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Citation:

Ocampo Pérez, John Albeiro; d'Eeckenbrugge, Geo Coppens. 2017. Morphological characterization in the genus *Passiflora* L.: an approach to understanding its complex variability. *Plant Systematics and Evolution* 303(4): 531-558.

Publisher's DOI:

<http://dx.doi.org/10.1007/s00606-017-1390-2>

Access through CIAT Research Online:

<http://hdl.handle.net/10568/80128>

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Morphological characterization in the genus *Passiflora* L.: an approach to understanding its complex variability

Morphological characterization in the genus *Passiflora*

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Abstract

Morphological variation was studied in 124 accessions from 61 species of genus *Passiflora*, using variance component and principal component analyses (PCA) on 43 quantitative traits, and neighbor joining cluster analysis on 85 qualitative traits. Coefficients of variation were generally higher for subgenus *Decaloba*, indicating stronger differentiation when compared with subgenera *Passiflora*. Twenty-four quantitative descriptors showing high variation at the subgenus level were selected for the PCA. The five principal components retained 84% of the total variation, being the first (32%) closely associated with flower length (hypanthium, nectary-chamber, androgynophore) and secondarily with floral cup constriction above the nectary chamber. The second (27%) is associated with flower width (length of bracts and length of corolla and corona-elements) and bract shape, and the third (14%) with peduncle branching, stem width and leaf length, which relates it clearly with variation between subgenera *Astrophea* and *Deidamioides*. 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 consistently our species sample using a strictly phenetic approach. Eight of the nine subgenera established by Killip represented in our sample were supported by the morphological analysis, although subgenus *Deidamioides* is only supported in the quantitative analysis. Our results support seven of the eight Killip's subgenera of our sample, but no infrasubgeneric classifications. However, Feuillet & MacDougal's classification of subgenus *Decaloba* was partly supported and converged on many points with previous phylogenetic results obtained with DNA sequences.

Key words *Passiflora*, systematics, morphological descriptors, principal component analysis, plant genetic resources.

Introduction

1 With more than 576 species, *Passiflora* L. is by far the most important genus in the family Passifloraceae,
2 both numerically and economically. It is mostly distributed in the Neotropics, from coastal zones up to
3 4,300 m.a.s.l. in Andean páramos; only 23 species are native to the Old World in Southeast Asia,
4 Australia and Oceania (Killip 1938; Ulmer and MacDougal 2004). The origin of Passifloraceae is very
5 ancient from 65.5 million years ago (Paleocene) and seems to follow a biogeographic scenario proposed
6 for several plant groups, originating in Africa, crossing to Europe/Asia and arriving in the New World by
7 way of land bridges (Muschner et al., 2012). The chromosome base number varies among $x = 6$ and $x = 9$
8 (De Melo et al. 2001), and the average genome size is 1.03 pg (Yotoko et al. 2011).

11 Passionflowers are herbaceous or woody vines usually climbing with tendrils, but a few are trees or
12 shrubs. Other typical vegetative traits include alternate leaves, axillary stipules, and petiolar and/or
13 laminar nectary glands. In addition, the genus exhibits several unique floral features such as an
14 androgynophore, a complex corona constituted by one or several concentric rows of filaments, and a
15 limen-operculum system limiting access to the nectary chamber, with impressive interspecific variation in
16 size, shape and colors (Killip 1938). Their wide morphological variation seems to be the result of their
17 habitat diversity as well as their co-evolutionary relationships with many organisms, including a wide
18 range of pollinators as small and large insects, birds and bats (Ulmer and MacDougal 2004).

21 Many species exhibit interesting fruits, pharmacological properties (e.g. sedative effect) and/or
22 ornamental potential. More than 80 *Passiflora* species produce edible fruits, all of them belonging to
23 subgenus *Passiflora* (Yockteng et al. 2011). The two botanicals forms of *P. edulis* Sims, *flavicarpa*
24 Degener (yellow passion fruit) and *edulis* (purple passion fruit) are by far the most important crops in the
25 family, with a world production estimated at ca. 640.000 tons. Other cultivated passion fruits are *P.*
26 *tripartita* var. *mollissima* (Kunth) Holm-Nielsen & Jørgensen (curuba de Castilla), *P. tarminiana* Coppens
27 & Barney (curuba India), *P. ligularis* Juss. (sweet granadilla), *P. maliformis* L. (granadilla de piedra or
28 stone granadilla), *P. quadrangularis* L. (giant granadilla), *P. popenovii* Killip (granadilla de Quijos),
29 *P. alata* Curtis (fragrant granadilla) and *P. setacea* DC (sururuca). The high potential of *Passiflora* for
30 crop diversification and economic development induced research institutions of different countries to
31 prioritize the characterization and evaluation of wild and cultivated populations (Cerqueira-Silva et al.
32 2016), and develop strategies for conservation and improvement of these genetic resources.

