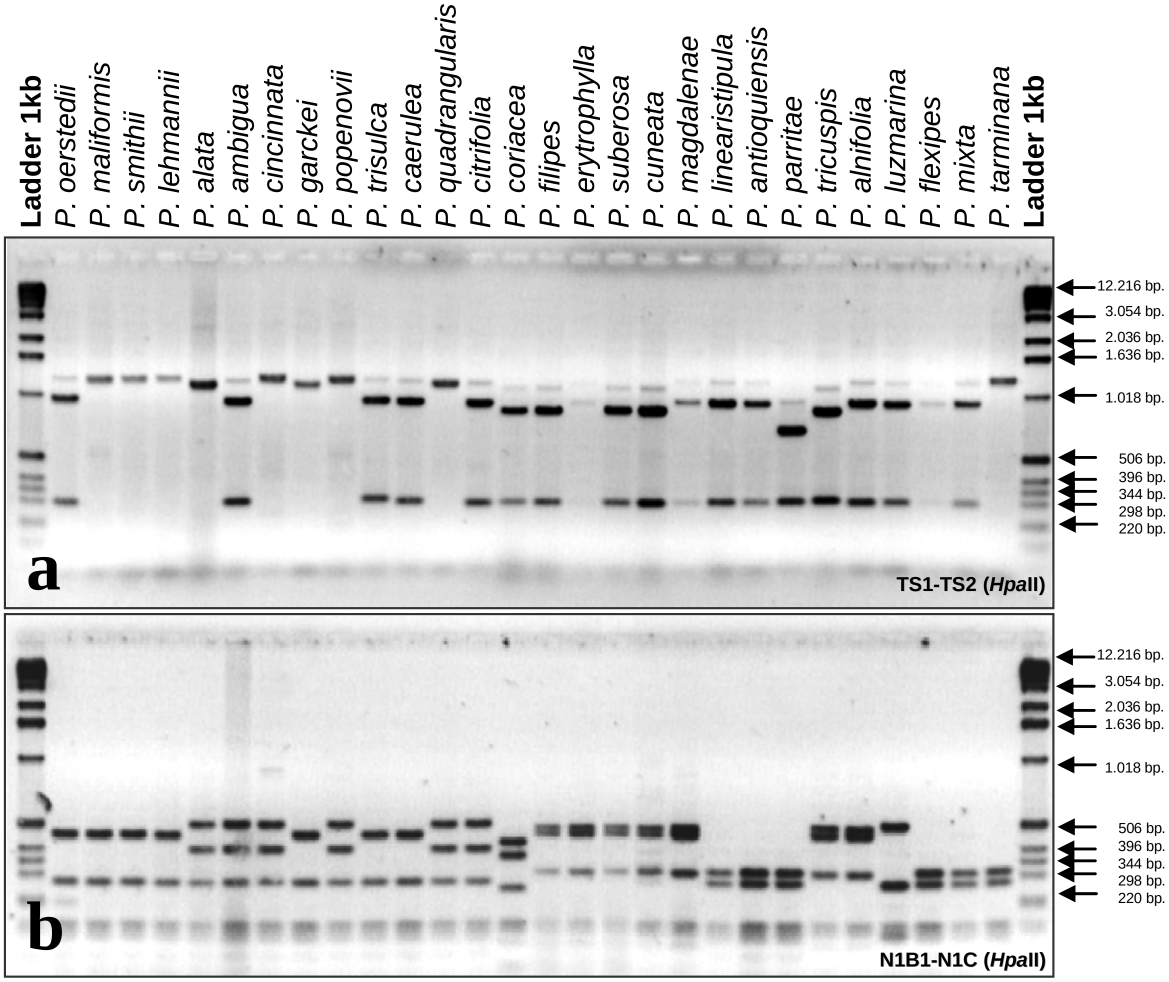


Figure 2. Interspecific variation for cpDNA (a) and mtDNA (b) among different *Passifora* species.

V.1.4.3. *PCR-RFLP haplotypes*

A total of 280 chloroplast haplotypes and 372 mitochondrial haplotypes were found (Table 3). Their global patterns of distribution among genera and subgenera are summarized in Table 4.

For the chloroplast, the TS1-TS2 region displayed more variation (177 haplotypes) than the PC1-PC2 region (103 haplotypes). Chlorotypes clearly distinguished subgenus *Decaloba* from the rest of the sample, as its species exhibited two or three specific haplotype patterns in all fragment/enzyme combinations. Subgenus *Astrophea* showed specific chlorotypes after the restriction of the TS1-TS2 region with *Rsa* I and *Taq* I. Subgenus *Distephana* was differentiated by the TS1-TS2/*Taq* I combination. Subgenera *Dysosmia, Manicata* and *Tacsonia* shared haplotypes for many combinations, so they cannot be clearly distinguished from each other. Subgenus *Tacsonia* appeared highly uniform for most combinations. Within subgenus *Passiflora*, most species of series *Laurifoliae* presented specific restriction patterns of the TS1-TS2 fragment (*Hha* I, *Rsa* I, and *Taq* I. Several combinations (*Hinf* I and *Taq* I) allowed distinguishing another morphological group, the typical representatives of series *Tiliifoliae* (*P. ligularis*, *P. palenquensis*, *P. tiliifolia*, *P. seemannii*). The outgroup (*Adenia*, *Barteria* and *Smeathmannia*) showed specific chlorotypes in most combinations. When this was not the case, they usually showed similarities with species of subgenus *Passiflora*.

A higher number of mtDNA haplotypes were observed, 245 for the N41-N42 region and 127 for the N1B-N1C region. Subgenus *Decaloba* again displayed many specific haplotypes, however it shared several mitotypes with *Barteria* and *Smeathmannia*. All accessions of subgenus *Tacsonia* but four were clearly differentiated by highly specific and uniform mitotypes for the N1B-N1C regions. The four exceptions were Ecuadorian accessions of *P. pinnatistipula*, *P. matthewsii*, *P. luzmarina* and *P. cumbalensis,* sharing most restriction patterns with subgenus *Passiflora*. Subgenus *Murucuja* was differentiated by the N1B-B1C/*Hha* I combination.

In most species represented by several individuals, intraspecific variation was observed for both cpDNA and mtDNA. Although represented by two accessions only, *P. foetida* and *P. vitifolia* displayed the highest diversity of haplotypes. Other remarkable cases are those of *P. ligularis, P. maliformis, P. alata*, *P. caerulea*, and *P. sphaerocarpa*.

Table 4. Global distribution of the haplotypes among the genera and subgenera studied.

Primers	***Hinf* I**	***Rsa* I**	***Hpa* II**	***Hae* III**	***Hha* I**	***Taq* I**
PC1 – PC2	*Decaloba* two groups - *Adenia* - *Barteria* - *Smeathmannia* - other subgenera	Impossible to interpret	*Decaloba* three groups - other subgenera	*Decaloba* - *Adenia* - *Smeathmannia* - other subgenera	*Decaloba* three groups - *Passiflora* two groups - *Tacsonia* two groups - other subgenera	*Decaloba* - other subgenera
TS1 – TS2	*Decaloba* two groups - *Passiflora* four groups - (*Barteria* - *Smeathmannia*) - other subgenera	*Decaloba* three groups - *Passiflora* four groups - *Astrophea* - other subgenera	*Decaloba* two groups - *Passiflora* three groups - *Adenia* - (*Barteria* - *Smeathmannia*) - other subgenera	*Decaloba* three groups - *Passiflora* two groups - other subgenera	*Decaloba* two groups - *Passiflora* two groups - other subgenera	*Decaloba* three groups - *Passiflora* two groups - *Distephana* - *Astrophea* - *Adenia* - (*Barteria* - *Smeathmannia*) - other subgenera
N41 – N42	*Decaloba* two groups - *Passiflora* - *Astrophea* - (*Barteria* - *Smeathmannia*) - other subgenera	*Decaloba* three groups - *Passiflora* two groups - *Adenia* - other subgenera	*Decaloba* two groups *Passiflora* four groups - *Tacsonia* two groups - *Barteria* two groups - other subgenera	*Decaloba* two - *Passiflora* five groups - *Adenia* - other subgenera	*Decaloba* two groups - *Passiflora* three groups - *Barteria* two groups - other subgenera	Impossible to interpret
N1B – N1C	*Decaloba* three groups - *Passiflora* two groups - *Tacsonia* two groups - (*Barteria* - *Smeathmannia*) - *Adenia* - other subgenera	*Decaloba* two groups - *Passiflora* two groups - *Tacsonia* - (*Barteria* - *Smeathmannia*) - *Adenia* - other subgenera	*Decaloba* two groups - *Passiflora* two groups - *Tacsonia* two groups - (*Barteria* - *Smeathmannia*) - other subgenera	*Decaloba* two groups - *Passiflora* two groups - *Tacsonia* two groups - other subgenera	*Decaloba* two groups - *Passiflora* two groups - *Tacsonia* two groups - *Murucuja* - *Adenia* - other subgenera	*Decaloba* two groups - *Tacsonia* - *Barteria* two groups - *Adenia* -

V.1.4.4. *Principal co-ordinates analysis*

The first two axes of the PCO on cpDNA data accounted for 59% of the total variation (Figure 3). They allowed visualizing a strong structure in the diversity under study, as the genera *Adenia*, *Barteria*, and *Passiflora* subgenera *Astrophea*, *Calopathanthus*, *Dysosmia*, *Distephana*, *Manicata*, *Passiflora*, *Tacsonia*, *Tacsonioides* and *Tryphostemmatoides*, and *P. deidamioides* occupy the left half of the principal plan, while the species of *Passiflora* subgenera *Apodogyne*, *Decaloba*, *Murucuja*, *Pseudomurucuja* and *Psilanthus* form a very well separated group, placed in a quite extreme position on the right, only the accessions of *Smeathmannia* and *P. lancetillensis* (subgenus *Deidamioides*) taking intermediate positions. Within genus *Passiflora*, only subgenus *Astrophea* is individualized. The subgenera on the right side form a wide group that we shall call the "*Decaloba* group", by analogy with the "*Decaloba* clade" obtained in previous molecular work (Muschner et al., 2003; Yockteng, 2003; Yockteng & Nadot, 2004, Hansen et al., 2006) and with the subgenus *Decaloba* of the new classification (Feuillet & MacDougal, 2003). In the same way, the major group on the left will be called the "*Passiflora* group". In the latter, only a small group dominated by species of subgenus *Passiflora* series *Laurifoliae* are separated from a bulk comprising species of subgenera *Tacsonia*, *Manicata*, *Calopathanthus*, *Dysosmia*, *Distephana* and *Tacsonioides*. *P. gracillima* (subgenus *Tryphostemmatoides*) is positioned between the '*Passiflora* group' and subgenus *Astrophea*.

V.1.4.5. *Cluster analysis*

The Neighbor-Joining tree obtained with cpDNA data shows three major, well-supported clusters, within genus *Passiflora* (Figure 4). The first one corresponds to the '*Passiflora* group', i.e. subgenera *Calopathanthus*, *Deidamioides, Distephana*, *Dysosmia*, *Dysosmioides*, *Manicata*, *Passiflora, Tacsonia*, and *Tacsonioides*, the second one to subgenus *Astrophea*, the third one to the '*Decaloba* group', i.e. most species of subgenera *Apodogyne, Decaloba, Murucuja, Pseudomurucuja* and *Psilanthus*. *P. gracillima* (subgenus *Tryphostemmatoides*) appears in basal position, forming a fourth cluster of its own. The position of *P. lancetillensis* (subgenus *Deidamioides*) is undefined, as it is placed on a long branch between the outgroup and the '*Decaloba* group' clusters, the outgroup itself taking an undefined position among the three *Passiflora* major clusters.

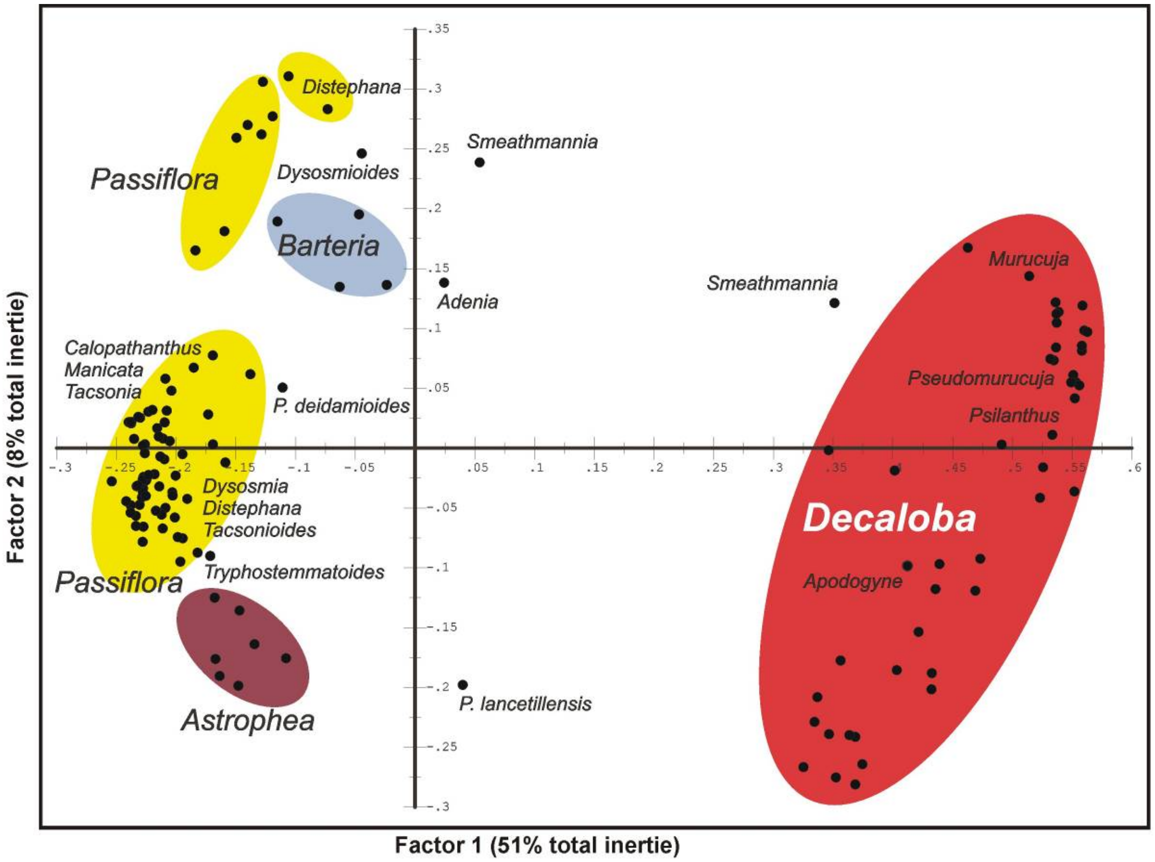


Figure 3. Principal co-ordinates on cpDNA data (PC1-PC2 and TS1-TS2 regions) estimated with 268 CAPS marker.

The *Astrophea* cluster shows no particular substructure, however accessions are logically grouped by species. Within the '*Decaloba* group', *P. karwinskii* (section *Pseudodysosmia*) and the Australian species (section *Eudecaloba*) take a basal position. After their separation, the '*Decaloba* group' is split in two loose subclusters. The first one contains small branches corresponding to particular sections as *Pseudodysosmia* and *Cieca* or to series *Auriculatae* of section *Decaloba* (*P. auriculata* and *P. jutasanchensis*). The second subcluster gathers species of subgenera *Murucuja*, *Pseudomurucuja*, *Psilanthus*, section *Pseudogranadilla* of subgenus *Decaloba* and series *Apetalae*, *Miserae*, *Punctatae*, *Sexflorae*, and *Luteae* of section *Decaloba*. This weak structure related to such low-level infrageneric taxa contrasts with the complete lack of differentiation among higher-level divisions of Killip, i.e. the subgenera constituting the ‘*Decaloba* group’. Thus, *P. trinervia* (subgenus *Psilanthus*), *P. murucuja* (subgenus *Murucuja*), *P. tulae* (subgenus *Murucuja*), and *P. perfoliata* (subgenus *Pseudomurucuja*) are well integrated among species of subgenus *Decaloba*. In addition, different accessions from a same species do not cluster close together, as in *P. bicornis*, *P. magdalenae*, *P. biflora* and *P. tricuspis*. Within the ‘*Passiflora* group’, resolution is very poor, and the substructure very weak. Branches are short and not supported. The only clear subcluster roughly corresponds to the small division of the ‘*Passiflora* group’ in the PCO principal plane. Species from a same subgenus do not tend to form even loose subclusters, with the partial exception of *tacsos* that show a higher uniformity. Even intraspecific variation can be compared in many cases to interspecific variation.

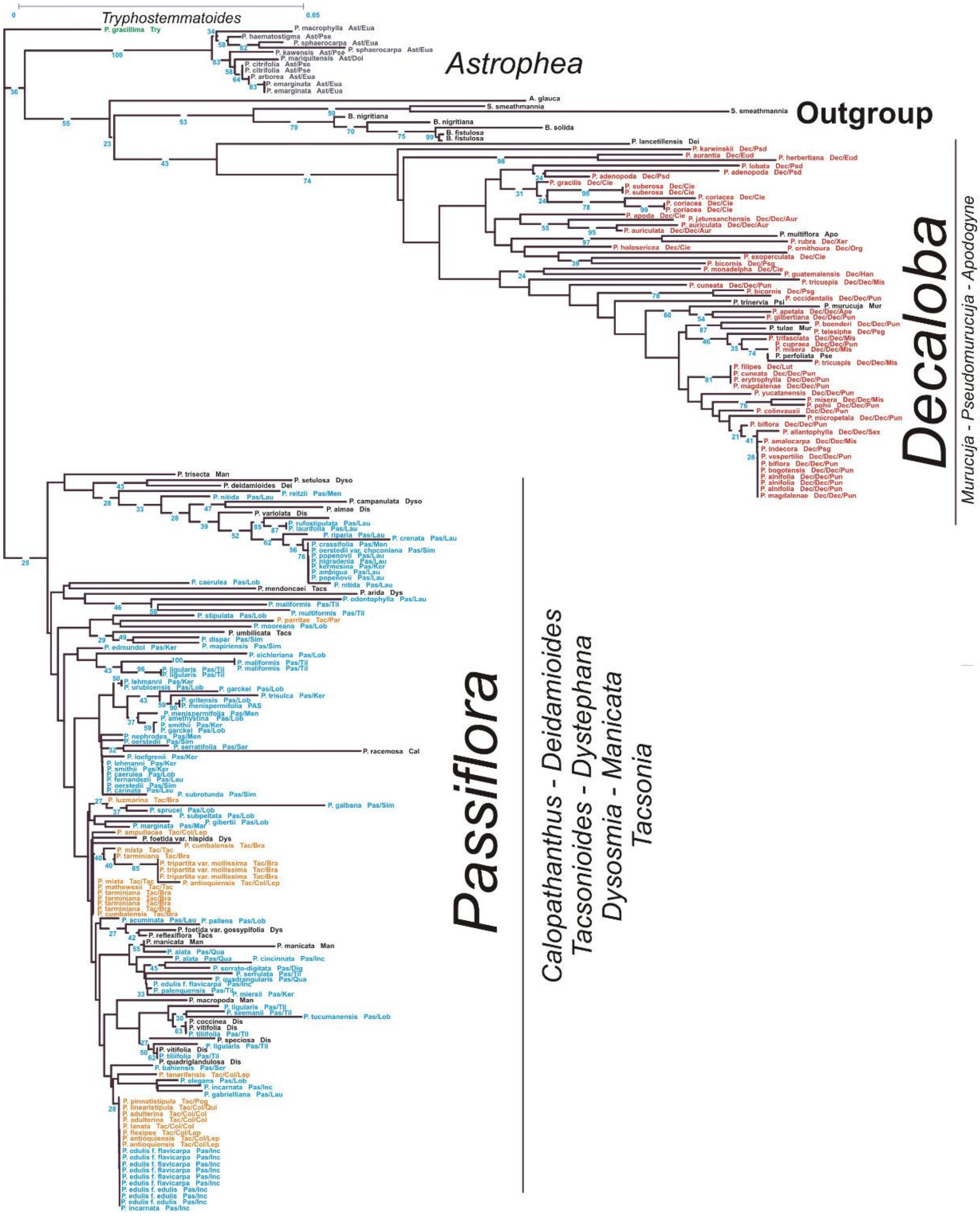


Figure 4. Phenogram derived from on cpDNA (PC1-PC2 and TS1-TS2 regions) data illustrating the distribution of the different *Passiflor*a subgenera studied. Boostrap values above 20% are indicated under branches.