35 The high diversity of character combinations related to nectary glands, stipules, corona, operculum
36 and limen have been heavily used to delimit infrageneric divisions in *Passiflora* taxonomy, separating
37 subgenera, sections, and series. Although most species appear well delimited, there are many cases in low
38 level taxa as sections and series, where two or more species are very difficult to distinguish. The largest
39 monograph and most important reference work was that of Killip (1938) who described 355 American
40 species plus 20 species in 1960, placing them in 22 subgenera. Escobar (1988a,b, 1989, 1990, 1994)
41 reviewed subgenera *Astrophea*, *Distephana*, *Manicata*, *Rathea* and *Tacsonia*, merging subgenera
42 *Tacsoniopsis* and *Tacsonia*, subdivided into sections and series, and proposing one additional subgenus,
43 *Porphyropathanthus*. MacDougal and Feuillet (2004) have proposed a new infrageneric classification of
44 *Passiflora*, taking into account the Old World species and recognizing only four subgenera, *Astrophea*
45 (unchanged; trees and shrubs, rarely lianas), *Decaloba* (vines with small flowers and fruits, the latter
46 usually black), *Deidamoides* (vines, with two-flowered peduncles, not clearly defined as a morphological

group) and *Passiflora* (vines to lianas, with large flowers and fruits). This classification needs to be revised, and completed with the explicit inclusion of many more species. Thus, Krosnick et al. (2009) with DNA molecular data recognized a fifth subgenus, *Tetrapathea* (vines, inflorescences, small flowers and fruits, yellow-green to red at maturity) from Oceania.

Both classifications of Killip (1938) and Feuillet and 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 are very common), 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 the taxonomy of the genus.

On the other hand, the first molecular studies carried out on significant *Passiflora* species samples have consistently validated three of the four major subdivisions proposed by MacDougal and Feuillet (2004). The results of Muschner et al. (2003), on nuclear ribosomal internal transcribed spacers (ITS-1 and ITS-2) and plastid *trnL-trnF* intergenic spacer, Yockteng (2003) on chloroplast *matK*, Yockteng and Nadot (2004) on chloroplast-expressed glutamine synthetase (*nepGS*), Hansen et al. (2006), on sequences analysis of the chloroplast (*rpoC1* and *trnL-trnT*), and Krosnick et al. (2013), on nuclear (nrITS and *nepGS*) and chloroplast (cp *trnL-F* and *ndhF*), all 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 and Nadot (2004) are split in two widely divergent branches. In addition, the latter study indicated that four other small subgenera, *Dysosmia* (DC.) Killip, *Tryphostemmatooides* (Harms) Killip, *Polyanthea* (DC.) Killip, and *Tetrapathea* (DC.) Rchb., should also be recognized. Another study carried out by Muschner et al. (2012) on the phylogeny, biogeography and divergence times in 106 species and four subgenera of *Passiflora* with plastidial, mitochondrial and nuclear genomes, showed that the genus *Passiflora* is monophyletic. In addition, subgenus *Deidamioides* as described by MacDougal and Feuillet (2004) emerged as paraphyletic. They also situated the divergence among the four subgenera in *Passiflora* from 33 to 38 million years ago, during the Andes uplifting process.

Recently, Krosnick et al. (2013) studied the phylogenetic relationships of subgenus *Decaloba* using 148 taxa and four molecular markers (nrITS, *nepGS*, cp *trnL-F* and *ndhF*). The results showed that subgenus *Decaloba* is monophyletic and contains seven major lineages that generally correspond to currently recognized supersections. These studies have provided many new insights into the evolution of *Passiflora* but reveal as many new challenges that need to be addressed. Furthermore, such phylogenetic molecular studies cannot give us a definitive answer on the relationship between morphologically ill-defined species and species groups.

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 their 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 on 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 same descriptor list was used to study morphological variation in the three most common cultivated (*P. tarminiana* and *P. tripartita* var. *mollissima*) 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). A very detailed descriptor list was also used by Porter-Utley (2014) to study supersection *Cieca* Feuillet and MacDougal of subgenus *Decaloba*, and particularly the species complex around *P. suberosa* L. and *P. coriacea* Juss. Seventy quantitative traits were measured finding 33 to 39 descriptors that could be categorized and gathered with qualitative traits for neighbor joining cluster analyses of the different subsamples.

On the other hand, there was considerable incongruence between molecular (ITS sequences) and morphological phylogenies which was mostly attributed to a smaller sample size 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 species, with the exception of two species not consistently classified, *P. foetida* L., a problematic species in all classifications, and *P. miersii* Mast.

In conclusion, despite the interest to complete an objective classification of a plant family with a huge morphological richness and complexity, only few research teams have developed and applied the necessary methodology. However, this methodology tends to be much more laborious than in plain molecular characterizations, due to the need of field germplasm collections from 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 carrying out *in situ* characterization which must then 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 material (Ocampo et al. 2007, 2010), a wide species sample could be gathered. However, practical limitations allowed describing accessions of only 51 of the 171 reported species from eight subgenera for the genus in the country. A few non-native species were added extending the sample to 61 species. 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 populations.

Materials and methods

Study area

The morphological study was carried out in three germplasm collections located in different ecological regions in Colombia according to environmental adaptations of species: El Cerrito (Tenerife) (2,700 m.a.s.l., 3°43'51.49"N; -76° 4'36.56"W) and El Cerrito (El Moral) in the department of Valle del Cauca (2,400 m.a.s.l., 3°42'53.80"N; -76° 4'37.67"W), and Buenavista (Paraguacito) in the department of Quindío (1,200 m.a.s.l., 4°23'47.57"N; -75°44'3.54"W).

Plant materials

The total sample was composed of 261 individuals representing 124 populations and 61 species of the *Passiflora* genus corresponding to nine of the 22 Killip subgenera (electronic supplementary material), of the four McDougal & Feuillet subgenera (Table 1). Geographic distribution was taken into account in the selection of accessions of a species. Narrow endemics as *P. trinervia* (Juss.) Poir.) are represented only by one population, and widespread species as *P. edulis* f. *flavicarpa* by one population per region. Three plants per were grown from seeds for each populations, at a distance of 3 m between rows and 3 to 5 m within rows, according to adult plant size. In this study we followed the two taxonomic treatment of the genus *Passiflora* proposed by Killip (1938, with emends by Escobar 1988a,b; 1989; 1994 and MacDougal 1994) and Feuillet and MacDougal (2013), as a point of comparison and discussion of our data.

Data collection

The descriptor list was developed in various stages by experts of Bioversity International (Regional Office for the Americas) and Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD), with adaptations to include the wide diversity of our collections. It included 43 quantitative and 84 qualitative descriptors that are presented synthetically in Table 2. These were assessed on three individuals per populations and five measures were taken for quantitative characters (in millimeters) for each individual plant. Color characters were recorded with the Royal Colour Chart (Royal Horticultural Society 2002). Quantitative fruit traits were not taken into account as they are often submitted to convergent selection processes both in wild and in cultivated species.

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, populations, and individuals. To identify characteristics that contributed highly to differentiation 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 variation in size. The selected descriptor set was submitted to a principal component analysis (PCA) applying the varimax normalized rotation option using the STATISTICA 10.0 software (Hill and Lewicki 2006), retaining those factors with an eigenvalue superior to one, and the individuals were projected onto the first three PCA axes.

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 among 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 and Nei 1987) using the coefficient of dissimilarity of Sokal & Michener and calculating bootstrap values from 1,000 replicates with the DARwin 6.0 software (Perrier et al. 2003). This phenetic approach was preferred because of the relatively poor information on morphological evolution in *Passiflora*.

Results

Quantitative variation

As expected, a very high variability was observed among the 124 populations. Table 3 gives mean values and coefficients of variation for the whole sample per subgenus. Coefficients of variation are generally higher for subgenus *Decaloba* compared with *Passiflora* that have comparable representation in number of species. This higher relative variation can be seen much clearer in inflorescences (18 out of 20 traits) and shape ratios (10 out of 13 ratios), than for vegetative parts (9 of 21 descriptors), suggesting a higher interspecific differentiation in subgenus *Decaloba* as compared to the other two.

The relative variance components for 57 quantitative descriptors shows that all present a residual variance under 25% and then a high repeatability (Fig. 1). Many descriptors appear to be efficient in discriminating among subgenera. Thus, the proportion of variance at this level exceeds 50% for 27 descriptors, including stem diameter, leaf margin serration, 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 and 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 among and within populations rarely contributes more than 20% of the total.

Correlations and principal components analysis (PCA)

A Pearson correlation (r) matrix shows high coefficients ranging between 0.71 and 0.97 among dimensions of certain floral components 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 27 quantitative descriptors showing high variation at the subgenus level, 24 were selected for the PCA discarding three of them to avoid redundancy between shape ratios and the original traits. Five principal components were retained, representing 84% of total variation (Table 4). The first component (32%) is primarily 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 with subgenus *Deidamioides*, on one hand, and all other subgenera. The fourth one (5%) is associated with the number of nectaries on leaf margins, which essentially relates it in supersection *Distephana*. The last one (5%) is only correlated with leaf serration.

Fig. 2 shows the accessions in the three first axes showing a clear grouping by subgenus and supersection. The representatives of supersection *Tacsonia* are placed on the right along the first axis, in relation to their long and wide flowers. A few accessions, with shorter flowers as *P. luzmarina* Jørgensen and *P. pinnatistipula* Cav., appear closer to the origin of this axis, together with *P. manicata* individuals. *P. trinervia*, of subgenus *Decaloba* (supersection *Decaloba*) is placed even further on the right thanks to its very long floral tube; additionally, 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-related axis 1, but by the second, flower width-related, axis 2. On this second axis, we find the large-flowered *P. alata* Curtis and *P. quadrangularis* (section *Quadrangulares* of subgenus *Passiflora*) at one extreme, and those of the small-flowered *P. arbelaezii* and *P. gracillima* Killip of subgenus *Deidamioides* at the other one. As expected, the third axis clearly differentiates subgenera *Astrophea* and *Deidamioides* from the five others. In general, subgenera *Passiflora*, *Decaloba*, *Astrophea* and *Deidamioides*, as likewise the supersections *Tacsonia* (subg. *Passiflora*) and *Decaloba* (subg. *Decaloba*) are clearly separated in the main tridimensional space. As expected, *P. manicata* (section *Manicata*) takes an intermediate position between the supersection *Tacsonia* and the other sections of subgenus *Passiflora*. This species not only combines morphological traits typical of both subgenera, but also intermediate eco-climatic requirements, as it may be found at lower elevations than *tacsos* (*Tacsonia*), but higher elevations than representatives of subgenus *Passiflora*. The representatives of the supersection *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. Other species taking a particular position are *P. foetida* and *P. vesicaria* of subgenus *Passiflora* (supersection *Stipulata* / section *Dysosmia*), placed near both subgenera *Passiflora* (other supersections) and *Decaloba*, but closer to the former.

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 in at least one subgenus, while polymorphic among other subgenera. Three 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, and 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.