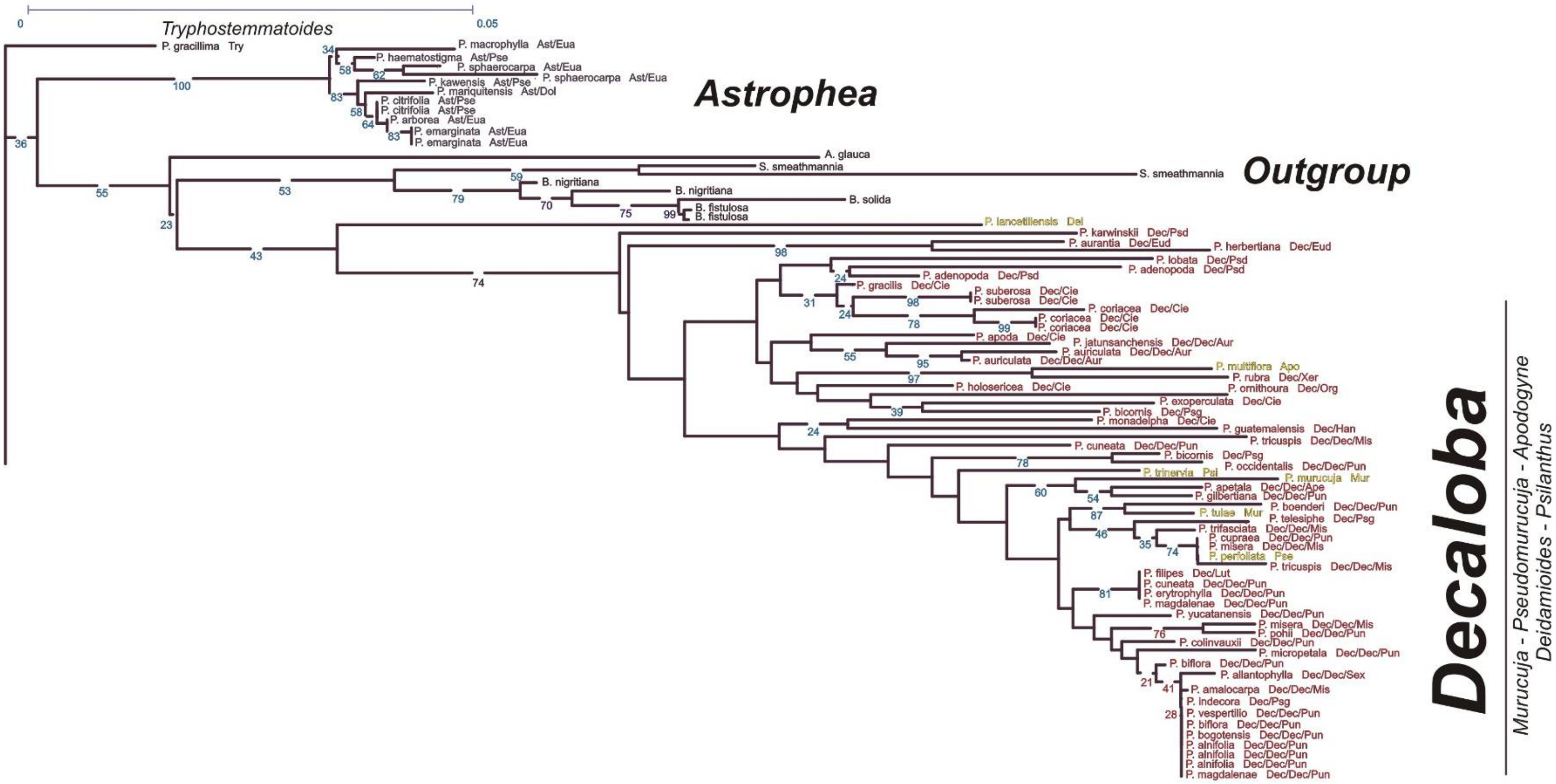


Figure 4a. Cluster analysis on cpDNA data, '*Decaloba* group', subgenera *Astrophea* and *Tryphostemmatoides*, and outgroup genera.

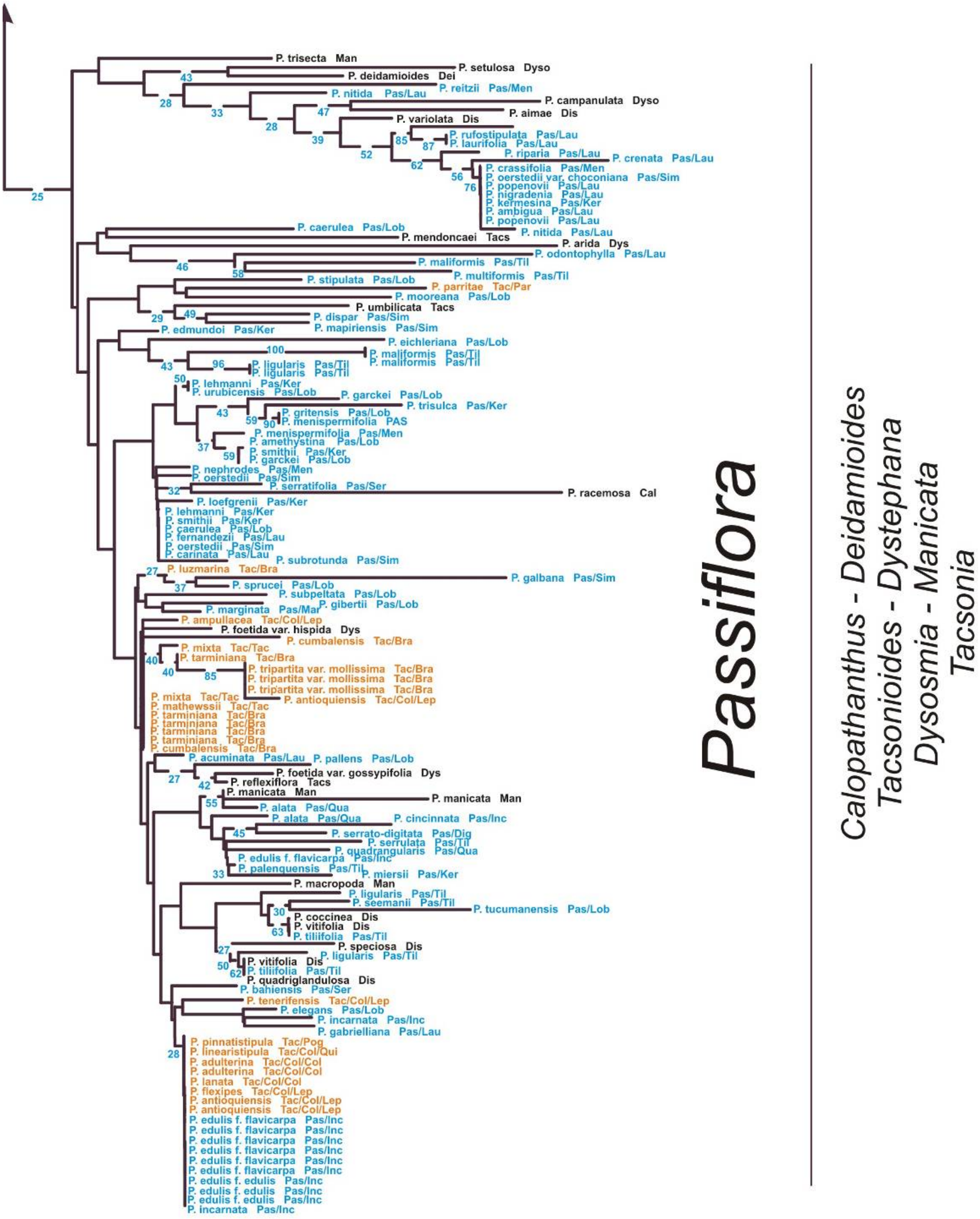


Figure 4b. Cluster analysis on cpDNA data, '*Passiflora* group'. Subgenus *Tacsonia* in clear-brown.

The dendrogram obtained with mtDNA data separates four poorly to moderately supported clusters (Figure 5). As for cpDNA, a first large cluster corresponds to the '*Decaloba* group'. Its accessions are grouped by species, with the only exception of *P. adenopoda.* Again the Australian *P. aurantia*/*P. herbertiana* are paired, as is the case for *P. suberosa* and *P. coriacea*. The numerous accessions of section *Decaloba* series *Punctatae* and *Miserae* tend to form a subcluster, while species of subgenera *Apodogyne*, *Murucuja*, *Pseudomurucuja* and *Psilanthus* are diluted in subgenus *Decaloba*. The other major clusters are different from those evidenced by cpDNA data.

The '*Passiflora* group' is split among three clusters. The largest one includes a subcluster composed of all species of subgenus *Astrophea,* but two. *P. gracillima* (subgenus *Tryphostemmatoides*) is basal to this *Astrophea* subgroup. Within this wide *Passiflora-Astrophea* cluster, accessions tend to cluster by species, although strong divergences may appear within particular species, as is the case for *P. alata* and *P. vitifolia*. Some loose subclusters can be interpreted, as one dominated by part of the series *Laurifoliae*, a branch grouping the most typical species of series *Tiliifoliae* (*P. ligularis*, *P. palenquensis*, *P. seemannii* and *P. tiliifolia*), a branch grouping four species of subgenus *Distephana*, and a branch bearing three Ecuadorian and one southern Colombian accessions of subgenus *Tacsonia*. On the other hand, the most typical representatives of series *Incarnatae*, i.e. the two forms of *P. edulis* and *P. incarnata*, are clearly separated on the tree. Another surprising splitting is that of the morphologically uniform series *Quandrangulares*, with the divergence of *P. alata* and *P. quadrangularis*.

A third important cluster is consistently composed by the majority of species from series *Menispermifoliae*, *Kermesinae,* and *Lobatae*. However, at lower levels, this morphological consistency is lost, as indicated by the separation of the very similar *P. lehmannii*, *P. trisulca* and *P. smithii*. Even more surprising is the separation of the morphologically very close *P. gibertii* and *P. subpeltata*, the latter on a smaller, distinct cluster, together with two other representatives of series *Lobatae*.

The fourth subcluster is very uniform, as it includes all species of subgenus *Tacsonia*, except the four Ecuadorian accessions mentioned above and an accession of *P. pinnatistipula*, also from Ecuador, which appears associated with the morphologically very similar *P. macropoda* in the *Passiflora-Astrophea* cluster.

A few species constitute a cluster of their own. Among them, we find again *P. deidamioides*, (subgenus *Deidamioides*), but this time at the base of the *Decaloba* cluster, *P. umbilicata* (subgenus *Tacsonioides*), *P. serratifolia* and *P. multiformis* (subgenus *Passiflora*), and *P. haematostigma* (subgenus *Astrophea*), adding to an already difficult interpretation of the mitochondrial tree. Two other surprising informations are the positioning of *P. lancetillensis* within the *Decaloba* cluster and the splitting of the two varieties of *P. foetida*, var. *hispida* appearing in the *Passiflora-Astrophea* cluster and var. *gossypifolia* appearing in the *Lobatae-Menispermifoliae-Kermesinae* cluster. Last but not least, the African Passifloraceae of the sample again take an abnormal position for an outgroup.

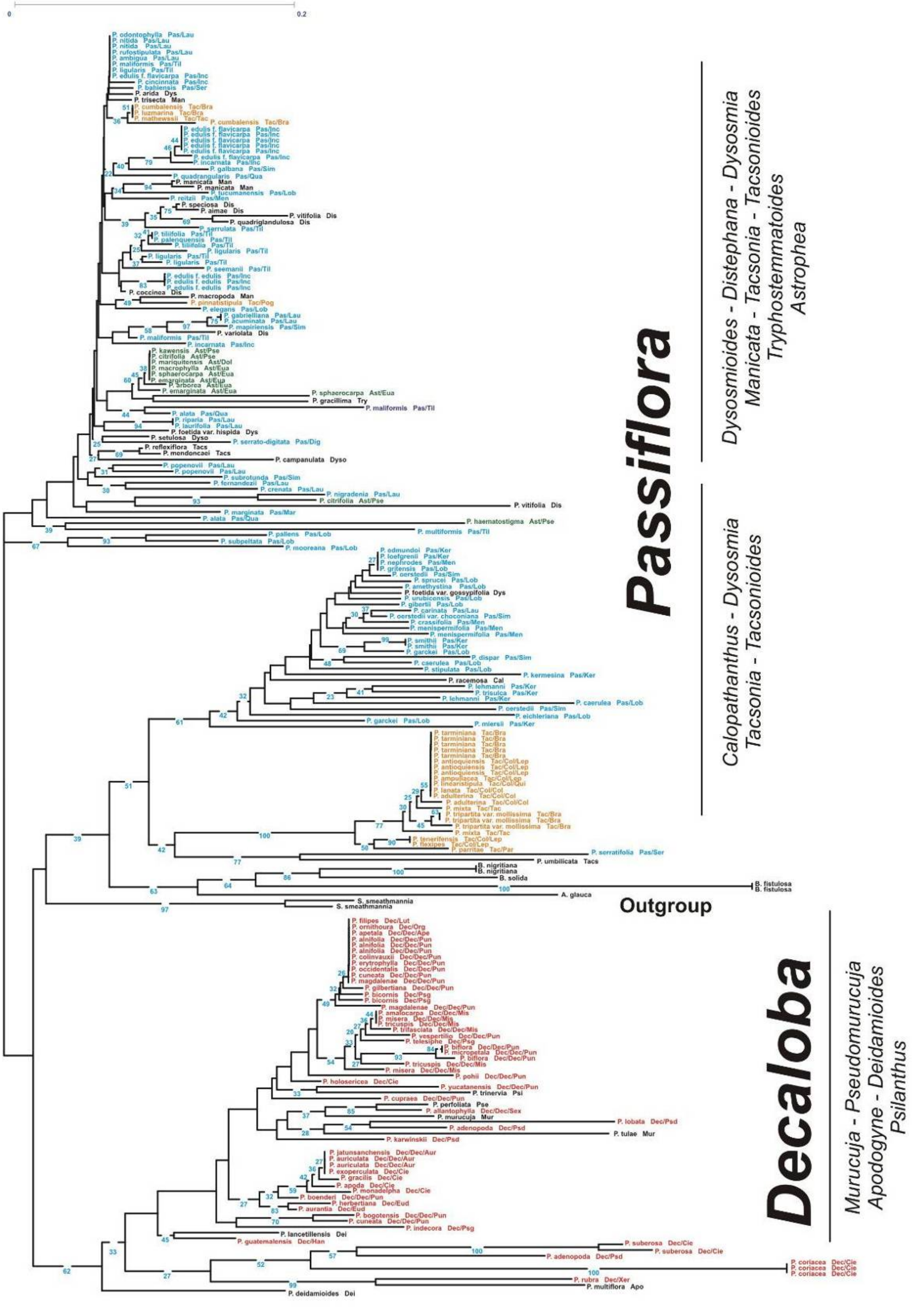
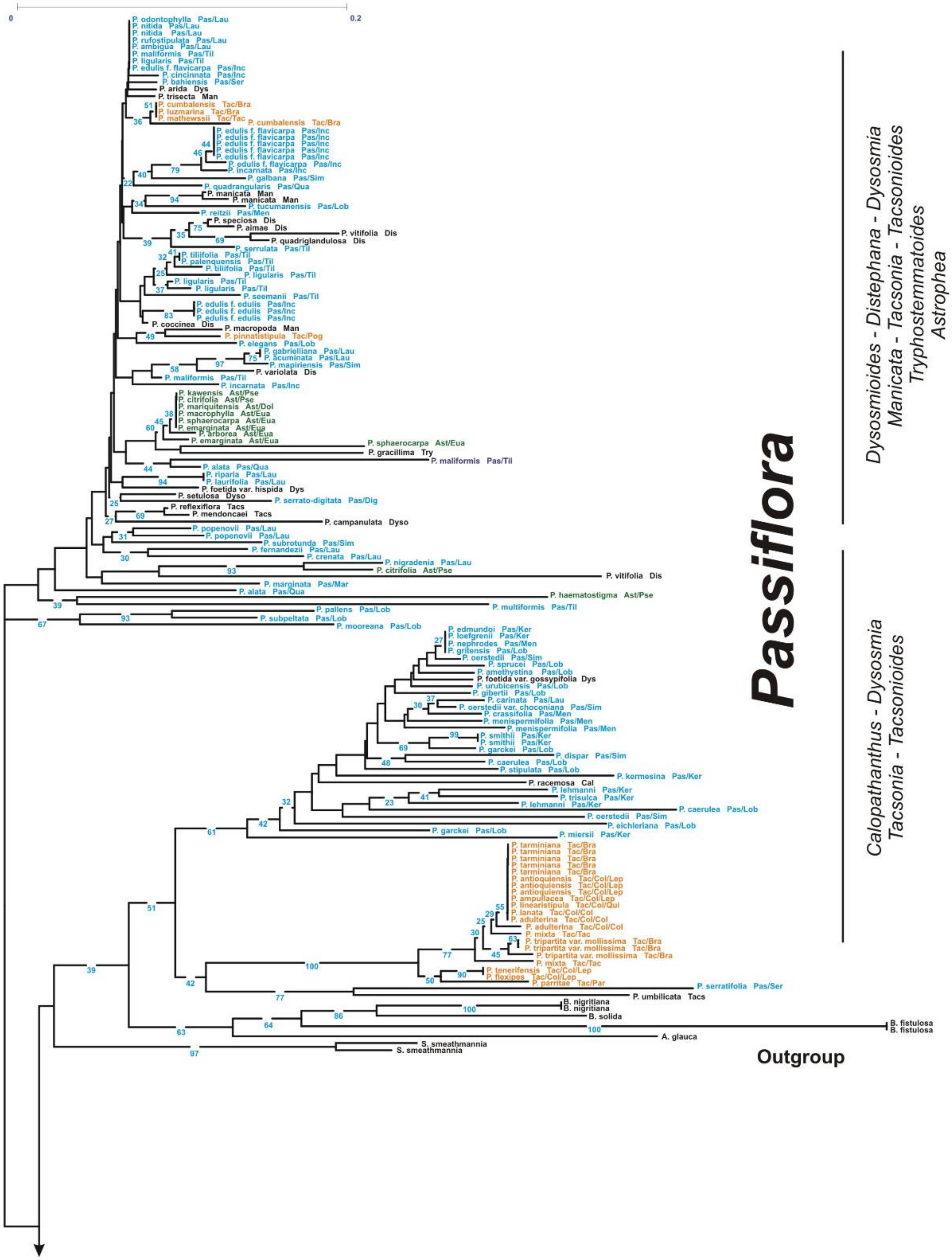


Figure 5. Phenogram derived from on mtDNA (N41-N42 and N1B-N1C regions) data illustrating the distribution of the different *Passiflor*a subgenera studied. Boostrap values above 20% are indicated under branches.



Fugure 5a. Cluster analysis on mtDNA data, '*Passiflora* group' and subgenera *Astrophea* and *Tryphostemmatoides*.

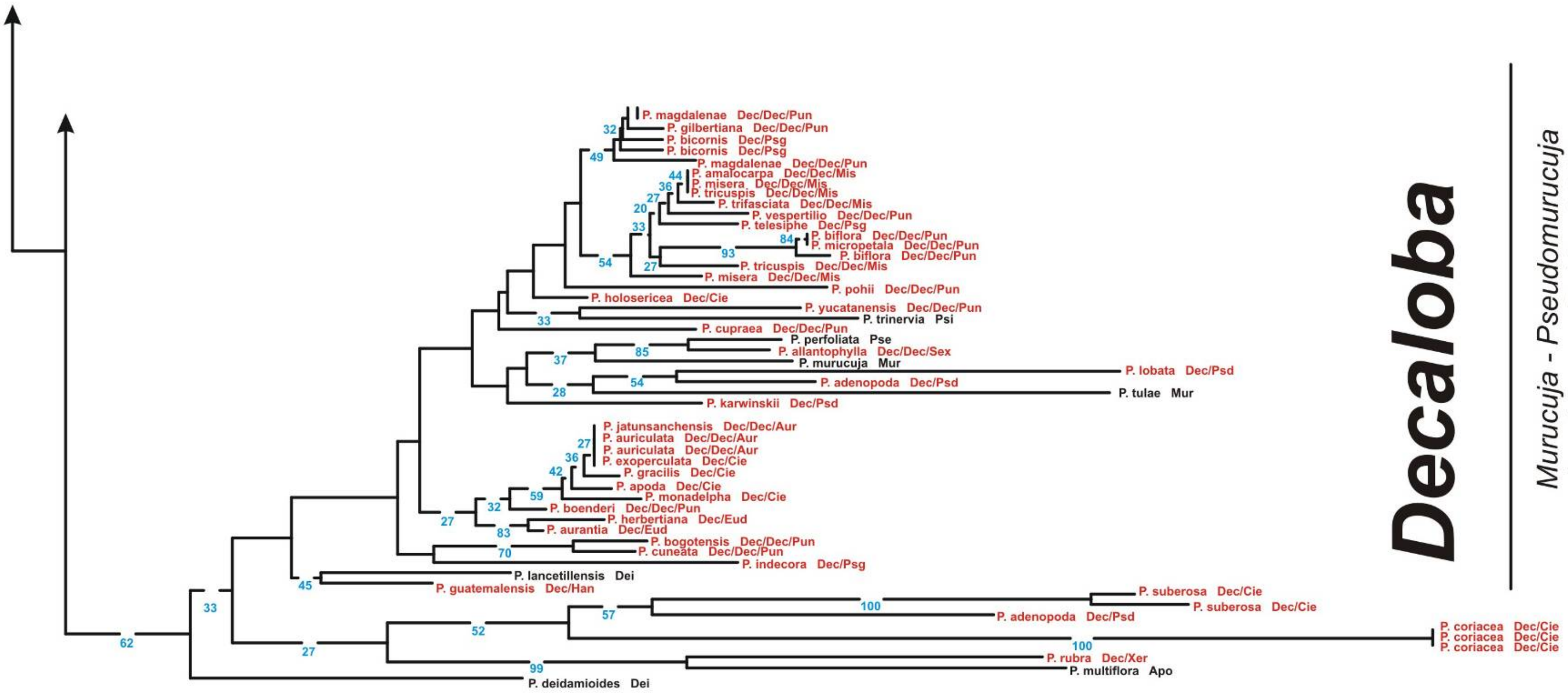


Figure 5b. Cluster analysis on mtDNA data, '*Decaloba* group'.

V.1.5. Discussion

V.1.5.1. *Chloroplast DNA diversity*

Concerning cpDNA diversity, our results are globally consistent with those previously obtained by Muschner et al. (2003) on *trnL-F* sequences, by Yockteng (2003) with *mat*K sequences (for the best resolved branches of the tree), and Hansen et al. (2006) with *trnL-trnT* sequences, as we observed three major groups, clearly corresponding to the three major clades of these phylogenetic studies and to the three major subgenera proposed by Feuillet & MacDougal (2003). The clusters/clades corresponding to subgenus *Astrophea* appear well differentiated and uniform in all studies. Within the '*Decaloba* group', there appears no structure corresponding to Killip's subgenera *Apodogyne, Decaloba, Murucuja, Pseudomurucuja* and *Psilanthus,* so their fusion into a unique subgenus is again justified by our cpDNA data. The marginal position of the Australian species can be interpreted by an ancient isolation. The two loose subclusters observed after their separation, are partly paralleled by subclades in the *trnL-F* and *trnL-T* trees. In the first one, we can recognize the association between *P. coriacea* and *P. suberosa* and, more distantly, with *P. capsularis* and *P. morifolia*; while subclades including species of series *Organenses*, *Miserae* and *Punctatae* of subgenus *Decaloba* and/or subgenera *Murucuja* and *Pseudomuruja* are observed in both trees. This subdivision within the *Decaloba* group is not very reliable, mostly because of the intraspecific variation that sometimes results in the placement of accessions of the same species in different subclusters or branches (e.g. *P. adenopoda* and *P. bicornis*). However it appears much more consistent with the classification of subgenus *Decaloba* proposed by Feuillet & MacDougal (2003) than with Killip's, as all the species grouped in the second subcluster are classified in supersection *Decaloba* - section *Decaloba* by the former authors.

In the three cpDNA studies, the '*Passiflora* group/clade' is the one showing the loosest structure and the highest number of inconsistencies between morphological and genetic similarities. The subgenera that compose it are not differentiated as their species tend to be widely dispersed among poorly supported subclusters/subclades, with the exception of *P. foetida* (subgenus *Dysosmia*), whose accessions appear as a well supported sister group of the '*Passiflora* clade' in the *mat*K tree of Yockteng (2003), while the representatives of this very particular subgenus are not individualized, neither in the *trnL-F* tree of Muschner et al. (2003) nor in our study. In our tree, the three accessions of *P. foetida* and *P. arida* even appear very dispersed within the '*Passiflora* group'. This observation can be generalized to most species represented by several accessions, which underlines that intraspecific variation is of the same order as interspecific and even intersubgeneric variation. Only two small clusters are supported by bootstrap values exceeding 50% and minimal taxonomic interpretation. One includes all species of series *Laurifoliae* of subgenus *Passiflora*, except *P. fernandezii* and *P. odontophylla*, plus three species of other series, *P. crassifolia* (series *Menispermifoliae*) *P. kermesina* (series *Kermesinae*), *P. oerstedii* var. *choconiana* (series *Simplicifoliae*). The other one includes three accessions of *P. tripartita* var. *mollissima* and one of *P. antioquiensis*.

Killip's subgenus *Tryphostemmatoides* is supported by the placement of *P. gracillima* in our tree, in an independent branch, but slightly closer to subgenus *Astrophea*. Its close relative, *P. tryphostemmatoides*, was placed among the arborescent and semi-arborescent species of subgenus *Astrophea* in the *mat*K study of Yockteng (2003) and as a sister group of subgenus *Astrophea* in the nuclear ncpGS tree of Yockteng & Nadot (2004). Thus, the three datasets converge in providing reasons to maintain these small herbaceous vines in a distinct subgenus, surprisingly associated with the arborescent or semi-arborescent species of subgenus *Astrophea*. Feuillet & MacDougal classified them as a section of their fourth subgenus, *Deidamioides*. However, the type species of this subgenus, i.e. *P. deidamioides*, is placed in the *Passiflora* group in our tree, which contradicts this view. *P. lancetillensis* and *P. microstipula*, two species of subgenus *Deidamioides sensu* Killip, were transferred to a supersection *Pterosperma* of subgenus *Decaloba* in the new classification. In our study, *P. lancetillensis* is placed at the base of the *Decaloba* group, but in a distant position, as in the phylogenetic trees of Muschner et al. (2003) and Hansen et al. (2006). In the latter, *P. microstipula* was very strangely dispersed, with one accession close to *P. lancetillensis,* and two accessions in the '*Passiflora* clade', a fact that was later attributed to a case of heteroplasmy (Hansen et al. 2007). In any case, neither the contours of Killip's subgenus *Deidamioides*, nor its splitting between subgenus *Deidamioides* and supersection *Pterosperma* by Feuillet & MacDougal (2003) are clearly supported by cpDNA data.

V.1.5.2. *Mitonchondrial DNA diversity*

The results on mtDNA diversity are consistent with those from cpDNA on two main points at the intersubgeneric level. These are the clear separation of the '*Decaloba* group' and the unexpected placement of the outgroup species, at a comparable distance. Within the '*Decaloba* group' cluster, we recognize several structural traits observed on cpDNA, such as a better grouping of accessions by species, as compared to the situation in the '*Passiflora* group', the integration of subgenera *Apodogyne, Decaloba, Murucuja, Pseudomurucuja* and *Psilanthus*, the formation of a subcluster supporting the section *Decaloba* of subgenus *Decaloba* in the new classification, and associations between particular species as *P. suberosa* and *P. coriacea* or the two Australian species. A third important convergence at the subgeneric level is the grouping of *P. gracillima* (subgenus *Tryphostemmatoides*) with most species of subgenus *Astrophea*.

The splitting of the '*Passiflora* group' and the insertion of the *Astrophea-Tryphostemmatoides* cluster in its largest division are the two most striking divergences with all chloroplastic and nuclear DNA, as well as morphological data (except for the separation of tacsos), and cannot be explained on the basis of any of the two subgeneric classifications. The largest cluster resulting from the division of the '*Passiflora* group' shows some loose clustering for species from subgenus *Distephana* (four of its six representatives), series *Tiliifoliae*, or simply for accessions from a same species, whereas other clear morphological groups are split, as series *Quadrangulares* and *Incarnatae*. The most uniform cluster dissident from the '*Passiflora* group' is constituted by the bulk of subgenus *Tacsonia* species. The five other accessions of this subgenus, placed in the largest '*Passiflora* group' subcluster, share a common recent Ecuadorian or southern-Colombian origin, constituting a particular case of geographic structure in the data. Interestingly, *P. umbillicata*, of the subgenus *Tacsonioides*, also characterized by a relatively long hypanthium, is placed at the base of the *Tacsonia* subcluster, while *P. manicata* is placed in the larger *Passiflora-Astrophea* cluster. The third '*Passiflora* group' cluster seems less easy to interpret, however it integrates remarkably the series *Kermesinae*, *Simplicifoliae*, *Lobatae*, and *Menispermifoliae*. All these series are differentiated in Killip's key by their foliaceous, semi-ovate to semi-oblong stipules, "attached on one side above base, hence often appearing reniform". As for the *Tacsonia* cluster, some representatives of these series are placed in the larger *Passiflora-Astrophea* cluster: *P. galbana*, *P. mapiriensis* and *P. subrotunda* (*Simplicifoliae*), *P. elegans*, *P. tucumanensis* (*Lobatae*), *P. reitzii* (*Menispermifoliae*). In addition, three species of series *Lobatae*, *P. mooreana*, *P. pallens* and *P. subpeltata* form a small independent cluster. In conclusion, the series *Kermesinae*, *Simplicifoliae*, *Lobatae*, and *Menispermifoliae* can be compared to those of subgenus *Tacsonia* for their relative divergence from the bulk of the '*Passiflora* group', however they show a much higher differentiation, both between divergent clusters and within their two specific clusters. The presence of *P. racemosa*, the unique species of Killip's subgenus *Calopathanthus*, among the species of these four series, is not really surprising, considering the shape of its stipules. In contrast, the presence of one of the accessions of *P. foetida* in this same cluster is very surprising.

As in the cpDNA tree, the relative distances between genus *Passiflora*, or its main divisions, and the outgroup, as well as the placement of the latter, do not provide any support to the monophyly of the genus.

V.1.5.3. *Divergences in the evolutions of chloroplast and mitochondrial genomes*

The analyses of chloroplastic and mitochondrial fragments gave very different pictures on the genetic structure of genus *Passiflora*. Differences appear at all levels, in the position of the outgroup, the relative position of four subgenera, and the relationships between species.

According to cpDNA data, the three genera of the outgroup are placed near the *Decaloba* cluster, giving more emphasis to its separation from the two other subgenera. In the mtDNA tree, they are placed between divisions of the '*Passiflora* group'. In addition, while *Adenia* appears more closely related to *Smeathmannia* for the chloroplast sequences, it appears more closely related to *Barteria* for the mitochondrial sequences.

The divergences between both datasets have opposite consequences for *Astrophea* and *Tacsonia*, the former being clearly differentiated by cpDNA but not so for mtDNA, and the latter being clearly differentiated by mtDNA and diluted in the '*Passiflora* group' in the cpDNA tree. Subgenus *Tryphostemmatoides* appears associated with subgenus *Astrophea* in both datasets. Its independence in the cpDNA tree is blurred in the mtDNA tree as both get integrated in the '*Passiflora* group'. The fourth case concerns the small subgenus *Deidamioides*. It is more complex as its two representatives are separated in both analyses, *P. lancetillensis* appearing in basal position close to the '*Decaloba* group', while its type species, *P. deidamioides*, is placed in the '*Passiflora* group' in the cpDNA tree, but at the base of the '*Decaloba* group' in the mtDNA tree.

At the infrasubgeneric level, clustering of chlorotypes and haplotypes appear globally consistent for the '*Decaloba* group', while we found replicas of the intersubgeneric discrepancies within the '*Passiflora* group'. Thus series *Laurifoliae* and *Incarnatae* tend to differentiate in the cpDNA tree, but not in the mtDNA tree, while the reverse is true, and clearer, for series *Tiliifoliae* and the *Kermesinae-Lobatae-Menispermifoliae-Simplicifoliae* series.

The divergence in the information obtained from chloroplast and mitochondrial genomes could be due to differences in their rate of evolution and mode of transmission. While most phylogenetic studies are based on the chloroplast genome because of its maternal transmission and slow evolution, as compared to the nuclear and mitochondrial genomes, which makes them less sensitive to hybridization events, this assumption has been contradicted in a significant number of cases. In their review of the question, Harris and Ingram had already shown in 1991 that mutation and hybridization/introgression may generate considerable intraspecific variation, constituting a potential problem for cpDNA-based phylogenetic reconstructions. According to their revision, 27% of the families and 21% of the genera show potential for biparental inheritance, and 23% of the species show only biparental inheritance, suggesting the existence of a continuum rather than an alternative mode of transmission. A few studies have also shown the possibility of intraindividual variation (heteroplasmy), resulting from biparental transmission, as in *Pelargonium* (Metzlaff et al., 1981), *Oryza sativa* (Moon et al., 1987), *Medicago* (Lee et al., 1988), *Musa* (Fauré et al., 1994), *Cucumis* (Harvey et al., 1998) and *Actinidia* (Chat et al., 2004). In *Actinidia*, where transmission of chloroplasts is paternal while that of mitochondria is maternal, chloroplastic phylogenetic information provides clear evidences of conflicts with morphological classification and striking incongruences have been observed between maternal and paternal phylogenies, evidencing reticulate evolution related to frequent hybridization events, sometimes involving distant species (Chat et al., 2004). *Passiflora* probably constitutes a very similar case, where reticulate evolution could account for the fast radiation in the genus, as well as the lack of clear morphological discontinuities at subgeneric levels, while variable patterns in transmission and evolution of organellar genomes explain striking incongruences between different datasets, reflecting multiple origins of species.

Indeed, since the observations of Corriveau & Coleman (1988) led them to suspect biparental plastid transmission in *Passiflora*, several molecular studies have pointed to a high frequency of paternal or biparental inheritance of the chloroplast genome in the genus. Studying a case of genome-plastome incompatibility in *Passiflora* hybrids, Mráček (2005) showed that biparental transmission of chloroplasts resulted in heteroplasmy of the whole plant, down to the single leaf level, and perhaps even the single cell level. The case of heteroplasmy reported by Hansen et al. (2007) involves two “extremely divergent chloroplast types” in a single individual. All species where biparental and/or paternal transmission was detected belong to the ‘*Passiflora* group’ (including subgenus *Dysosmia*), while the only cases studied in subgenus *Decaloba* evidenced maternal transmission (Do et al., 1992; Mráček, 2005; Muschner et al., 2006) or predominantly maternal transmission (Hansen et al., 2007), which would then explain lower intraspecific variation in the latter. More studies are needed to ascertain whether this was coincidence or one more fundamental difference between the ‘*Decaloba* group’ and the ‘*Passiflora* group’. Concerning mitochondrial inheritance, mtDNA was maternally transmitted in the five hybrids studied by Muschner et al. (2006).

For *Passifloraceae* phylogenetic studies, the consequences of paternal/biparental transmission of chloroplasts would include all the most severe problems anticipated by Harris & Ingram (1991), i.e. high intraspecific and intraindividual variation, random survivorship of lineages from a polymorphic progenitor (lineage sorting), reticulate evolution of the chloroplast genome through hybridization and introgression, all factors that, interfering with interspecific genetic differentiation, may explain the confuse situation, particularly in the ‘*Passiflora* group’. The differentiation among the major group/clades (‘*Passiflora’*, ‘*Decaloba’*, *Astrophea*) would limit genetic exchanges between them, explaining the distances observed in most studies. If the maternal transmission of mtDNA observed by Muschner et al. (2006) were further confirmed, this genome would become essential in the elucidation of the relations between *Passiflora* species. However, the numerous cases of wide intraspecific variation for mtDNA in our data suggest that there is no such clearcut difference in the transmission of the two organellar genomes.

V.1.5.4. *Diversity of organellar genomes and* Passiflora *systematics*

Obviously, the central expectation in the recent molecular studies of *Passiflora* was that they would give key elements for the understanding of its evolution and the definition of its subgeneric divisions, compensating for the pitfalls in the morphological diversity analysis. What they have produced instead is a series of divergent pictures of *Passiflora* diversity, one for each genome, plus one from morphological diversity, while providing strong evidence for reticulate evolution in the genus and, very likely, the whole family. The divergences between corresponding datasets are such that they disqualify any intent of deriving a consensual picture by simply piling up these datasets in a global analysis. In other words, there is no basis for a consensus tree. All we can do is trying to draw the clearest lessons from the different analyses.

While all inferior divisions of the two competing taxonomical treatments only appear occasionally supported by molecular and morphological data, revealing our general tendency to overclassification, the three main divisions of the new classification proposed by Feuillet & MacDougal appear clearly in all molecular studies. The situation for smaller clades is less clear. The fourth subgenus, *Deidamioides*, is not supported, while our data confirm the statement of Yockteng & Nadot (2004) supporting the persistence of the small subgenus *Tryphostemmatoides*.