Our Colombian 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 *Deidamioides* 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. subg. *Astrophea*). *P. vitifolia* Kunth (subgenus *Passiflora* / supersection *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* and *P. vesicaria* (subgenus *Passiflora* / section *Dysosmia*) only by their pinnatisect bracts, and *P. trinervia* (subgenus *Decaloba* / supersection *Decaloba*) 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* (except *P. trinervia*) and *Passiflora* do not show unique traits, however they are clearly segregated by combinations of non-exclusive traits. Thus, in subgenus *Decaloba*, the presence of a flat hypanthium is only shared with subgenus *Tryphostemmatoides*, and the relatively small flower size with subgenera *Astrophea*, *Deidamioides* and the section *Dysosmia* of subgenus *Passiflora*. On the other side, subgenus *Passiflora* share wide flowers and the general presence of petiolar nectaries. The last three and subgenus *Decaloba* (*P. trinervia*, section *Decaloba*) 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 *P. trinervia* and *Tacsonia* species, with the exceptions of *P. pinnatistipula*, *P. luzmarina* and *P. manicata* related to their pollinators (hummingbirds). 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*, *Deidamioides*, *Astrophea*, and *Passiflora* (supersection *Distephana*), and highly complex coronas (more than three rows) are typical in subgenera *Passiflora* (except supersec. *Tacsonia*). Bracts are foliaceous in subgenera *Passiflora* and *Tacsonia*. Fruit shape is generally globose to short ovate/obovate in subgenera *Astrophea*, *Decaloba* (except *P. trinervia*), *Deidamioides* and *Passiflora* (supersections *Passiflora*, *Distephana* and *Stipulata*), and oval to fusiform in the supersections *Tacsonia* (*tacsos* with the exception of *P. pinnatistipula*) and *Decaloba* (*P. trinervia*). Fruit color seems also an interesting trait, with a particular frequency of blackish fruits in subgenus *Decaloba*, however this descriptor was not observed in all species.

Certain species show unusual trait combinations in their subgenus. This is particularly clear in subgenus *Decaloba*, where *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 as well as 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 species show petiolar nectaries while the last two lack such glands in all their organs and produce an elongated fruit with a bright red color.

Cluster analysis on the reduced descriptor list

Fig. 3 presents a *Neighbor Joining* dendrogram obtained from the observations on the first set of descriptors. The three best-represented subgenera, i.e. *Passiflora*, *Astrophea* and *Decaloba*, and the supersection *Tacsonia* (except section *Manicata*) 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 the supersections *Distephana*, *Tacsonia* and *Manicata* (subgenus *Passiflora*), i.e., species presenting large flowers and fruits as well as petiolar nectaries and foliaceous bracts, with a base chromosome number of $n = 9$. They are further divided between the carpenter bee-pollinated species (subgenus *Passiflora*) and the hummingbird-pollinated species of the supersections *Tacsonia* and *Distephana*. The consistency of this sub-classification compensates for the low associated bootstrap values.

On the opposite side of the tree we find subgenera whose species produce small to medium sized 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 expected from the number of their rare traits, the tree species of subgenus *Astrophea* appear very uniform and clearly separated in a very distant cluster. *P. trinervia* (subgenus *Decaloba*) is placed on another long branch inserted at the same position. A third much larger cluster is constituted by all the species of subgenera *Deidamioides* and *Decaloba*, except for *P. trinervia* and *P. adenopoda* (subgenus *Decaloba*). The latter species is placed on a well-separated branch inserted in an intermediate position between the *Passiflora*-*Distephana*-*Tacsonia*-*Manicata* clusters and the *Astrophea*-*Decaloba*-*Deidamioides* clusters. Indeed, this species shows several unusual features and trait combinations when compared to *Decaloba* as a group. *P. foetida* and *P. vesicaria* (subgenus *Passiflora*) take a very similar intermediate position and appear well differentiated from one another, supporting the recent revision of section *Dysosmia* (Vanderplank 2013). Although the branch bearing the representatives of subgenus *Deidamioides* (*P. gracillima* and *P. arbelaezii*) is relatively long, it is clearly inserted within subgenus *Decaloba*, suggesting that the qualitative morphological differentiation of subgenus *Deidamioides* is fragile. This is consistent with the very low number of traits supporting it, but contrasting with the PCA results for quantitative traits.

The first set of qualitative data also allows distinguishing some structures 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., another one to large-flowered species of supersection *Passiflora* i.e. *P. edulis* f. *flavicarpa*, *P. incarnata*, and *P. cincinnata* Mast., a different one to series *Quadrangulares* (*P. quadrangularis* and *P. alata*) and typical representatives of series *Tiliifoliae* (*P. tiliifolia* and *P. ligularis*). Another main branch relates to typical representatives of series *Laurifoliae* (*P. popenovii* and *P. nitida*), one to accessions of *P. maliformis*, and

another one to species of section *Kermesinae* (*P. lehmannii* and *P. smithii*). Killip's series *Lobatae* is shared between the *Incarinatae* 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 them as *P. mathewsii* (Mast.) Killip, and *P. luzmarina*. A second one includes species of Escobar's section *Colombiana* (eg. *P. tenerifensis* and *P. linearistipula*), and the last one includes the relatively short-tubed species *P. pinnatistipula* and *P. manicata*. Within the *Decaloba-Deidamioides* cluster, one branch corresponds to section *Cieca* (*P. coriacea* and *P. suberosa*), whose species are not clearly distinguished, and another one to section *Xerogona* (*P. capsularis* and *P. rubra*). *P. guatemalensis*, the only representative of supersection *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 another one for all its other representatives.