All studies on cpDNA diversity have indicated a higher differentiation within the '*Decaloba* group/clade', and a better relation between genetic and morphological diversities. In addition, our data show a better relation between chlorotype and mitotype diversities in this group. This may be attributed to one or several of three causes. A first hypothesis is that this taxon is more ancient than the other major groups/clades, which would be consistent with the fact that it is present also in Asia and Australia, while the others are of strictly American origin. A second one would be that these mostly herbaceous vines present a shorter generation time, contributing to a faster evolution (Yockteng, 2003). A third likely explanation is that maternal transmission of cpDNA is the most common case in the '*Decaloba* group'. In addition, if both genomes are mostly transmitted in similar ways, it also explains why mtDNA and cpDNA trees are relatively congruent only in this group.

The '*Passiflora* group/clade', as defined by cpDNA and nuclear DNA data, appears as the group where reticulation events have the wider impact on radiation and evolution. Its division in three clusters in the mtDNA tree is the most difficult point to interpret. In this division, the only logics we can see follow ecological adaptation and morphological differentiation. The best-differentiated and most uniform cluster corresponds to subgenus *Tacsonia*. This taxon is composed of species specifically adapted to the cool conditions of Andean highlands, between 2,500 and 4,000 m.a.s.l, and pollination by the long-billed hummingbird *Ensifera ensifera*. They have developed a particularly long hypanthium, so the presence of the long-tubed *P. umbillicata* in a neighbor branch of the tree is not surprising. This young group clearly constitutes the most efficient adaptative answer of

Passiflora to the rise of the Andes, as they are responsible for a species diversity peak along the elevational gradient (see Chapter III). Their recent evolution explains their mtDNA and morphological uniformity (see Chapter IV). The formation of a geographic subcluster by four accessions of *Tacsonia* from Ecuador and southern Colombia within the largest cluster of *Passiflora*, close to lowland species, indicates the possibility of capture of mitochondrial genetic material through relatively wide hybridization, although this appears much less frequent than exchanges of chloroplast material.

The relative separation of series *Kermesinae*, *Simplicifoliae*, *Lobatae*, and *Menispermifoliae* shows a similar correspondence with morphological traits (stipule shape) and ecoclimatic adaptation, although the climatic trend is less marked. Most species represented in this cluster are vines adapted to the mild climates of Andean hillsides, between 1,200 and 2,000 m, or of subtropical regions of southern South America (northern Argentina to Brazilian Minas Gerais).

By contrast, the *Passiflora-Astrophea-Tryphostemmatoides* cluster is a composite group, including the trees and treelets of subgenus *Astrophea* and all vigorous lianas of subgenera *Passiflora* and *Distephana*, mostly originating from tropical lowlands or Andean foothills, plus their close relatives from other climates. Thus, in the series *Incarnatae*, *P. incarnata* is adapted to the temperate or subtropical conditions of the southern USA, while *P. edulis* f. *edulis* is adapted to the mild conditions of southern South America. In the series *Tiliifoliae* we find two high hillside species, *P. tiliifolia* and *P. ligularis* (1,500-2,500m). Interestingly, we also find species of the reniform stipule cluster and species that are intermediate between subgenera *Passiflora* and *Tacsonia*, as *P. manicata* (subgenus *Manicata*), *P. pinnatistipula* (a *tacso* with a shorter tube, less reduced corona and round fruit) and *P. macropoda* (very similar to the latter, with an even shorter tube and a more complex corona). *P. pinnastipula* is known to cross spontaneously with typical *tacsos*, although most of the resulting *P.* x *rosea* hybrids are sterile.

Subgenera *Astrophea* and *Tryphostemmatoides* are much less divergent from the '*Passiflora* group' than the '*Decaloba* group'. They are only slightly differentiated by mtDNA, while their restriction profiles only diverge for the cpDNA fragment (*trn*S-*trn*fM regions), which suggests that their separation was more recent than that of the '*Decaloba* group'. As their chromosome number is 2*n* = 24, this is consistent with the scheme of genome evolution proposed by De Melo et al. (2001). According to these authors, the 2*n* = 20 (subgenus *Dysosmia*) and 2*n* = 18 ('*Passiflora* group') evolved from the 2*n* = 12 of the '*Decaloba* group' via a duplication followed by descendent disploidy (Figure 6). The tree proposed by De Melo et al. (2001) would be more parsimonious if we accept that the divergence of the '*Decaloba* group' is more ancient than that of *Adenia* (2*n* = 12), or, in other words, if we accept that genus *Passiflora* is not monophyletic. This latter possibility is consistent with the cpDNA studies of Muschner et al. (2003), Hansen et al. (2006) and our cpDNA data, as well as the geographic distributions of these taxa.

The question of *Passiflora* monophyly unavoidably imposes to remember that *Decaloba* and *Astrophea* were once generic names and the possibility of reconsidering the relative status of the three major clades. Morphology, biogeography, cytogenetics and possibly differences in inheritance of plastid genomes converge with molecular data in differentiating the '*Decaloba* group/clade' and, to a lesser degree, clades corresponding to the current subgenera *Astrophea* and *Tryphostemmatoides*. The future of lower-level divisions, as sections and series, will obviously depend on the answer to the main question. In a hypothetical simplified genus *Passiflora*, many problems would be solved spontaneously. For example, *Tacsonia* or *Distephana* would very logically recover a subgeneric status, reducing the need for lower taxonomic levels. On the other hand, whatever the levels of the divisions in the classification, some species will remain problematic, such as *P. manicata* and *P. pinnatistipula*, which show morphological affinities with both Killip's subgenera *Tacsonia* and *Passiflora*, nuclear DNA affinities with the former (Segura et al., 2002; Yockteng & Nadot, 2004) and mtDNA affinity with the latter.

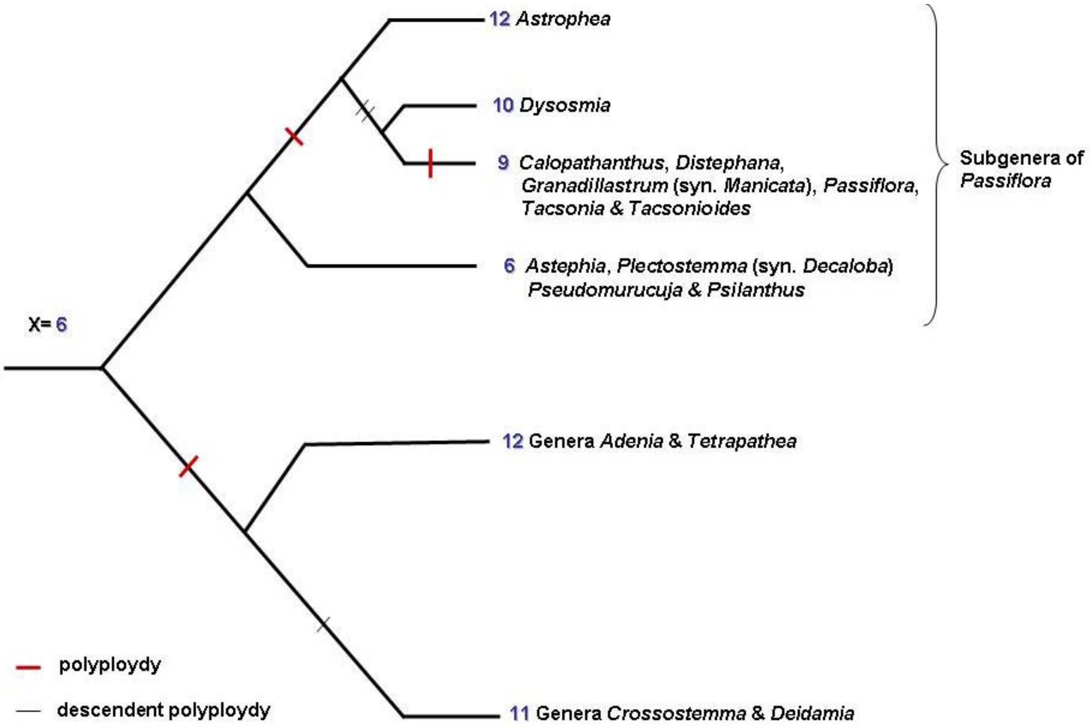


Figure 6. Probable relationships among main haploid numbers known in *Passiflora* subgenera and other Passifloraceae genera, as proposed by De Melo et al. (2001).

V.1.6. Conclusions

The clear conflicts observed between classifications based on morphological, chloroplast DNA and mitochondrial DNA data can be explained by a combination of reticulate evolution and biparental/paternal transmission of organellar genomes in *Passiflora* and probably the whole family. This situation appears further complicated by differences in the transmission between the chloroplastic and the mitochondrial genomes, the latter being probably more frequently maternal. There is even a possibility that organellar transmission differs among subgenera. In particular, the situation in subgenus *Decaloba sensu* Feuillet & MacDougal should be further assessed.

This situation imposes particular caution in using molecular data for the resolution of the many problems in *Passiflora* systematics and evolution. Only major divisions have been confirmed by the molecular studies. On one hand, these tend to confirm the necessary simplification of *Passiflora* taxonomy and the strong reduction in the number of subgenera, as undertaken by Feuillet & MacDougal (2003). On the other hand, the monophyly of the genus is questioned by the data, a problem which must be solved before any significant taxonomic modification. The possibility of restoring genera *Decaloba*, as established by Roemer in 1846, and *Astrophea*, by Reichenbach in 1828 (Killip, 1938), should be considered.

Interspecific relations appear particularly confusing in the large-fruited species of the '*Passiflora* clade', which includes all the passion fruits presenting economic importance or breeding potential. In the absence of a strong structure, this entire group can be considered as genetic resources for developing new passion fruit species and cultivars. Breeders should not suspect interspecific barriers *a priori*. On the contrary, the '*Decaloba* clade' and subgenus *Astrophea* should not be attributed the same potential for fruit crop development.

V.1.7. Acknowledgements

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General discussion

1. Discussion

1.1. *Biogeography and conservation*

Colombia has been subject to many studies focused on inventories of plant species groups (Gentry, 1993; Silverstone-Sopkin & Ramos, 1995; Galeano et al., 1998; Rangel, 1995, 2002). Passifloraceae have been inventoried in taxonomical works by Escobar (1998a,b, 1989, 1990 inedited) and Hernández & Bernal (2000). As compared to the latter, we have added new information on geographical distribution of each taxon and extended the list to a total of 167 Passifloraceae species, from three genera and the five biogeographic regions, with reports of 26 species new to Colombia. Our list ranks Colombia as the country with the highest richness of Passifloraceae, followed by Brazil with 127 species. Colombian species richness and diversity is more than twice that of Peru and Venezuela, two countries of similar surface and latitude. Given its much smaller area, Ecuador also presents an impressive diversity. Thus, the northern Andes of Colombia and Ecuador clearly constitute the center of diversity for the genus *Passiflora*.

Escobar (1988a) had already underlined that 40% of the New World Passifloraceae are found in the Andes. Indeed, radiation has been very active in the northern Andes, with particular contribution of recent and fast evolving groups, such as subgenus *Tacsonia*, particularly adapted to highlands in comparison to other infrageneric groups. Not surprisingly, among the more than 41 *tacso* species in Colombia and Ecuador, 21 (14%) are endemics. Colombian highlands are also rich in representatives of subgenus *Decaloba*. On the whole, habitats between 1000 and 3,000 m account for only 27% of the Colombian land area, but 81% of the species of Passifloraceae are found there. With 123 species, the Andean region concentrates the highest richness, mainly between 1000 and 2,000 m. The increase of species richness and endemism with the elevation is generally interpreted as a result of the increasing isolation and decreasing habitat surface in high mountain regions, leading to small, fragmented populations which are prone to speciation (Simpson, 1975; Jørgensen et al., 1995). Another contribution to the particular species richness in Colombia and Ecuador is that of the Pacific Coast region, continuous with the similar highly diverse ecosystems of Central America (Chocó-Darién/Western Ecuador hotspot of Myers et al., 2000), and receiving one of the highest rainfalls in the world, in strong contrast with the conditions prevailing in the westerns Andes and coast of Peru that are arid or semi-arid, or the drier and more contrasted climate of Venezuela.

The distribution of Passifloraceae has been drastically affected by deforestation, principally in the Andean region, as their favorite habitats correspond to areas with a long history of livestock and agriculture that now supports extensive plantations of coffee, sugar cane, rice, bananas, and potatoes. Forests in the northern Andes are currently one of the major conservation priorities on a global scale due to their fragility, biological richness, high rates of endemism and multiple anthropogenic threats (Olson & Dinerstein, 1998). As Passifloraceae display very high species richness, endemism and extinction risk in this area, and given their multiple ecological interactions with many organisms, as well as their economic potential, this family should constitute both an important target of conservation efforts and a good indicator of their success. This appears particularly important as we have shown that the conservation of Passifloraceae and their habitat is not taken into account by the current system of protected areas in the Colombian Andes, due to a general lack of correspondence between the modeled distribution of Passifloraceae diversity and these areas, as presented in Figure 8 (Chapter III). Instead, the striking superposition of areas of high Passifloraceae diversity on certain Colombian coffee growing zone ecotopes (Figure 9; Chapter III) points to the need of developing a completely different approach, integrating agriculture, tourism, watershed management, and nature conservancy at the landscape level, in a region whose conservation is of utmost importance for the country.

1.2. *Morphological and molecular diversity*

As a first major point, we can underline that the major morphological divisions observed in our study find support in the genetic studies. The cytological groups are always validated, with the clear separation of subgenera *Astrophea* (*n* = 12), *Tryphostemmatoides* and *Decaloba* (*n* = 6) between themselves and from subgenera *Passiflora*, *Tacsonia*, and *Distephana* (*n* = 9). Concerning subgenus *Tryphostemmatoides*, the consistency between morphological and genetic studies is clear only when considering our quantitative analysis, where it is associated with subgenus *Astrophea* mostly on peduncle traits (third principal component). This trait is represented also in the qualitative descriptors, however its effect is blurred by the high number of traits shared with subgenus *Decaloba*. While the comparison is difficult for subgenus *Tryphostemmatoides*, it is impossible for subgenus *Psilanthus*, because of insufficient data and the unlikely placement of *P. sanguinolenta* in the '*Passiflora* clade' in the ncpGS study. The two species, *P. adenopoda* and *P. foetida*, that take an intermediate position in the general "morpho-cytological" pattern, or their close relatives, are consistently placed in intermediate positions, in most phylogenetic studies, *P. adenopoda* or *P. morifolia* (section *Pseudodysosmia* of subgenus *Decaloba*) appearing basal to a general '*Decaloba* clade' and *P. foetida* (subgenus *Dysosmia*) basal to the general '*Passiflora* clade'.

The comparison becomes more difficult at lower, infra subgeneric, levels. Subgenus *Decaloba* appears better structured than the other subgenera, and shows similarities in morphological and molecular diversity patterns, with the grouping of Killip's sections *Punctatae* and *Miserae*, and the differentiation of species of sections *Xerogona*, *Cieca*, and series *Auriculata* and, less clearly, *Sexflorae*. The placement of *P. adenopoda* in the different trees questions the inclusion of section *Pseudodysosmia*, while the structure observed among representatives of several sections provides support to some simplification, but not for as many fusions as those operated in the new morphological classification of Feuillet & MacDougal (2003). In any case, more species should be gathered in a same phenetic study before revising objectively the morphological classification.

Within the $n = 9$ group, molecular and morphological data diverge partially, as studies of DNA sequences allow the distinction of a *Tacsonia-Manicata* group and fail to separate clearly subgenus *Distephana*, placing both of them within a *Passiflora* clade, while morphological analysis supports these three subgenera at the same level of differentiation. The fact that species of subgenera *Distephana*, *Tacsonia* and *Manicata* have developed ornithophyly is obviously related to their strong morphological differentiation, which does not minor the importance of their morphological separation from subgenus *Passiflora*. Whether their probable evolution from a "*Passiflora*-like" common ancestor justifies their inclusion in the bee-pollinated subgenus *Passiflora*, as proposed in the new classification, is just the same classical question about considering birds as dinosaurs. In the end, it seems a problem of putting more emphasis on the adaptative forces commanding evolution or more emphasis on the genetic structure that subtend them. Concerning subgenus *Passiflora sensu* Killip, no structure appears at the interspecific level that could result in clear subdivisions into series. The study of sequence variation for the ncpGS gene provides the only tree with reasonably well-supported structure at this level, however several obvious abnormalities question the robustness of the information. Our morphological observations only confirm closer associations between the most typical representatives of some series, however the number of contradictions with the classification and the lack of a clear hierarchy in the branch structure point to the difficulty of the work and the risk of under- or overclassification, leading to chose between a limited number of poorly supported series or a great number of poorly represented series. Similarly, the structure of the *Tacsonia-Manicata* branch does not support clearly sections and series in subgenus *Tacsonia*, however it allows differentiation between two groups of *tacsos*, one corresponding to common species that probably have their center of diversity in Ecuador, as is obvious for *P. cumbalensis*, *P. luzmarina* and *P. matthewsii*, and very likely for *P. mixta*, *P. tripartita* and *P. tarminiana* (Segura et al., 2005), and another cluster only including species endemic to Colombia, with a slight but clear differentiation related to extreme variation for peduncle length.

1.3. *Importance of reticulate evolution in* Passiflora

Many Passifloraceae species are cross-compatible (Vanderplank, 2000; Ulmer & MacDougal, 2004). Based on morphological observations, Escobar (1980) stated that also in nature these interspecific hybridizations occasionally occur in areas where species distributions overlap. In the molecular analyses presented here, several discrepancies were observed between chloroplast and mitochondrial DNA phenograms, suggesting both recent and ancient hybridization and introgression events and corroborating the observations of Escobar (1980). These data clearly suggest that evolution in *Passiflora* is reticulate rather than exclusively dichotomous and branching. Especially the origin of *P. foetida* provides an excellent example of reticulate evolution and once more illustrates the importance of hybridization in speciation within *Passiflora*. Such phenomena are well-documented and considered fairly common in the evolution of plants (Van Droogenbroeck et al., 2004; Chat et al., 2004; Vriesendorp & Bakker, 2005).

The combination of significant reticulate evolution, with a biparental/paternal inheritance of the choloroplast genome and, although to a lesser extent, the mitochondrial genome, particularly in the '*Passiflora* group', is the most likely explanation to the observations of wide intraspecific, and even intra-individual, organelle DNA variation, or conversely morphologically distant species sharing very similar organellar genomes, indicating captures of chloroplasts and mitochondria, and the resulting striking inconsistencies between the ITS, *mat*K, ncpGS and *Trn*L/*trn*T phylogenies published so far (Muschner et al., 2003; Yockteng, 2003; Yockteng & Nadot, 2004; Hansen et al., 2006; see Annex 4a-d). Taking into account these elements, the molecular phenograms presented in the present thesis can serve as a base for further exploration of the genetic diversity and interspecific relationships, phenotypic evolution, historical ecology and phylogeography of the wide *Passiflora* diversity.

At another level, the results presented in this work are also valuable for the development of better *in situ* and/or *ex situ* conservation strategies of *Passiflora* diversity. The extent of natural hybridization occuring in the different areas of sympatry should be considered when dealing with *Passiflora* genetic resources. Although hybridization has long been recognized as an important factor in the evolution of plant species, the harmful effects of hybridization have also led to the extinction of many populations and species (Allendorf et al., 2001; Barton, 2001). Such effects of hybridization can be most problematic in the situation when a rare *Passiflora* species comes into contact with a more abundant one. Such cases could get more common as the abundance of several *Passiflora* species has been reported to decline steadily. Thus, in Colombia, we have determined that three Passifloraceae species can be considered extinct and 70% of the species are threatened

(Chapter II). Conservation programs, not only in Colombia, should be aware of such effects in preserving the genetic integrity of Passifloraceae species in the long term.