Discussion

Morphological and molecular diversity

To appreciate the organization of *Passiflora* morphological diversity, we can compare some of the interspecific associations or divergences with results obtained in phenetic studies based on biochemical and molecular markers, on samples including some of the species we studied. A first series of genetic studies were carried out on smaller samples, mostly from Colombia. 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* 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 is 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 a 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 our morphological cluster. This result is still the same when the comparison is extended to subgenus *Manicata* and comparing them to the ones 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 *Tiliifolia* of subgenus *Passiflora* (Ocampo et al. 2004) and in the same way it does not support the inclusion of this species in series *Laurifoliae* according to Feuillet & MacDougal (2013).

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 *matK* sequences, Yockteng and 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*, a second one formed around subgenus *Decaloba*, and a third one formed around subgenus *Passiflora*. Species of the supersection *Tacsonia* form a subclade within the *Passiflora* clade (i.e. all studies except that of Muschner et al. 2003). *P. vitifolia* and other representatives the supersection *Distephana* in 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 positions of the three major clades differ 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. (2003), but closer to the *Decaloba* clade in the *trnL-trnT* tree of Hansen et al. (2006) while the *Decaloba* clade appears closer to the *Passiflora* clade in the sample of Yockteng (*ncpGS* and *matK* trees). *P. foetida* (section *Dysosmia*) 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 *matK* sequences. *P. adenopoda* is basal to the *Decaloba* clade in the *ncpGS* tree as well as in the ITS study of Krosnick and Freudenstein (2005). *P. morifolia* Mast., another species of section *Bryonioides* 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 and Nadot (2004) and the ITS study of Krosnick and Freudenstein (2005), subgenus *Deidamiioides*, represented by *P. tryphostemmatoides* Harms and by *P. arbelaezii* L. Uribe respectively, is placed close to subgenus *Astrophea*. Strangely, in the study of Yockteng and Nadot (2004) (*ncpGS* tree), *P. sanguinolenta* Mast. is placed in a *Passiflora* subclade dominated by representatives of series *Tiliifolia*. According to Killip (1938), the placement of this species in subgenus *Psilanthus* is "anomalous"; indeed, his suggestion to consider its relation with *P. rubra* was validated by the phylogeny of Krosnick et al. (2009),

Within the *Decaloba* clade we can recognize the higher level of divergence between subclusters, i.e. the association between representatives of series *Punctatae* and *Miserae* (Killip's classification) 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 last two species are closely associated with *P. sexflora* in the *ncpGS* tree. Additionally, these results are consistent with the ones found by Krosnick et al. (2013) and Milward-de-Azevedo et al. (2014) regarding their position in the series and they also support subgenus *Decaloba* as monophyletic.

As in our morphological study, the *Passiflora* clade identified in phylogenetic studies generally shows loose relations among species. The interpretation of the poorly supported subclades is very uneasy, with the partial exception of the *ncpGS* tree presented by Yockteng and Nadot (2004), where branches are better defined although not easier to interpret, given for example the dispersion of species belonging to series *Incarnatae* and *Laurifoliae* (Killip's classification). 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 a clear separation of subgenera *Astrophea* ($n = 12$) and *Deidamioides* and *Decaloba* ($n = 6$), both among themselves and from subgenera *Passiflora*, *Tacsonia*, and *Distephana* ($n = 9$). Concerning subgenus *Deidamioides*, 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 also represented in the qualitative descriptors but its effect is blurred by the high number of traits shared with subgenus *Decaloba*. While the comparison is difficult for subgenus *Deidamioides*, it is impossible for *P. trinervia*, which is not duly represented in molecular studies. The species *P. adenopoda* and *P. foetida* and their close relatives that take an intermediate position in the general morpho-cytological pattern are consistently placed in intermediate positions. In most phylogenetic studies *P. adenopoda* or *P. morifolia* (supersection *Bryonioides* of subgenus *Decaloba*) appear basal to a general *Decaloba* clade, and *P. foetida* and *P. vesicaria* (section *Dysosmia*) basal to the general *Passiflora* clade (Krosnick et al. 2013).

The comparison becomes more difficult at lower infrasubgeneric levels. Subgenus *Decaloba* appears better structured than the other subgenera, and its morphological and molecular diversity patterns appear consistent, with the grouping of Killip's sections *Punctatae* and *Miseriae*, and the differentiation of species of sections *Xerogona*, *Cieca*, and series *Auriculata*, and less clearly *Sexflorae*. 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* (section *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* are $2n = 20$ (De Melo et al. 2001; Yockteng and Nadot 2004). According to De Melo et al. (2001) and De Melo and Guerra (2003), *P. foetida* appears cytologically quite isolated but closer to the $n = 9$ group, its smaller chromosomes and articulate 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*. In any case, more species should be gathered in a same morphological study before revising objectively the morphological classification.

Within the $n = 9$ group, molecular data with DNA sequence studies partially allow the distinction of a *Tacsonia-Manicata* group and fail to separate clearly the supersection *Distephana* (or subgenus according to Killip), 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* according to Killip's classification have developed ornithophily 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, it is just the same classical question about considering birds as dinosaurs. In the end, it seems an issue of giving more emphasis to the adaptative forces commanding evolution or to the genetic structure that subtends them. Concerning subgenus *Passiflora* sensu Killip, no clear structure appears at the interspecific level that could result in clear subdivisions into the 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, although 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 over classification, which will lead 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 supersection *Tacsonia*, but 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 including only species endemic to Colombia with a slight but clear differentiation related to extreme variation for peduncle length. On the other hand, *P. vitifolia* remained as a good representative of the uniform supersection *Distephana*, so its position does not support its downgrading to a supersection within subgenus *Passiflora* proposed by Feuillet and MacDougal (2003).