1.4. *Phylogeography*

As discussed in the Chapter III, South America and especially the biodiversity hotspot described as ‘the Tropical Andes’ have higher plant species diversity than any other habitat on the planet. How this diversity arose is unexplained. One theory suggested that species richness in the tropics is the result of the gradual accumulation of species over a long geological period, with low rates of extinction in stable equatorial climates (Stebbins, 1974). However, more recent discoveries suggest that Neotropical climates were unstable over the past 2 million years during the Pleistocene (Whitmore & Prance, 1987). Cyclical glacial events led to periods of cooler and/or drier climate in which forest species may have withdrawn to small refugial pockets. According to this view, the present species diversity could be more recent, resulting from speciation through allopatric differentiation of populations in separate refugia (Haffer, 1982). Other recent geological phenomena that have been suggested as driving neotropical speciation are the uplift of the northwestern Andes from about 5 million years ago and the bridging of the Isthmus of Panama some 3.5 million years ago (Simpson & Todzia, 1990). Gentry (1989) speculated that nearly half of the Neotropical flora might be accounted for by explosive speciation. This rapid diversification is characteristic of plant evolution on the South-American continent since its isolation from Africa, Meso-America and Antarctica-Australia during the late Cretaceous and early Tertiary Period, about 60 to 70 million years ago (Burnham & Graham, 1999; Dino et al., 1999). These geographic connections allowed high exchange of flora, according to fossil registers of many families (Taylor & Taylor, 1993; Taylor, 1995). In the genus *Passiflora* this exchange is evident with the presence of the subgenus *Tetrapathea* and the section and series *Hollrungiella*/*Eudocaloba* (of subgenus *Decaloba*) in Oceania and South Asia.

Taking into account all these elements, it is most likely that isolation and adaptive radiation into ecologically extreme habitats at the time of the Andean uplift also have led to rapid diversification and differentiation in the genus *Passiflora*. The relatively wide size and restricted distribution of the genus *Passiflora* and paleobotanical data from 17-20 millions of years (Miocene) provide support to this hypothesis (Dorofeev, 1963). As illustrated by Richardson et al. (2001), molecular evidence can be useful in assessing the validity of phylogeographical hypotheses. The sequence analyses reported by Muschner et al. (2003), Yockteng (2003), Yockteng & Nadot (2004), Hansen et al. (2006) and our results with cp/mtDNA, revealed only low levels of sequence divergence among *Passiflora* taxa, suggesting that these have diversified recently. In particular all molecular data place the species of the highland subgenus *Tacsonia* (with a cylindrical elongate floral tube) within the '*Passiflora* group'. However, in the mtDNA phenogram, this subgenus forms a well-supported independent group. This stronger differentiation of mtDNA appears consistent with a faster evolution of the mitochondrial genome, as compared to the chloroplast genome, the particular altitudinal distribution of subgenus *Tacsonia* and the hypothesis of a rapid diversification and differentiation in the genus *Passiflora* in relation to the uplift of the Andes.

Conclusions
&
future prospects

1. Conclusions

With 167 reported species, Colombia is the country with the highest Passifloraceae richness. This richness is concentrated in the Andean region, particularly in the departments of Antioquia, Valle del Cauca and Cundinamarca. Comparisons with other countries indicate that the northern Andes of Colombia and Ecuador constitute the center of diversity for the most important genus *Passiflora*.

Collections of Passifloraceae have not been uniform as a consequence of difficulty of access and/or chronic social conflict in many areas. They have been much denser in the central coffee growing zone, Antioquia, Valle del Cauca and Cundinamarca. The southern and northeastern Andes, and the Caribbean have been little explored. For the lowland forests of the Pacific, the Orinoquian and the Amazonian, data are so poor that they are misleading. Despite the resulting sampling bias, collecting parameters clearly point to the concentration of observed Passifloraceae diversity in the Andes, and more particularly the central coffee growing zone.

The analysis of species distribution areas shows a trend for a wider dispersion of species occurring at low and intermediate elevations. On the contrary, narrow endemics are more frequent among highland species.

The modeled species richness map allowed identifying nine richness spots of variable size, three of which, located in the southern and southeastern Andes of Colombia, correspond to collection gaps, as they were not detected in the analysis of observed diversity. Another probable collection gap, not detected by diversity modeling, corresponds to the Sierra Nevada de Santa Marta, an isolated mountain range with both high diversity and endemism. The proportion of endemics living in high richness spots is lower than the proportion of all species used for modeling, confirming the lack of relation between diversity concentration and endemism reported in other studies. If this is further substantiated in different groups of organisms, it could limit the application of the biodiversity hotspot concept, as the best-protected areas for diversity would not necessarily provide protection to a high proportion of narrow endemics.

Passifloraceae diversity is not conserved by the current network of Colombian protected areas. On the contrary, it is particularly concentrated on certain ecotopes of the coffee growing zone, i.e. highly disturbed habitats, so any conservation effort must be integrated in local management strategies at the landscape level. Passifloraceae may provide an interesting indicator to evaluate the outcome of such efforts.

In the absence of a clear set of morphological criteria for discriminating at the different hierarchic levels of the infrageneric classification of *Passiflora*, we have used a quite exhaustive list of 43 quantitative and 83 qualitative descriptors. A shorter list of 32 qualitative traits, selected after analyzing variation among Killip's subgenera, allowed classifying our 60-species sample consistently, using a strictly phenetic approach. Eight of the nine Killip's subgenera represented in our sample are supported by the morphological analysis, although subgenus *Tryphostemmatoides* is only supported in the quantitative analysis. By contrast, the simplification proposed by Feuillet & MacDougal is not clearly supported in our analyses, except for the possible inclusion of *P. manicata* in subgenus *Tacsonia*, as this species is intermediate with subgenus *Passiflora* for quantitative traits but very similar to *tacsos* for most qualitative traits.

Chloroplast and mitochondrial molecular trees provide clear evidence of conflicts with morphological classifications. This suggests that the infrageneric classifications that have been established in the past by Killip (1938), Escobar (1988a,b, 1989) and Feuillet & MacDougal (2003) do not reflect the molecular evolutionary history of the genus *Passiflora,* at least with respect to the supersections and series. Moreover, the frequent occurrence of reticulation events in the evolution of *Passiflora* could explain the lack of morphological discontinuities at subgeneric levels, while variable patterns in transmission and evolution of organellar genomes explain striking incongruences between different datasets, reflecting multiple origins of species.

Breeding programs aimed at producing interspecific hybrids involving the cultivated species of *Passiflora* should therefore focus on the species belonging to the same clade as subgenus *Passiflora*. According to our results, the '*Decaloba* clade' and subgenus *Astrophea* do not constitute interesting genetic resources for passion fruit breeding.

These results constitute potentially crucial inputs for the development of a coherent strategy for the conservation and use of these genetic resources. Studies of *Passiflora* diversity in the Andean countries, and the maps presented here, will be used in future prospecting and identifying sites for *in situ* conservation, and more generally guiding government conservation strategies.

2. Future prospects

The low level of exploration in parts of the Andes, the Amazonian and the Orinoquian raises expectations that Colombia may still harbor many unknown species. Future studies should encompass new regions, including protected areas and current conflict zones. Indeed, a better knowledge of this diversity, and its distribution, is urgent for the *in situ* conservation of this threatened richness, targeting the conservation of these resources as well as their habitat. Both aspects may even be combined if the genus *Passiflora* can be used as an indicator of biodiversity in the Andean region, as was the objective of a project in the coffee growing zone. Another important aspect is its direct valorization as a germplasm resource for crop diversification programs, implying the need for a better understanding of its morphological and genetic diversity.

Another direction that should be considered is the sequencing of regions different from those analyzed in this study. By doing so, the value of the phenograms obtained in this work can be assessed and further complemented. A promising source is the nuclear ribosomal internal transcribe spacers (ITS). This region has been widely used in plant phylogenetics because of their high rate of nucleotide substitutions and their power in elucidating infrageneric relations (Taberlet et al., 1991; Alvarez & Wendel, 2003) Also, the ITS have already been used in *Passiflora* species by Muschner et al. (2003) with success, although the size and composition of the sample limited the interpretation at the level of subgenera. It would also be necessary to increase the number of species and in particular to include Asian members of *Passiflora* as well as species of subgenera not represented in our analysis.

Given the importance of hybridization and introgression in the evolution of the genus *Passiflora*, more studies are also needed to investigate and document hybridization in *Passiflora*, and its potential implications in the taxonomic problems concerning the genus and the whole family. Detailed studies should focus on the morphologically variable taxa, along with their close relatives in areas where they co-occur. A large number of different methods can provide valuable information regarding hybridization, such as:

- Artificial hybridizations in many species.
- Investigation and characterization of pollen viability and seed germination in artificially produced hybrids.
- Molecular techniques to confirm the hybrid origin of some taxa, combined with cytogenetic techniques, including chromosome counts, flow cytometry, fluorescence *in situ* hybridization (FISH) and genomic *in situ* hybridization (GISH).

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ANNEXES

Annex 1. Infrageneric classification according to Killip (1938) with emends of Escobar (1988, 1989) and MacDougal (1994).

Genus *Passiflora* L.	**507 species**
1 - Subgenus *Adenosepala* Killip	**01**
2 - Subgenus *Apodogyne* Killip	**01**
3 - Subgenus *Astephia* Killip	**01**
4 - Subgenus *Astrophea* (DC.) Masters	**46**
Section *Botryastrophea* (Harms) Killip	11
Section *Cirrhipes* Killip	01
Section *Dolichostemma* Killip	02
Section *Euastrophea* (Harms) Killip	15
Section *Leptopoda* Killip	01
Section *Pseudoastrophea* (Harms) Killip	16
5 - Subgenus *Calopathanthus* (Harms) Killip	**01**
6 - Subgenus *Chloropathanthus* (Harms) Killip	**01**
7 - Subgenus *Deidamioides* (Harms) Killip	**02**
8 - Subgenus *Distephana* (Juss.) Killip	**11**
9 - Subgenus *Dysosmia* (DC.) Killip	**11**
10 - Subgenus *Dysosmioides* Killip	**04**
11 - Subgenus *Granadilla* (Medic.) Masters	**97**
Series *Quadrangulares* Killip	02
Series *Digitatae* Killip	01
Series *Tiliafoliae* Killip	10
Series *Marginatae* Killip	01
Series *Laurifoliae* Killip	13
Series *Serratifoliae* Killip	04
Series *Setaceae* Killip	01
Series *Pedatae* Killip	01
Series *Incarnatae* Killip	06
Series *Palmatisectae* Killip	01
Series *Kermesinae* Killip	08
Series *Imbricatae* Killip	02
Series *Simplicifoliae* Killip	14
Series *Lobatae* Killip	29
Series *Menispermifoliae* Killip	04
12 - Subgenus *Manicata* (Harms) Escobar	**05**
13 - Subgenus *Murucuja* (Medic.) Masters	**04**
14 - Subgenus *Plectostemma* Masters	**154**
Section *Cieca* (Medic.) Mast.	25
Section Mayapathanthus Killip	01
Section *Decaloba* (DC.) Mast.	91
Series *Auriculatae* Killip	02
Series *Heterophyllae* Killip	02
Series *Sexflorae* Killip	04
Series *Apetalae* Killip	02
Series *Luteae* Killip	03
Series *Organenses* Killip	07
Series *Miserae* Killip	05
Series *Punctatae* Killip	47
Series *Eudecaloba***	19
Section *Hahniopathanthus* (Harms) Killip	03
Section *Hollrungiella***	01
Section *Mayapathanthus* (Harms) Killip	01
Section *Pseudodysosmia* (Harms) Killip	18

Section *Pseudogranadilla* (Harms) Killip	06
Section *Xerogona* (Raf.) Killip	08
15 - Subgenus *Polyanthea* (DC.) Killip	**01**
16 - Subgenus *Porphyropathantus* Escobar	**01**
17 - Subgenus *Pseudomurucuja* (Harms) Killip	**04**
18 - Subgenus *Psilanthus*, Killip	**04**
19 - Subgenus *Rathea* (Karsten) Killip	**02**
20 - Subgenus *Tacsonia* (Juss.) Triana & Planchon	**48**
Section *Ampullacea* Escobar	01
Section *Boliviana* Escobar	01
Section *Bracteogama* DC Prodr.	12
Section *Colombiana* Escobar	19
Series *Leptomischae* Escobar	08
Series *Colombianae* Escobar	09
Series *Quindiensae* Escobar	02
Section *Fimbriatistipula* Escobar	02
Section *Parritana* Escobar	02
Section *Poggendorffia* Triana & Planchon	01
Section *Tacsonia* Escobar	05
Section *Tacsoniopsis* Triana & Planchon	03
Section *Trifoliata* Escobar	02
21 - Subgenus *Tacsonioides* (DC.) Killip	**05**
22 - Subgenus *Tacsoniopsis* (Tr. & Planch) Killip	**01**
23 - Subgenus *Tetrapathea**	**01**
24 - Subgenus *Tryphostemmatoides* (Harms) Killip	**03**

(Harms, 1925; de Candolle, 1822; Hutchinson, 1967; Green, 1972)* and (de Wilde, 1972)**.

Annex 2. Infrageneric classification according to Feuillet & MacDougal (2003).

Genus *Passiflora* L.	**520 species**
1- Subgenus *Astrophea* (DC.) Masters	**57**
Supersection *Astrophea*	*27*
Section Astrophea	10
Section Capreolata MacDougal & Feuillet	15
Section Leptopoda Killip *ex* Feuillet & Cremers	02
Supersection *Pseudoastrophea* (Harms) Feuillet & MacDougal	30
Section *Pseudoastrophea* (Harms) Killip	17
Section *Botryastrophea* (Harms) Killip	13
Series *Botryastrophea* (Harms) MacDougal & Feuillet	06
Series *Carnae* Feuillet	07
2- Subgenus *Deidamioides* (Harms) Killip	**13**
Section *Polyanthea* DC.	01
Section *Deidamioides* (Harms) Feuillet & MacDougal	01
Section *Tetrastylis* (Barb. Rodr.) Harms	02
Section *Mayapathanthus* MacDougal & Feuillet	02
Section *Tryphostemmatoides* Harms	07
3- Subgenus *Decaloba* (DC.) Rchb.	**214**
Supersection *Pterosperma* Gilbert & MacDougal	04
Supersection *Hahniopathanthus* (Harms) MacDougal & Feuillet	05
Supersection *Disemma* (Labill.) MacDougal & Feuillet	21
Section *Octandranthus* Harms	17
Section *Disemma* (Labill.) MacDougal & Feuillet	03
Section *Hollrungiella* Harms	01
Supersection *Multiflora* (Small) MacDougal & Feuillet	09
Supersection *Auriculata* MacDougal & Feuillet	08
Supersection *Cieca* (Medic.) MacDougal & Feuillet	18
Supersection *Bryonioides* (Harms) MacDougal & Feuillet	20
Supersection *Decaloba* (DC.) MacDougal & Feuillet	119
Section *Decaloba* DC.	106
Section *Xerogona* (Raf.) Killip	13
4- Subgenus *Passiflora*	**236**
Supersection *Passiflora*	19
Series *Passiflora*	13
Series *Palmatisectae* Feuillet & MacDougal	01
Series *Pedatae* Killip *ex* Cervi	01
Series *Setaceae* Killip *ex* Cervi	04
Supersection *Stipulata* Feuillet & MacDougal	95
Section *Granadillastrum* Triana & Planch.	66
Section *Calopathanthus* Harms	01
Section *Tacsonioides* DC.	04
Section *Kermesinae* (Cervi) Feuillet & MacDougal	04
Section *Dysosmia* DC.	20
Supersection *Laurifolia* (Cervi) Feuillet & MacDougal	42
Series *Laurifoliae* Killip *ex* Cervi	21
Series *Quadrangulares* Feuillet & MacDougal	06
Series *Tiliifolia* Feuillet & MacDougal	14
Series *Marginatae* Killip *ex* Cervi	01
Supersection *Coccinea* Feuillet & MacDougal	14
Supersection *Distephana* (DC.) Feuillet & MacDougal	05
Supersection *Tacsonia* (Juss.) Feuillet & MacDougal	61
Section *Rathea* (Karst.) Harms	03
Section *Insignes* Feuillet & MacDougal	05

Section *Colombiana* Escobar	19
Series *Colombianae* Escobar	09
Series *Leptomischae* Escobar	08
Series *Quidiensae* Escobar	02
Section *Parritana* Escobar	02
Section *Fimbriatistipula* Escobar	02
Section *Tacsoniopsis* Triana & Planch.	02
Section *Elkea* Feuillet & MacDougal	15
Section *Tacsonia* (Juss.) Harms	05
Section *Boliviana* (Harms) Feuillet & MacDougal	02
Section *Trifoliata* Feuillet & MacDougal	01
Section *Manicata* (Harms) Feuillet & MacDougal	05

Annex 3. Species cultivated in Colombia.

A.3.1. *Passiflora edulis* Sims

Plant essentially glabrous throughout (except ovary); trilobate leaves (5-25 x 5-20 cm.); sepals white inside and green outside. This species presents two botanical form *flavicarpa* Degener and *edulis*, originally differentiated by the color (yellow and purple) and size of the fruit (8-12 x 5-10 cm and 5-8 x 4-6 cm respectively).

The yellow maracuja*,* *P. edulis* f. *flavicarpa* is very probably native of Brazil and is the most important passion fruit in the hot tropical areas, under the names of passion fruit, yellow granadilla, yellow maracuja, maracuyá, parchita maracuyá. The yellow maracuja requires high temperatures, between 20 and 34 ˚C, and develops better at lower altitudes. The principal producer is Brazil with 450.000 t.y^{-1}. Colombia reports 5.000 ha located from 0 to 1.200 m, with a production of 17 to 20 t.ha^{-1}.y^{-1}, mainly in the departments of Huila and Valle del Cauca. Between 60 and 70% of the Colombian production is processed into frozen juice, exported to the European market and the remainder is consumed *in natura*.

The purple maracuja, *P. edulis* f. *edulis* is native of southern Brazil to northern Argentina and Paraguay. It is now cultivated in most tropical areas with a mild climate (subtropics and tropical highlands). In Colombia, it grows up to 2.500 m. This form is known under the names of purple maracuja, gulupa, curuba redonda, maracuyá rojo, palchita. Colombia, Australia, USA, Kenya, and Zimbabwe are the principal producers with approximately 20.000 t, although the total area is unknown. In Colombia, about 100 ha area cultivated between 1.700 and 2.500 m, with reported yields between 10 and 12 t.ha^{-1} .y^{-1}.

According to Vanderplank (2000), the presently cultivated material originated from several fruits, found in a London market, whose seeds were sent to Argentina. In 1915, the progeny from these seeds passed through the USDA (United States Department of Agriculture) into the United States, which redistributed them to Australia and New Zealand. Yellow maracuja breeding has most often involved direct mass selection of this material with a narrow genetic base and its hybridization with genotypes of the purple form obtained from materials exported to Australia and Hawaii more than one hundred years ago.

The purple and yellow forms have frequently been crossed and spontaneous hybrids are found in Hawaii and Australia. The direction of crossing determines its success: *P. edulis* f. *flavicarpa* should be used as the male (Beal, 1975). The F_1 hybrids are intermediate, normal and vigorous (Nakasone et al., 1967). Meiosis is normal with the formation of nine bivalents, but the chiasma frequency is lower in the hybrid than in the parents, which suggests slightly reduced chromosomal homology. In the F_2, 6 to 8% of the plants were found to be abnormal (Beal, 1975). These data, as well as differences in the phenology and acclimatization of the two forms, indicate the beginning of differentiation, tempered by the fact that equally important divergences may be observed within the purple form in Brazil (Oliveira et al., 1987).

A.3.2. *Passiflora ligularis* Juss.

Vernacular names: sweet granadilla, granadilla.

Origin: Andes of Colombia to Peru.

Distribution: Mexico to Peru.

Plant glabrous with broad heart-shaped leaves (rarely trilobate), flowers white or pinkish white, fruit round to ovoid, 5 to 9 cm long, 4 to 7 cm in diameter, tapering towards the peduncle, with a thin, hard and brittle pericarp, light brown to orange, sometimes tinged of violet, with small light spots or stripes. Its light grey pulp is aromatic, slightly tangy and relished by consumers in raw form. This species is usually cultivated at altitudes of 1.400 to 2.200 m. near the Equator, with extremes of 800 and 3.000 m. It grows at average temperatures of 14 to 22^{o}C and a relative humidity of 70%. It can tolerate short and very light frosts. It is said to be tolerant to parasites and diseases of root and collar, but is susceptible to withering due to *Nectria haematococca* (anamorphic *Fusarium solani*) in poorly drained soils. A plantation is productive for four to eight years. The sweet granadilla commences flowering in the ninth month and production starts 75 to 80 days later. Colombia is the principal producer with 2.661 ha (2004) at a density of 400 plants per hectare and yields reach 45 to 50 t ha^{-1} y^{-1}. Currently, Colombia is exporting this fruit to Europe. There are no commercial varieties of the sweet granadilla. Although some superior types may be propagated by cuttings or grafting, multiplication is usually by seed and the plant allogamy maintains considerable variability in plantations.

A.3.3. *Passiflora tripartita* var. *mollissima* (Kunth) Holm-Nielsen & Jørgensen

Vernacular names: Banana passion fruit, curuba de Castilla, tacso, tumbo.

Origin: Andes of Venezuela to Bolivia (2.000 - 3.500 m).

Distribution: Venezuela to Argentina (mostly cultivated), New Zealand.

Plant pubescent, leaves deeply trilobate, 5-10 x 6-12 cm; flowers pendant, corolla variable in size, with pink to deep red sepals and petals, 2.5 to 4 cm long. The crown is reduced to a whorl of white tubercles on a red background. The floral tube is 6 to 11 cm long and 1.5 cm wide; fruit oblong, 6-5 cm x 3-5 cm. with rounded ends, weighing 50 to 150 g (average 80 g). The pericarp is pale yellow, occasionally green, somewhat pubescent, thin and supple but coriaceous. It is rich in pectin and can be processed if in a perfect state, without anthracnose spots. The pulp, constituting 60% of the fruit, is salmon-pink to dark orange, slightly acidic, very pleasantly scented but generally astringent. The plant grows at altitudes between 2.000 and 3.000 m, sometimes up to 3.600 m, at average temperatures of 12 to 15°C and relative humidity of 70 to 80%. It cannot adapt to warmer climates yet it is sensitive to extended periods of frost. Production begins at about 18 months. Commercial cultivation began in the 1950s. In Colombia, 1.795 ha are cultivated, with yield ranging from 7 $t.ha^{-1}.y^{-1}$ to 45 t, the latter under the most suitable conditions. The major phytosanitary problems are anthracnose, which spoils the fruit, and nematodes of the genus *Meloidogyne*. Being an allogamous species, its repeated self-fertilization results in a serious loss of vigor (Schöniger, 1986).

A.3.4. *Passiflora tarminiana* Coppens & Barney

Vernacular names: curuba india, tacso, tumbo

Distribution: Venezuela to Argentina, as a cultigen, naturalized in the USA (Hawaii; invasive species), New Zealand, Philippines, Ceylon, Papua New Guinea, tropical highlands of East Africa.

Plant glabrous; leaves trilobate, 7-9 x 12-18 cm; flowers pendent, petals bright pink to light pink; fruit fusiform 10-14 x 3.5-4.5 cm, pericap yellow to orange with dots except along the main vascular bundles. *P. tarminiana* is adapted to a wide range of elevations as compared to other species of the subgenus *Tacsonia* and have been introduced into numerous cool tropical and tropical montane areas other than its original Andean range, in some cases becoming an invasive weed. The hybrids with *P. mixta* and *P. tripartita* var. *mollissima* are fertile and show intermediate phenotypes (Primot et al., 2005). This species is tolerant to *Alternaria* and

Colletrotrichum. In Colombia, it is cultivated between 2.000 and 2.700 m with yields around 20-25 t.ha^{-1}.y^{-1}, although the cultivated area is not known, as it is frequently confused with *P. tripartita* var. *mollissiima.*

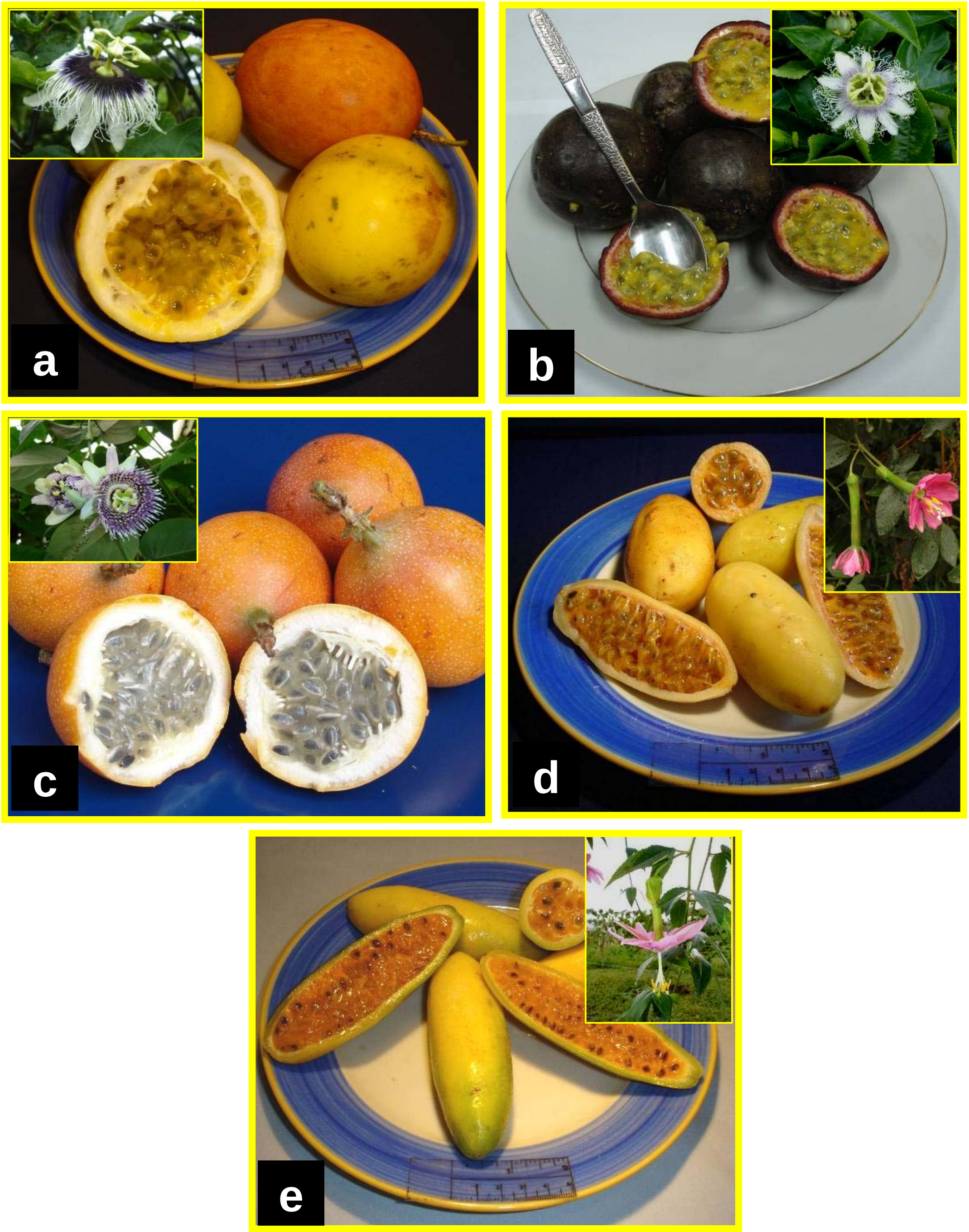


Figure 1. Species cultivated in Colombia: (**a)** *P. edulis* f. *flavicarpa*; (**b)** *P. edulis* f. *edulis*; (**c)** *P. ligularis*; (**d)** *P. tripartita* var. *mollissima*; (**e)** *P. tarminiana*.

A.3.5. *Passiflora quadrangularis* L.

Vernacular names: giant granadilla, badea, barbadine.

Distribution: West Indies to South America

Plant glabrous, stem stout, quadrangular, reaching 50 m in length; leaves simple, oval or oblanceolate, 10 to 25 cm long and 8 to 18 cm broad; the flowers may reach 12 cm in diameter: the inner face of the sepals and petals is white, pink, red or violet; the crown may reach 6 cm in length; the fruit is yellowish-green, sometimes with a pinkish tint, ovoid to oblong. It is 20 to 30 cm long, 10 to 18 cm broad, and weighs 2.8 kg on average, even reaching 4 kg. It develops in 62 to 85 days. The fruit mesocarp is 2 to 3 cm thick, soft and edible but bland. The pulp is transparent, white to orange, sweet and slightly tangy, the taste variable but always less pungent than that of maracuja. Manual pollination is often recommended. This species is tolerant to *Alternaria passiflorae* (McMillan & Graves 1992) and resistant to withering but highly susceptible to nematodes and *Xanthomonas* spp. (Oliveira & Ferreira, 1991; Vanderplank 2000). In Colombia 60 ha are cultivated between 0 to 1.000 m, with a yield of 16 to 18 t. ha^{-1} y^{-1}.

A.3.6. *Passiflora maliformis* L.

Vernacular names: stone granadilla, conch apple, granadilla de piedra, chulupa, coque en fer.

Origin: West Indies to Ecuador.

Distribution: West Indies to Ecuador, North Brazil.

Plants glabrous or finely pilosulous with leaves ovate, ovate-lanceolate, or sometimes orbicular ovate; flowers petals densely mottled with dark red-purple; fruits globose, 4 to 6 cm in diameter, green or orange green and rarely purple, pericarp hard to extremely hard.

The juice has excellent flavor, is very refreshing and valuable due its high content of ascorbic acid. This plant occurs naturally at mid-elevations (0 to 1.600 m), but in Colombia it is cultivated at 600 to 1.000 m on 97 ha, with yields of 11 to 14 t ha^{-1} y^{-1}, mainly in the Huila department where there is a local market.

A.3.7. *Passiflora alata* Curtis

Vernacular names: Fragrant granadilla, maracuja doce, Maracua.

Origin: Brazilian and Peruvian Amazon, Brazilian Planalto in forest galleries.

Distribution: Brazil, Peru and Colombia.

Plant glabrous with stem stout and quadrangular; leaves ovate or ovate-oblong 8-15 x 7-10 cm; flowers petals red inside and green outside; fruit ovoid or pyriform, 8 to 10 cm. long, yellow. In many regions of South America, *P. alata* is cultivated because of its edible fruit. Brazil is the principal producer with 50 $t.ha^{-1}. y^{-1}$ and an area of 120 ha. In Colombia, it has been cultivated traditionally in the Amazon and commercially in the North of the Valle del Cauca and Quindío departments from 1999, but its yield statistics are unknown. This species has given a number of hybrids, mainly with the closely related *P. quadrangularis*.

A.3.8. *Passiflora popenovii* Killip

Vernacular names: Granadilla de Quijos, granadilla caucana, curubejo.

Distribution: South of Colombia and Ecuador.

Plant glabrous, except the ovary and the outer surface of the calyx tube; leaves unlobed, oblong-ovate, 8.5 to16 cm long; fragrant flowers with white petals; fruit ovoid, 6 to 10 cm in diameter, epicarp thin and yellow. The sweet pulp and juice are highly regarded and is enjoyed for its rich aroma and taste. This species is cultivated in Colombia (Cauca and Nariño) and Ecuador (Tungurahua, Napo, Loja) between 1.400 and 2.100 m. and its fruits are offered in local markets in the months of April and May. This plant is regularly propagated by cutting. In Colombia, yields of 140 kg/plant are reported, but the cultivated area is not well known.

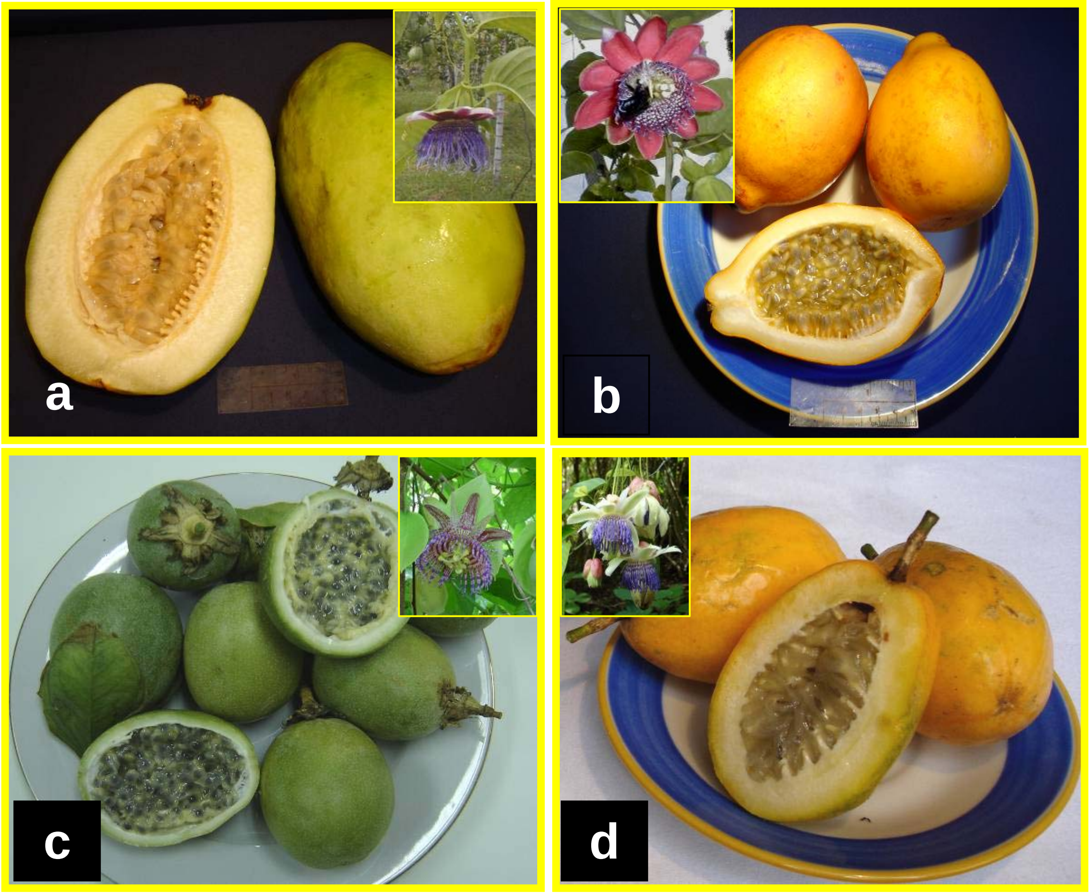
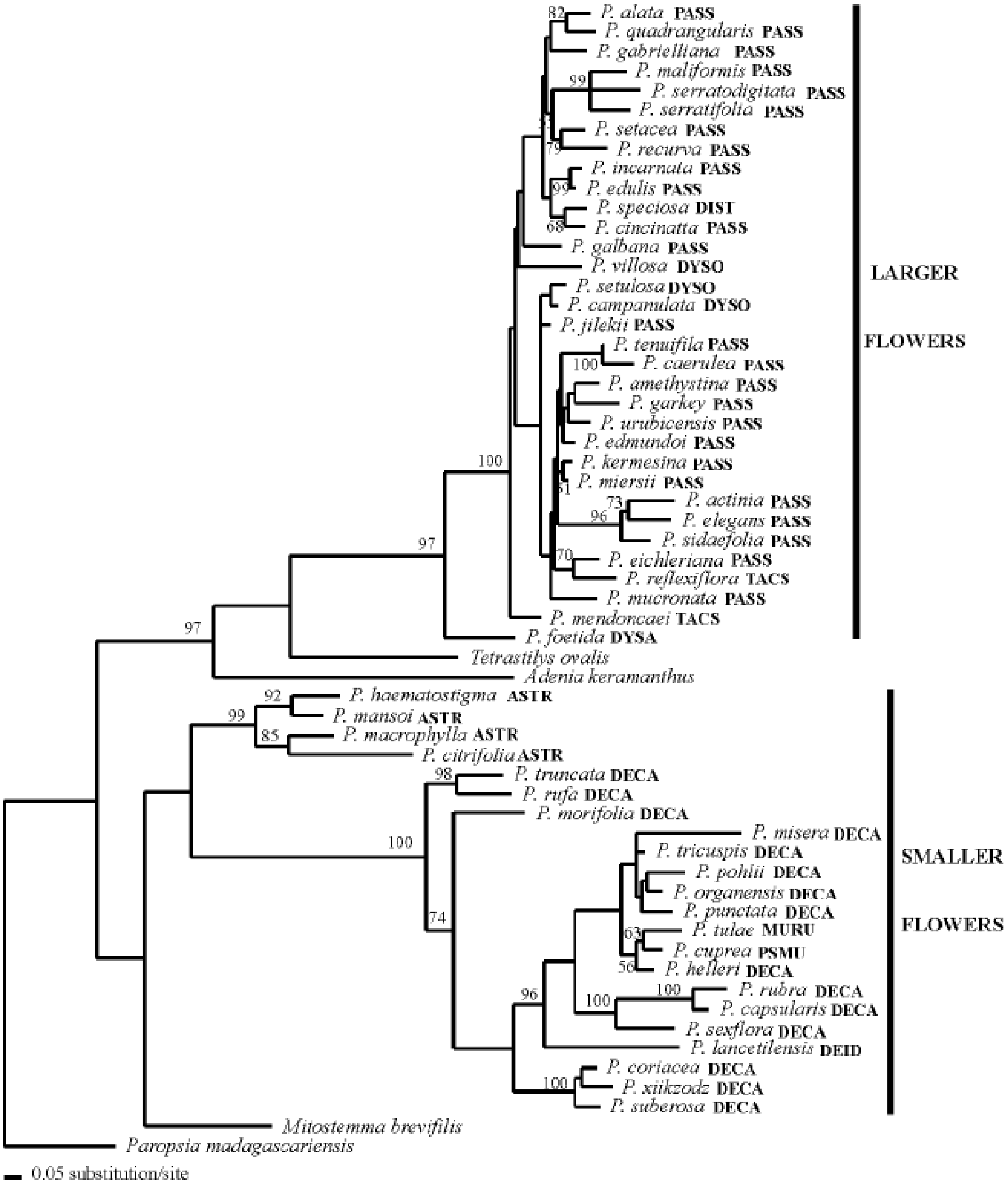
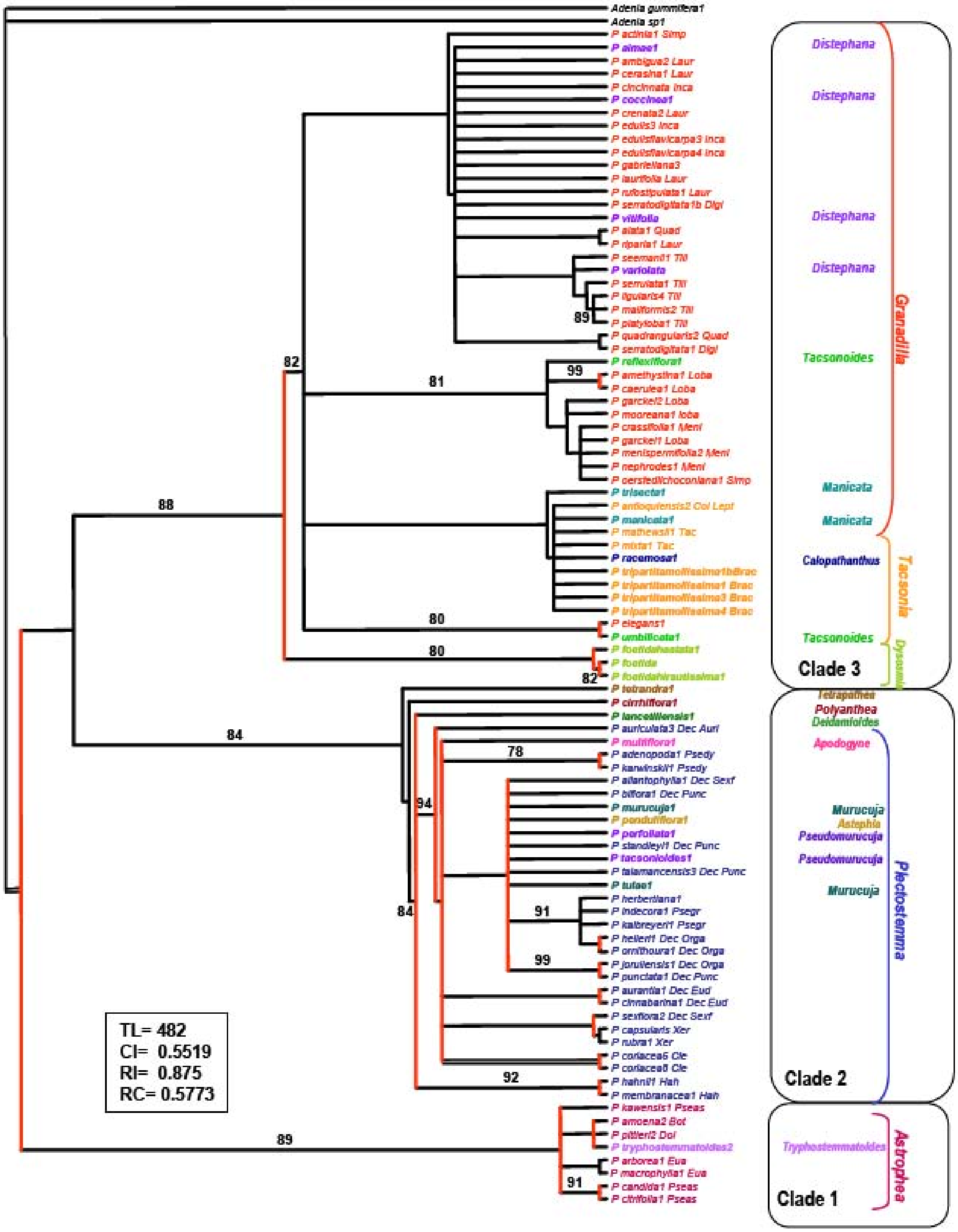