Conclusions

A shorter list of 32 qualitative traits selected after analyzing variation among Killip’s and Feuillet & MacDougal’s subgenera allowed to classify our 61 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 were not systematically analyzed, fruit size and color. Furthermore, the smaller number of descriptors providing valuable information used in this approach will also allow a reduction in the labor, time and resources spent in the characterization of genetic resources of genus *Passiflora*.

Eight of the nine of Killip’s subgenera represented in our sample are supported by the morphological analysis, although subgenus *Tryphostemmatoides* (*Deidamioides*) is only supported in the quantitative analysis. On the other hand, the simplification proposed by Feuillet and 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.

Comparing molecular results with 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, other features of considerable importance for their evolution were found. 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 can be seen even clearer. 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* (Killip's classification) 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* (Killip's classification) and its differentiation within the $n = 9$ group earlier in the history of *Passiflora*, as its species show no indication 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, Killip's classification), forming another striking case of convergence between species from very different evolutionary backgrounds.

Acknowledgements

This research has been funded by Colciencias and the Colombian Ministry for Environment, with support from the Research Center of the Colombian Coffee Grower Federation (Cenicafé) through the projects: 'Conservación y utilización de los recursos genéticos de pasifloras' and 'Estudio de la diversidad de las Passifloraceae y Caricaceae de la zona cafetera de Colombia'. The first author gratefully acknowledges the financial support from the Gines-Mera Fellowship Foundation (CIAT - CBN).

Compliance with Ethical Standards

- Funding:

This study was funded by Colombian Ministry for Environment (grant number CEN-303-2003)

- Conflict of Interest:

The authors declare that they have no conflict of interest

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Table 1 List of accessions of the genus *Passiflora* L. used in this study. Taxonomy according to
infrageneric classification proposed by Feuillet and MacDougal (2003)

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

Table 3 Mean values and coefficients of variation for all the descriptors per subgenera

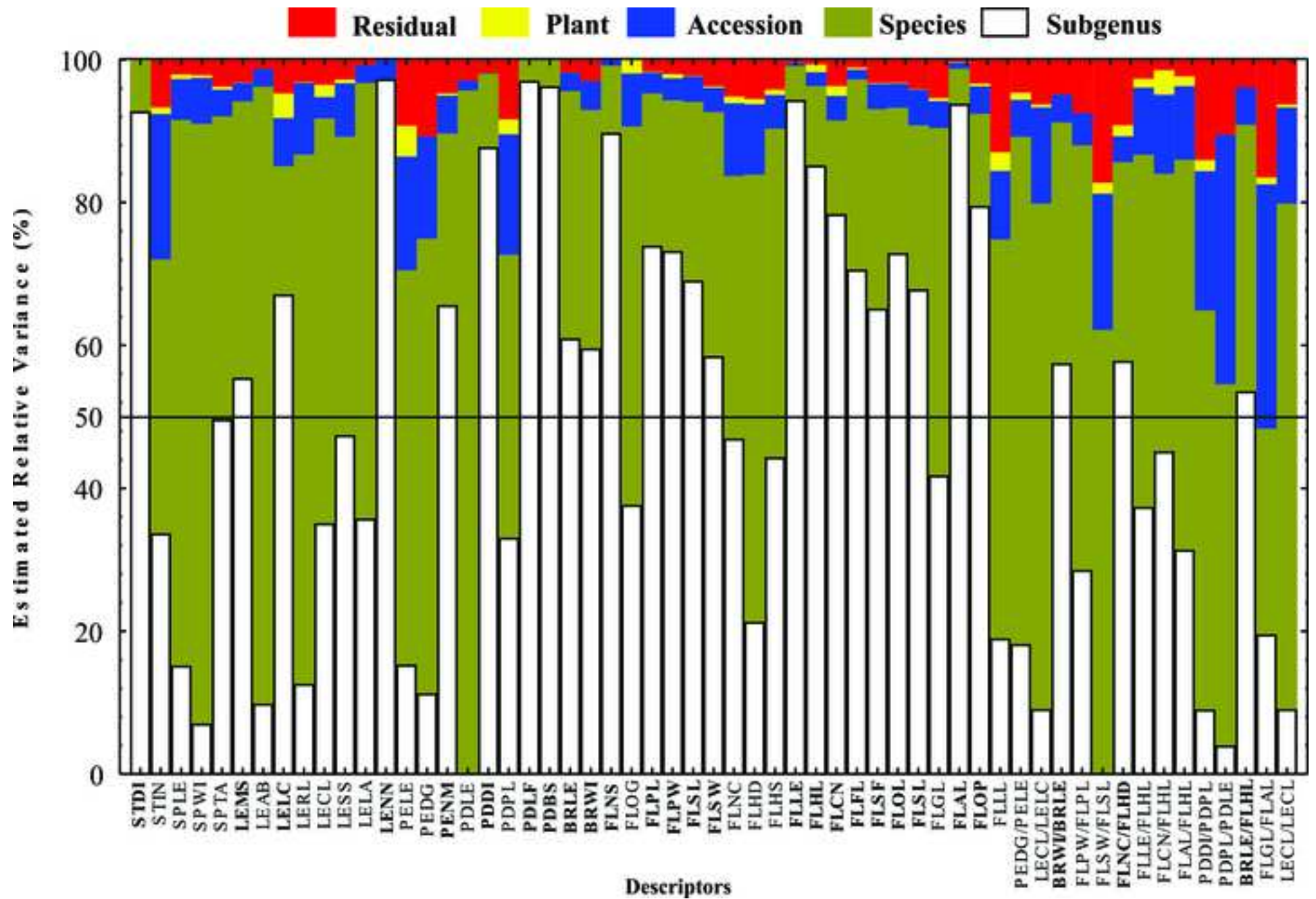
Table 4 Factor loadings from the principal component analysis (*varimax normalized rotation*) carried out
on 24 quantitative descriptors