Figure 2. Species cultivated in Colombia: (**a**) *P. quadrangularis*; (**b**) *P. alata*; (**c**) *P. maliformis*; (**d**) *P. popenovii*.

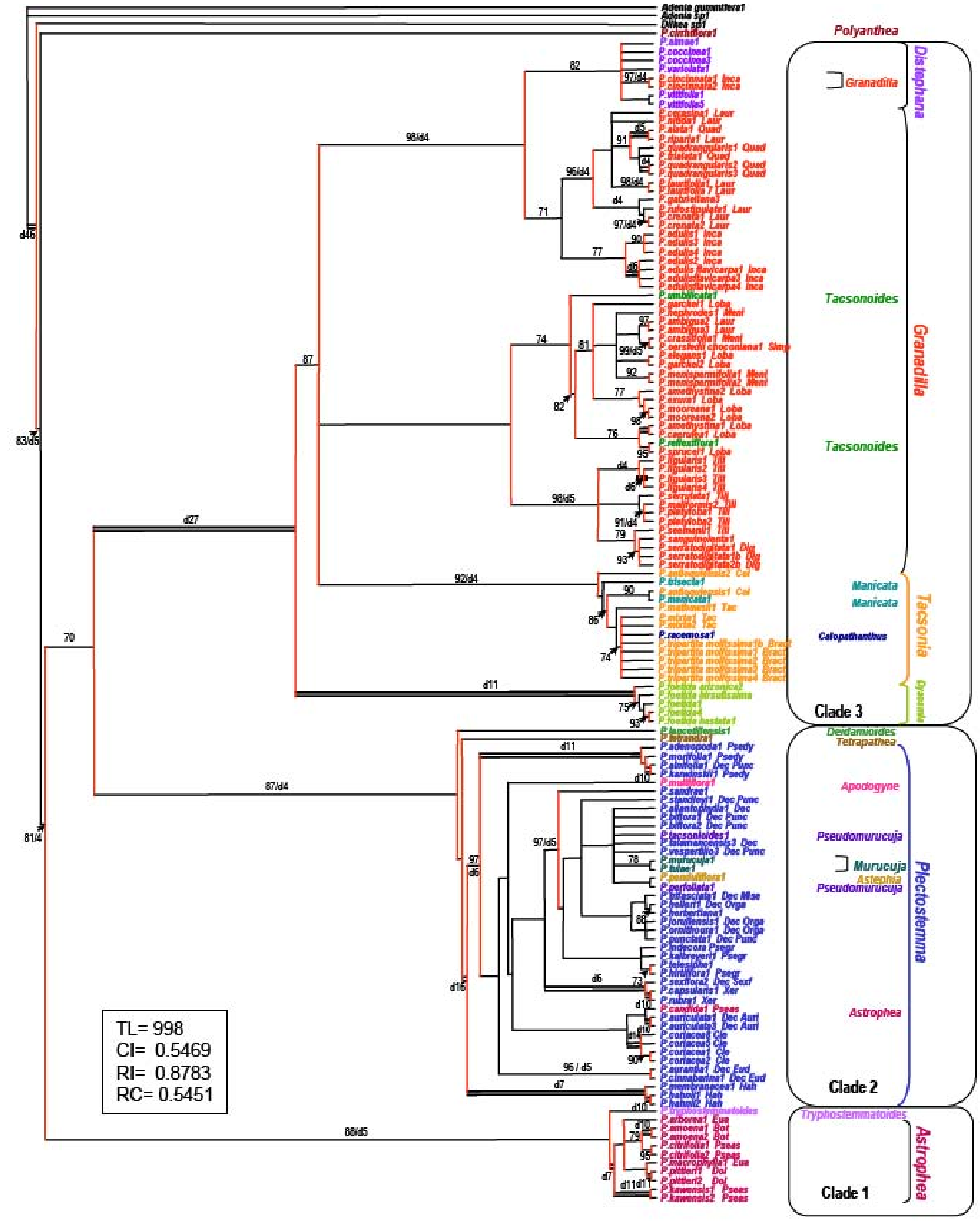
Annex 4. *Passiflora* molecular diversity. Dendrograms obtained in previous studies.



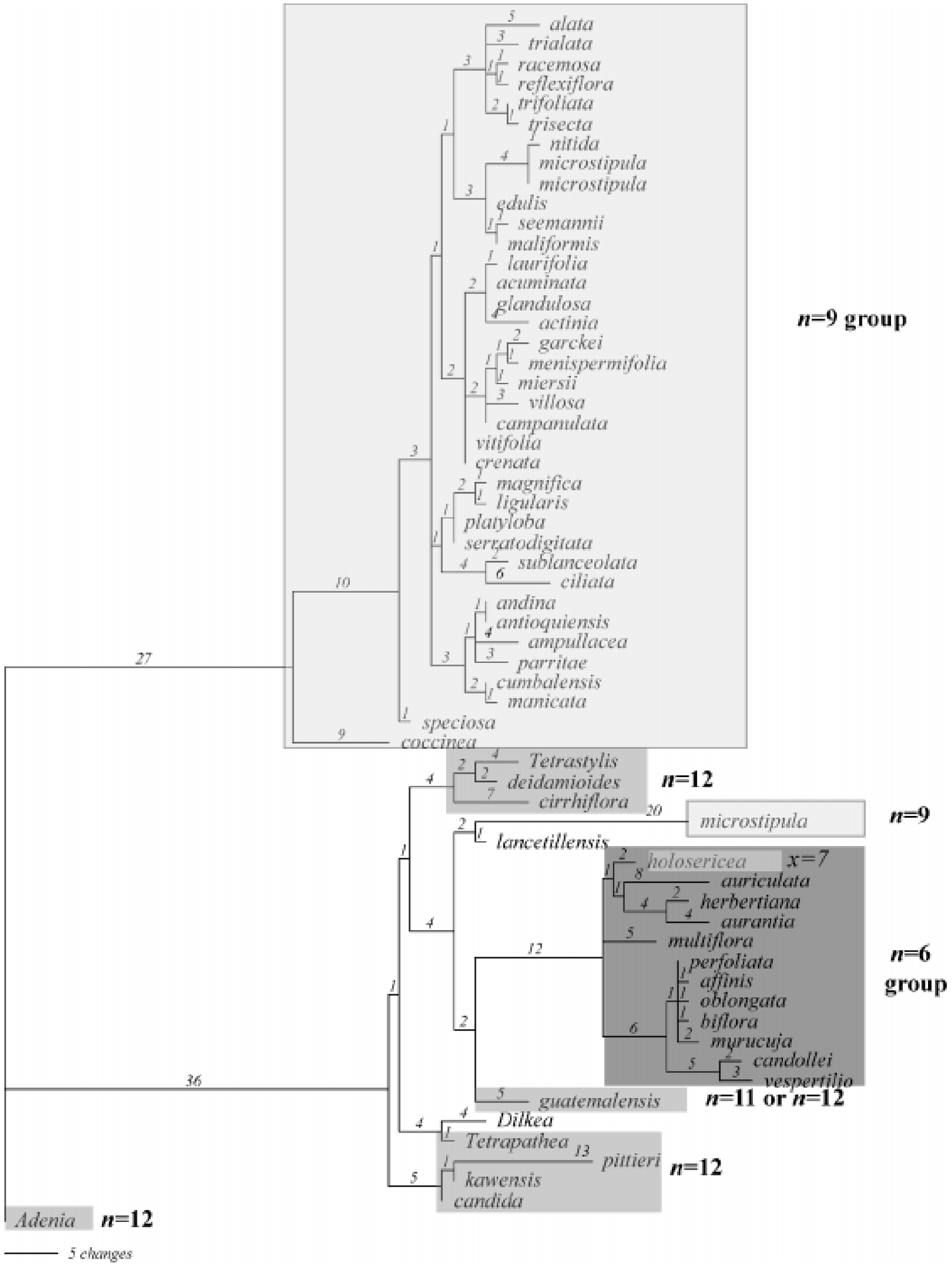
A.a. Phylogenetic tree *sensu* Muschner et al. (2003). Maximum-likelihood tree for the **ITS spacer** in *Passiflora* and outgroups. Numbers above branches are bootstrap support values (when higher than 50%) based on 1000 replicates. Abbreviations indicate the subgenera as follows: PASS 5 *Passiflora*; DIST 5 *Distephana*; TACS 5 *Tacsonioides*; DYSO 5 *Dysosmioides*; DYSA 5 *Dysosmia*; ASTR 5 *Astrophea*; DECA 5 *Decaloba*; MURU 5 *Murucuja*; DEID 5 *Deidamioides*; PSMU 5 *Pseudomurucuja*; ADOP 5 *Adopogyne*.



A.b. Phylogenetic tree *sensu* Yockteng (2003). Strict consensus tree of 3,536 most parsimonious trees based on the alignment of chloroplast-expressed mutarase K (***mat*k**) sequences. Bootstrap support values (BS) greater than 70% and decay indices greater than 4 are indicated above branches. Thick lines indicate BS values of 100%, dots indicate nodes supported by 100% in the Bayesian tree. The subdivisions according to Killip (1938) are indicated for each taxon. The sections and series names are abbreviated as follows: Cie, *Cieca*; Dec, *Decaloba*; Auri, *Auriculatae*; Sexf, *Sexflorae*; Orga, *Organenses*; Mise, *Miserae*; Punc, *Punctatae*; Eud, *Eudecaloba*; Xero, *Xerogona*; Psedy, *Pseudodysosmia*; Psegr, *Pseudogranadilla*; Hah, *Hahniopathanthus*; Lept, *Leptomischae*; Col, *Colombianae*; Bract, *Bracteogama*; Tac, *Tacsonia*; Quad, *Quadrangulares*; Digi, *Digitatae*; Tili, *Tiliafoliae*; Laur, *Laurifoliae*; Inca, *Incarnatae*; Simp, *Simplicifoliae*; Loba, *Lobatae*; Meni, *Menispermifoliae*; Doli, *Dolichostemma*; Euas, *Euastrophea*; Pseas, *Pseudoastrophea*. The three clades emerging from the analysis are indicated on the right.



A.c. Phylogenetic tree *sensu* Yockteng & Nadot (2004). Strict consensus tree of 32,573 most parsimonious trees based on the alignment of chloroplast-expressed glutamine synthetase (**ncpGS**) sequences. Bootstrap support values (BS) greater than 70% and decay indices greater than 4 are indicated above branches. Thick lines indicate BS values of 100%, dots indicate nodes supported by 100% in the Bayesian tree. The subdivisions according to Killip (1938) are indicated for each taxon. The sections and series names are abbreviated as follows: Cie, *Cieca*; Dec, *Decaloba*; Auri, *Auriculatae*; Sexf, *Sexflorae*; Orga, *Organenses*; Mise, *Miserae*; Punc, *Punctatae*; Eud, *Eudecaloba*; Xero, *Xerogona*; Psedy, *Pseudodysosmia*; Psegr, *Pseudogranadilla*; Hah, *Hahniopathanthus*; Lept, *Leptomischae*; Col, *Colombianae*; Bract, *Bracteogama*; Tac, *Tacsonia*; Quad, *Quadrangulares*; Digi, *Digitatae*; Tili, *Tiliafoliae*; Laur, *Laurifoliae*; Inca, *Incarnatae*; Simp, *Simplicifoliae*; Loba, *Lobatae*; Meni, *Menispermifoliae*; Doli, *Dolichostemma*; Euas, *Euastrophea*; Pseas, *Pseudoastrophea*. The three clades emerging from the analysis are indicated on the right.



A.d. Phylogenetic tree *sensu* Hansen et al. (2006). Phylogram of 1 of 200,000 trees from analysis A of ***trnL/trnT*** sequence data illustrating the distribution of chromosome numbers in the genus. Branch lengths represent character state changes and the number of changes is listed above each branch.

Annex 5. List of morphological descriptors in the genus *Passiflora* L.

PASSPORT

INSTITUTE CODE:

ACCESSION NUMBER:

ACCESSION NAME:

STATUS OF SAMPLE:

SCIENTIFIC NAME:

VERNACULAR NAME:

CULTIVAR ORIGIN:
1. Open pollination:
2. Artificial pollination:
3. Clonal selection:
4. Seedling selection:

COLLECTING DESCRIPTION:
1. Country of origin:
2. Province / state / Deparment:
3. Country
4. Collection site:
5. Latitude:
6. Longitude:
7. Altitude:

ENTHNOBOTANICAL DATA:

COLLECTOR:

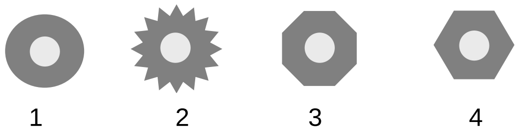
DATE:

NOTES:

1. STEM

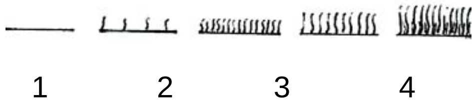
1.1 HABIT (STHA)
1. Liana (eg. *P. incarnata*)
2. Tree (eg. *P. emarginata*)
3. Shrub (eg. *P. macrophylla*)

1.2 EXTERNAL SHAPE (STSH)
1. Round
2. Striate
3. Subangulate
4. Angulate (e.g. *P. quadrangularis*)
5. Other (Specify)



1.3 ANTHOCYAN (STAN)
1. Absent
2. Medium (< 80%)
3. High (> 80%)

1.4 PUBESCENCE (STPU)
1. Glabrous
2. Few density
3. Tomentoso
4. Villous
5. Pilose



1.5 INTERNODE LENGTH (STIN)

mm	**mm**	**mm**	**mm**	**mm**

1.6 DIAMETERS (STDI)

mm	**mm**	**mm**	**mm**	**mm**

2. TENDRIL

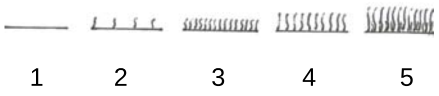
2.1 TENDRILS (TEPRE)
1. Absent
2. Present

2.2 SPIRAL SHAPE (TESH)
1. Cylindrical
2. Conic
3. Compound

4. Linear
5. Indefinite

2.3 PUBESCENCE (TEPU)

1. Glabrous
2. Low density
3. Tomentose
4. Villous
5. Pilose



2.4 ANTHOCYANIN (TEAN)

1. Absent
2. Medium (< 80%)
3. High (> 80%)

3. STIPULE

3.1 STIPULES (TEPR)

1. Present
2. Absent

3.2 DURATION (SPPE)

1. Permanent
2. Deciduous

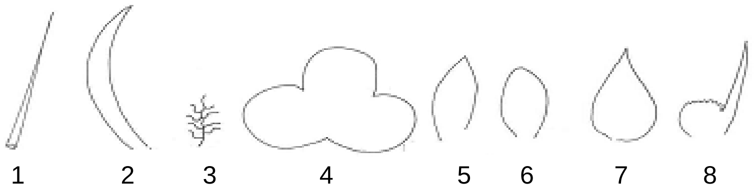
3.3 COLOR (SPCO)

3.4 PUBESCENCE (SPPU)

1. Glabrous
2. Low density
3. Tomentose
4. Villous
5. Pilose

3.5 SHAPE (SPSH)

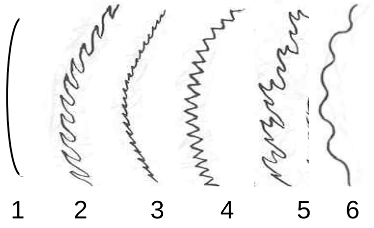
1. Setaceous
2. Linear
3. Pinnatisect
4. Lobed
5. Lanceolate
6. Oblate
7. Ovate
8. Reniform (or auricular)



9. Other (specify)

3.6 MARGIN (SPMA)

1. Entire
2. Serrate
3. Serrulate
4. Dentate
5. Doubly dentate
6. Crenate
7. Other (specify)

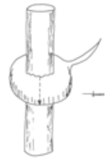


3.7 ANTHOCYANIN (SPAN)

1. Absent
2. Medium (< 80%)
3. Heigth (> 80%)

3.8 LENGTH (SPLE)

mm	**mm**	**mm**	**mm**	**mm**



3.9 WIDTH (SPWI) (including the arist)

mm	**mm**	**mm**	**mm**	**mm**

3.10 TERMINAL ARIST LENGTH (SPTA)

mm	**mm**	**mm**	**mm**	**mm**

4. PETIOLE

4.1 ANTHOCYANIN (PEAN)

1. Absent
2. Medium (< 80%)
3. High (> 80%)

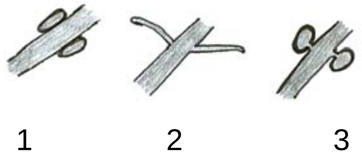
4.2 PUBESCENCE (PEPU)

1. Glabrous
2. Low density
3. Tomentose
4. Villous
5. Pilose

4.3 COLOR (PECO)

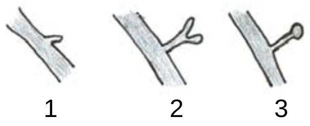
4.4 NECTARY SHAPE (PENS)

1. Discoid (e.g. *P. edulis* f. *flavicarpa*)
2. Extended (e.g. *P. ligularis*)
3. Spherical (e.g. *P. adenopoda)*
4. Other



4.5 STIPE OF NECTARIES (PESN)

1. Absent
2. Intermediate
3. Present



4.6 LENGHT (PELE)

mm mm mm mm mm

4.7 DISTANCE FROM BASE TO FIRST GLAND (PEDG)

mm mm mm mm mm

4.8 NECTARY GLAND NUMBER (PENM)

5. LEAF

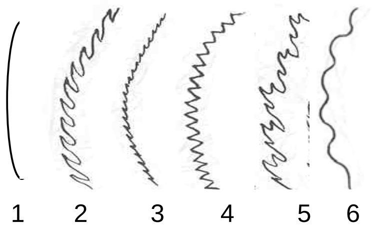
5.1 HETEROPHYLLY (LEPO)

1. Absent
2. Present

5.2 LOBE NUMBER (LELN)

5.3 MARGIN (LEMA)

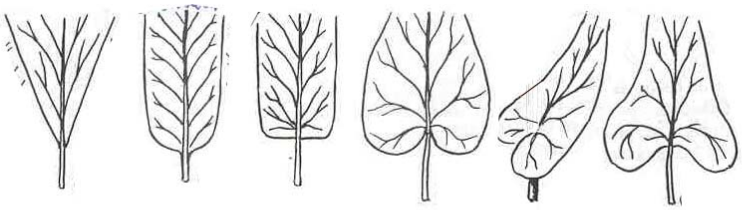
1. Entire
2. Serrate
3. Serrulate
4. Dentate
5. Doubly dentate
6. Crenate



7. Other (specify)

5.4 BASE SHAPE (LEBS)

1. Cuneate
2. Rounded
3. Truncate
4. Cordate (Heart-shaped)
5. Deeply cordate
6. Articulate
7. Other (specify)



5.5 APEX SHAPE (LEAS)

1. Rounded
2. Obtuse ($>90^o$)
3. Acute
4. Acute ($<45^o$)
5. Other (specify)

5.6 ACUMEN (LEPA)

1. Absent
2. Presence

5.7 PUBESCENCE ADAXIAL (LEAX)

1. Glabrous
2. Low density
3. Tomentose
4. Villous
5. Pilose

5.8 PUBESCENCE ABAXIAL (LEPB)

1. Glabrous
2. Low density
3. Tomentose
4. Villous
5. Pilose

5.9 ANTHOCYANIN - LAMINA (LEAL)

1. Absent
2. Medium (< 80%)
3. High (> 80%)

5.10 ANTHOCYANIN - NERVES (LEAN)

1. Absent
2. Medium (< 80%)
3. High (> 80%)

5.11 COLOR – ADAXIAL (LECA)

5.12 MARGIN SERRATION DENSITY (number on 2 cm) **(LEMS)**

mm	**mm**	**mm**	**mm**	**mm**

5.13 ANGLE BETWEEN LATERAL LOBES (LEAB)

mm	**mm**	**mm**	**mm**	**mm**

5.14 CENTRAL LOBE LENGTH (LELC)

mm	**mm**	**mm**	**mm**	**mm**

5.15 RIGHT LOBE LENGTH (LERL)

mm	**mm**	**mm**	**mm**	**mm**

5.16 CENTRAL LOBE WIDTH (LECL)

mm	**mm**	**mm**	**mm**	**mm**

5.17 DISTANCE BETWEEN LEAF SINUS AND PETIOLE INSERTION (LESS)

mm	**mm**	**mm**	**mm**	**mm**

5.18 HETEROBLASTY (LEPH)
0. Absent
1. Present

5.19 LAMINAR NECTARIES (LENL)
1. Absent
2. Present

5.20 NECTAR GLAND NUMBER ON LAMINA (LELA)

5.21 DISTRIBUTION OF LAMINAR NECTARIES (LEDN)
1. Along central lobe

2. On lateral lobes
3. Around lamina
4. Around apex
5. At base

5.22 PRESENCE OF MARGINAL NECTARIES (LEPN)

1. Absent
2. Present

5.23 NECTAR NUMBER ON LEAF MARGIN (LENN)

5.24 DISTRIBUTION OF LAMINAR MARGIN NECTARIES (LELM)

1. Base
2. Base and sinus
3. Margin
4. Other (specify)

5.25 NECTARY SHAPE (LENS)

1. Discoid (squashed)
2. Extended
3. Spherical
4. Other


1


2


3

6. PEDUNCLE

6.1 PUBESCENCE (PDPU)

1. Glabrous
2. Low density
3. Tomentose
4. Villous
5. Pilose

6.2 ANTHOCYANIN (PDAN)

1. Absent
2. Medium (< 80%)
3. High (> 80%)

6.3 BIFURCATION (PDBN)

1. Present
2. Absent

6.4 LENGTH (PDLE)

mm	**mm**	**mm**	**mm**	**mm**

6.5 DIAMETER (PDDI)

mm	**mm**	**mm**	**mm**	**mm**

6.6 PEDICEL LENGTH (PDPL)

mm	**mm**	**mm**	**mm**	**mm**

6.7 LENGTH TO FIRST BIFURCATION (PDLF)

mm	**mm**	**mm**	**mm**	**mm**

6.8 LENGTH TO SECOND BIFURCATION (PDBS)

mm	**mm**	**mm**	**mm**	**mm**

7. BRACT

7.1 UNION (BRUN)

1. Free
2. United at less than half
3. United at half
4. United at more than half

7.2 BRACT (BRPR)

1. Present
2. Absent

7.3 PERMANENCE (BRPE)

1. Permanent
2. Deciduous

7.4 PUBESCENCE (BRPU)

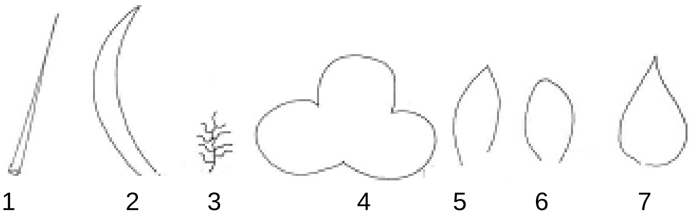
1. Glabrous
2. Low density
3. Tomentose
4. Villous
5. Pilose

7.5 POSITION OF PUBESCENCE (BRPP)
1. Absent
2. Adaxial
3. Abaxial
4. Both sides

7.6 COLOR (BRCO)

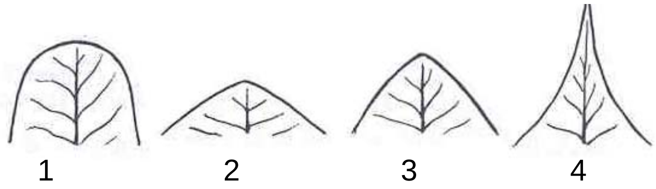
7.7 ANTHOCYANIN (BRAN)
1. Absent
2. Medium (< 80%)
3. High (> 80%)

7.8 SHAPE (BRSH)
1. Setaceous
2. Linear
3. Pinnatisect
4. Lobate
5. Lanceolate
6. Oblate
7. Ovate
9. Other (specify)



7.9 MARGIN (BRMA)
1. Entire
2. Serrate
3. Serrulate
4. Dentate
5. Doubly dentate
6. Crenate
7. Other (specify)

7.10 APEX SHAPE (BRAS)
1. Round
2. Obtuse (>90^{o})
3. Acute
4. Very acute (<45^{o})
5. Other



7.11 MARGIN NECTARIES (BRNM)
1. Present
2. Absent

7.12 LENGTH (BRLE)

mm mm mm mm mm

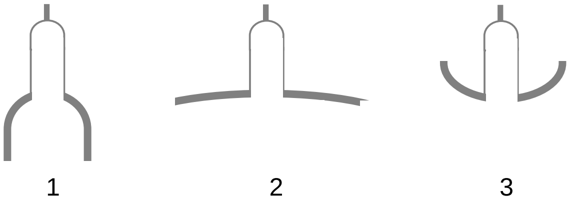
7.13 WIDTH (BRWI)

mm mm mm mm mm

8. FLOWER

8.1 CORONA TYPE (FLCY)
1. Tuberculous
2. Filamentous

8.2 COROLLA TYPE (FLCT)
1. Campanulate (e.g. *P. mixta)*
2. Intermediate (eg. *P. manicata*)
3. Reflex (eg. *P. tarminiana*)
4. Other (specify)



8.3 ORIENTATION (FLOF)
1. Pendular (eg. *P. antioquiensis*)
2. Intermediate (eg. *P. mixta*)
3. Erect (eg. *P. manicata*)

8.4 ORIENTATION (in Degrees to vertical) (FLOG)

8.5 PUBESCENCE ON COROLLA (FLPU)
1. Glabrous
2. Low density
3. Tomentose
4. Villous
5. Pilose

8.6 HYPHANTHIUM PUBESCENCE (FLHP)
1. Glabrous
2. Low density
3. Tomentose
4. Villous
5. Pilose

8.7 DOMINANT PETAL COLOR (FLCP)

8.8 CHLOROPHYLL ON EXTERIOR OF SEPAL (FLCS)

1. Absent
2. Present

8.9 KEEL-SHAPED SEPALS (FLKS)

1. Absent
2. Present

8.10 SEPAL AWN (CAS)

1. Absent
2. Present

8.11 UNION OF SEPALS (FLUS)

1. Free
2. United

8.12 PETALS (FLPP)

1. Present
2. Absent

8.13 PETAL LENGTH (FLPL)

mm	**mm**	**mm**	**mm**	**mm**

8.14 PETAL WIDTH (FLPW)

mm	**mm**	**mm**	**mm**	**mm**

8.15 SEPAL LENGTH (FLSL)

mm	**mm**	**mm**	**mm**	**mm**

8.16 SEPALS WIDTH (FLSW)

mm	**mm**	**mm**	**mm**	**mm**

8.17 DIAMETER OF NECTARY CHAMBER (FLNC)

mm	**mm**	**mm**	**mm**	**mm**

8.18 HYPANTHIUM DIAMETER ABOVE NECTARY CHAMBER (FLHD)

mm	**mm**	**mm**	**mm**	**mm**

8.19 HYPANTHIUM DIAMETER – DISTAL (FLHS)

mm	**mm**	**mm**	**mm**	**mm**

8.20 FLOWER LENGTH (FLLE)

mm	**mm**	**mm**	**mm**	**mm**

8.21 HYPHANTIUM LENGHT (FLHL)

mm	**mm**	**mm**	**mm**	**mm**

8.22 LENGHT OF NECTARY CHAMBER (FLCN)

mm	**mm**	**mm**	**mm**	**mm**

8.23 NUMBER OF CORONA SERIES (FLNS)

8.24 COLOR OF FILAMENTS AT BASE (FLCB)

8.25 COLOR OF FILAMENTS AT APEX (FLCA)

8.26 FILAMENT LENGTH (FLFL)

mm	**mm**	**mm**	**mm**	**mm**

8.27 DISTRIBUTION OF ANTHERS (FLDA)

1. Symmetry radial
2. Symmetry bilateral
3. Other

8.28 COLOR OF STAMINAL FILAMENTS (CFE)

8.29 STAMINAL FILAMENTS LENGTH (FLSF)

mm	**mm**	**mm**	**mm**	**mm**

8.30 OVARY PUBESCENCE (FLOP)

1. Glabrous
2. Low density
3. Tomentose
4. Villous
5. Pilose

8.31 COLOR OF OVARY (FLCO)

8.32 OVARY LENGTH (FLOL)

mm	**mm**	**mm**	**mm**	**mm**

8.33 COLOR OF STYLE (FLCS)

8.34 STYLE LENGHT (FLSL)

mm	**mm**	**mm**	**mm**	**mm**

8.35 COLOR DISTRIBUTION ON STYLES (FLDS)

1. Uniform
2. Specked
3. Apex
4. Base
5. Other

8.36 COLOR OF STIGMA (FLCG)

8.37 COLOR OF ANDROGYNOPHORE (FLCN)

8.38 COLOR DISTRIBUTION ON ANDROGYNOPHORE (FLDN)
1. Uniform
2. Speckled
3. Other

8.39 PUBESCENCE OF ANDROGYNOPHORE (FLPN)
1. Glabrous
2. Few density
3. Tomentose
4. Villous
5. Pilose

8.40 GYNOPHORE LENGTH (FLGL)

mm	**mm**	**mm**	**mm**	**mm**

8.41 ANDROGYNOPHORE LENGTH (FLAL)

mm	**mm**	**mm**	**mm**	**mm**

8.42 OPERCULUM LENGTH (FLOP)

mm	**mm**	**mm**	**mm**	**mm**

8.43 LIMEN LENGTH (FLLL)

mm	**mm**	**mm**	**mm**	**mm**

8.44 LIMEN MARGIN (FLML)
1. Flat-entire
2. Flat-serrate
3. Wavy-entire
4. Wavy-serrate

8.45 NECTARY CHAMBER RING (FLNR)
1. Absent
2. Present

8.46 HYPANTHIUM TYPE (FLHY)
1. Flat (eg. *P. suberosa*)
2. Campanulate (*P. ligularis*)
3. Tubular (*P. tarminiana*)

8.47 INTERNAL COLOR OF HYPHANTIUM (FLCI)

8.48 CLOROPHYLLA ON EXTERIOR OF HYPANTHIUM (FLCE)

1. Absent
2. Partial
3. Global

8.49 ANTHOCYANIN ON EXTERIOR OF HYPANTHIUM (FLAE)

1. Absent
2. Partial
3. Global

8.50 STYLES NUMBER PER FLOWER (NEF)

8.50 NECTARS ON SEPALS (FLNS)

1. Absent
2. Present

8.51 DOMINANT SEPAL COLOR (FLCP)

8.52 ANTHOCYANIN ON EXTERIOR OF SEPALS (FRSH)

1. Absent
2. Partial
3. Global

9. FRUIT

9.1 TYPE (FRTY)

1. Berry
2. Capsule

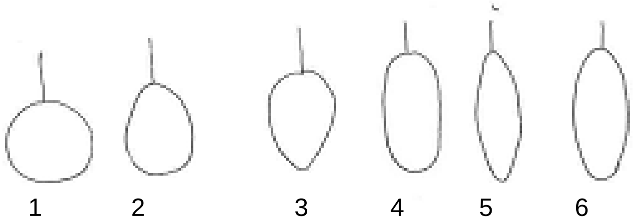
9.2 PIGMENTATION OF INMATURE FRUITS (FPFIM)

1. Uniform
2. Dotted
3. Lined
4. Other

9.3 DOMINANT COLOR OF THE RIPE FRUIT (FRCF)

9.4 SHAPE (FRSH)

1. Spherical / Round
2. Ovoid
3. Oblate
4. Oblong
5. Ellipsoid
6. Fusiform
7. Other



9.5 PUBESCENCE (FRPU)

1. Absent
2. Present

9.6 WEIGHT (FRWH)

	g		**g**		**g**		**g**		**g**

9.7 LENGTH (FRLE)

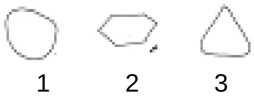
mm	**mm**	**mm**	**mm**	**mm**

9.8 DIAMETER (FRDM)

mm	**mm**	**mm**	**mm**	**mm**

9.9 TRANSVERSAL SECTION (FRTS)

1. Round
2. Hexagonal
3. Triangular
4. Other (specify)



9. PERICARP DIAMETERS (FREM)

mm	**mm**	**mm**	**mm**	**mm**

9.11 MESOCARP TEXTURE (FRMT)

1. Hard
2. Soft rough
3. Soft
4. Other

9.12 ARIL TASTE (FRAT)

1. Acid
2. Acid sweet
3. Sweet
4. Insipid
5. Other

9.13 SKIN WEIGHT (FRSW)

	g		**g**		**g**		**g**		**g**

9.14 SEEDS WEIGHT (FRSW)

	g		**g**		**g**		**g**		**g**

9.15 WEIGHT OF JUICE AND PULP (FRJP)

	g		**g**		**g**		**g**		**g**

9.16 SKIN TEXTURE (FRST)

1. Soft
2. Resistant to the pressure
3. Brittle

9.17 JUICE PH (FRPH)

9.18 TITRABLE ACIDITY (FRAT)

mg/100ml

9.19 TOTAL SOLUBLE SOLIDS (FRTS)

9.20 ASCORBIC ACID (FRVC)

mg/100ml

9.21 JUICE AROMA (FRAJ)

1. Weak
2. Intermediate
3. Strong

10. SEED

10.1 SURFACE TYPE (SEST)

1. Smooth
2. Reticulate
3. Other

10.2 ARIL COLOR (SEAC)

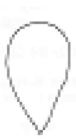
10.3 COAT COLOR (SECC)

10.4 SEED BRIGHTNESS (SEBS)

1. Mate
2. Intermediate
3. Brilliant

10.5 SEED SHAPE (SESS)

1. Obovate
2. Cordate
3. Pyramidal
4. Obcordate
5. Cuneate
6. Other (specify)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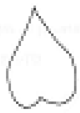
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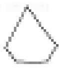
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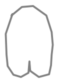
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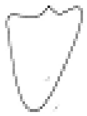
5

10.6 WEIGHT (100 seeds) (SEWH)

mm	**mm**	**mm**	**mm**	**mm**

10.7 LENGTH (SELE))

mm	**mm**	**mm**	**mm**	**mm**

10.8 WIIDTH (SEWI)

mm	**mm**	**mm**	**mm**	**mm**

10.9 NUMBER OF SEEDS PER FRUIT (SENF)

	g		**g**		**g**		**g**		**g**

11. POLLINATION SYNDROME

1. Hummingbirds (e.g. *P. mixta*, *P. vitifolia)*.
2. Bats (e.g. *P. mucronata*, *P. lobata*).
3. Hummingbirds and bats (e.g. *P. penduliflora*).
4. Bees (e.g. *P. alnifolia*, *P. filipes*).
5. Wasps (e.g. *P. edulis* f. *flavicarpa*, *P. quadrangularis*).
6. Bees and Wasps (e.g. *P. foetida*, *P. sphaerocarpa*).
7. Others (specify).

12. PEST AND DISEASE SUSCEPTIBILITY

12.1 PEST

12.2. FUNGI

12.3 BACTER

12.4 VIRUS

12.5 ABIOTIC STRESS SUSCEPTIBILITY

12.6 OTHERS DISORDERS