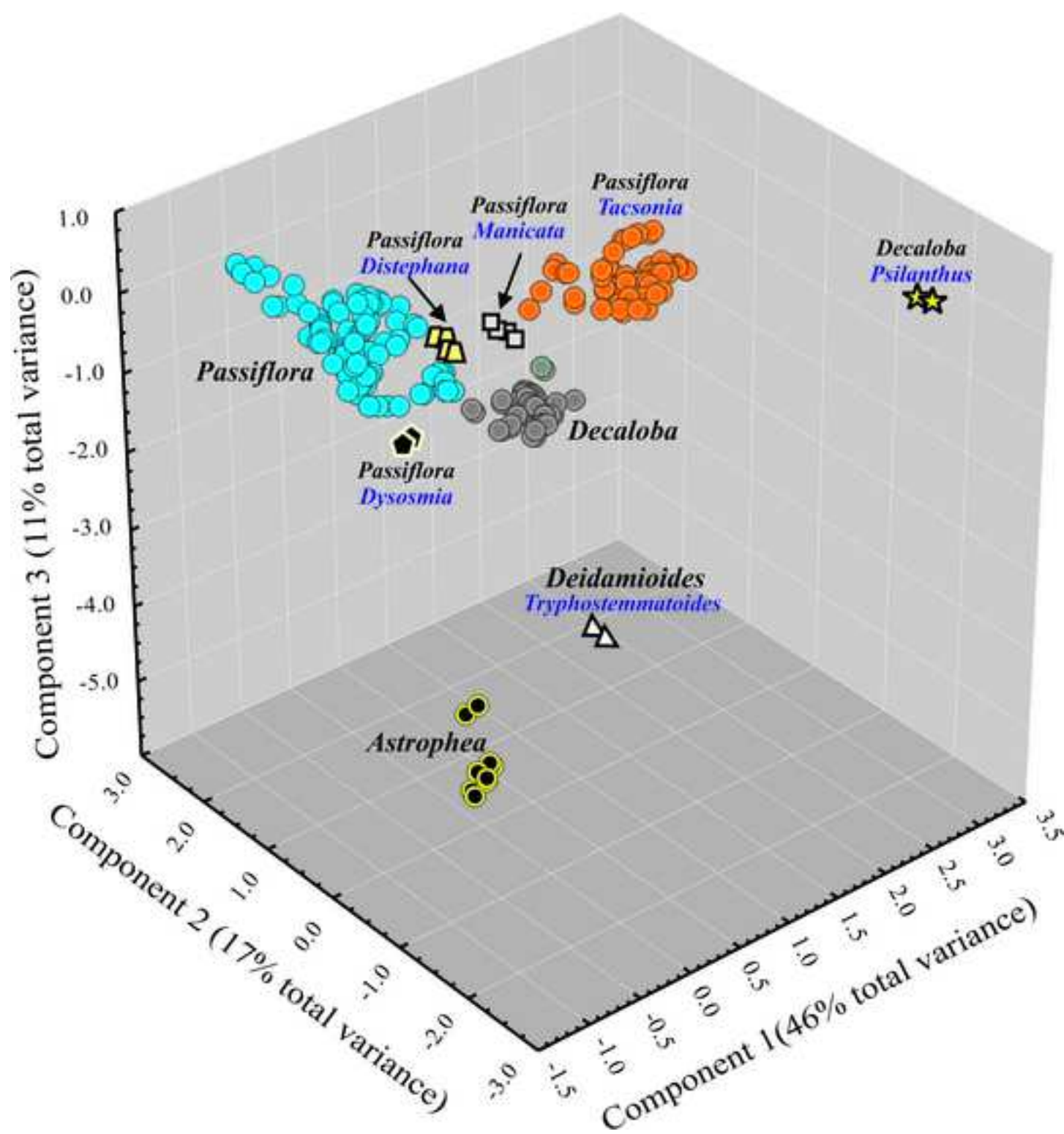
Table 5 Variation for 32 qualitative and four categorized quantitative descriptors in the different
subgenera sampled

Fig. 1 Relative variance components for 57 quantitative descriptors. Bold characters are used for traits
displaying more than 50% of variance among subgenera

Fig. 2 Tridimensional plot of the scores of *Passiflora* accessions for the first three quantitative variation
components. Colors refer to subgeneric classification

Fig. 3 Dendrogram obtained with a first set of qualitative data. Distances of Sokal & Michener. Images
courtesy of PhyloPic (phylopic.org)





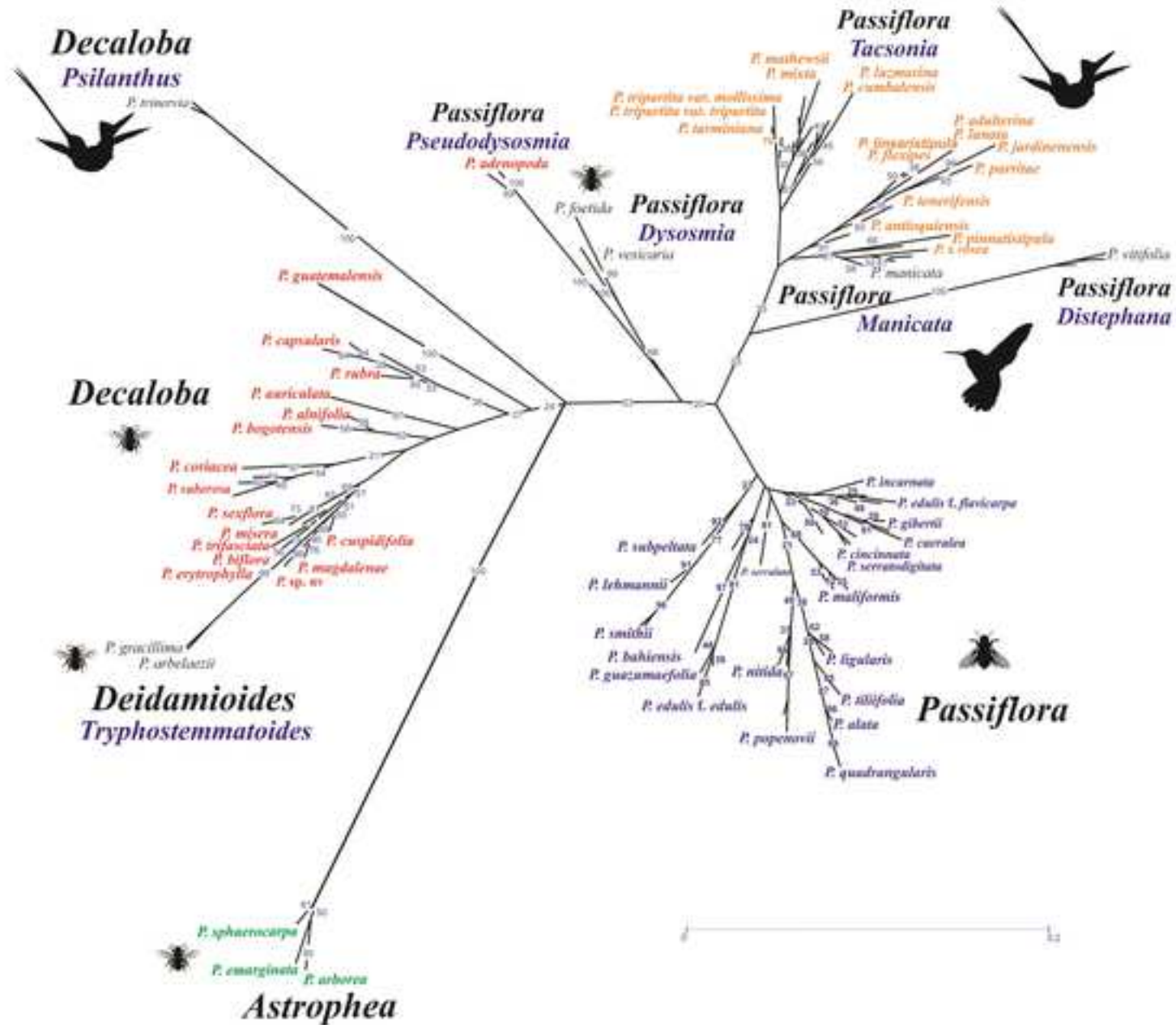


Table 1 List of accessions of the genus *Passiflora* L. used in this study. Taxonomy according to infrageneric classification proposed by Feuillet and MacDougal (2003).

Subgenus / Supersection / Section / Series / Species	Number of individuals	Country	Locality
Subgenus <i>Astrophea</i> (DC.) Masters, 1871			
Section <i>Astrophea</i>			
<i>Passiflora arborea</i> Spreng.	2	Colombia	Manizales (Caldas)
<i>Passiflora emarginata</i> Humb. & Bonpl.	2	Colombia	Manizales (Caldas)
<i>Passiflora sphaerocarpa</i> Triana & Planch.	2	Colombia	Cali (Valle del Cauca)
Subgenus <i>Deidamioides</i> (Harms) Killip, 1938			
<i>Passiflora arbelaezii</i> L. Uribe	1	Colombia	Quibdó (Chocó)
<i>Passiflora gracillima</i> Killip	1	Colombia	Salento (Quindío)
Subgenus <i>Decaloba</i> (DC.) Rchb., 1828			
Supersection <i>Auriculata</i> MacDougal & Feuillet			
<i>Passiflora auriculata</i> Kunth	2	Colombia	Victoria (Caldas)
Supersection <i>Bryonioides</i> (Harms.) MacDougal & Feuillet			
<i>Passiflora adenopoda</i> Moc. & Sessé ex D.C	2	Colombia	Buenavista (Quindío)
	2	Colombia	Ibagué (Tolima)
Supersection <i>Cieca</i> (Medic.) Feuillet & MacDougal			
<i>Passiflora coriacea</i> Juss.	2	Colombia	Palestina (Caldas)

<i>Passiflora suberosa</i> L.	2	Colombia	Cartago (Valle del Cauca)
	2	Colombia	Palmira (Valle del Cauca)
	2	Colombia	Ibagué (Tolima)
	2	Colombia	Jericó (Antioquia)
	2	Colombia	Manizales (Caldas)
	2	Colombia	Manizales (Caldas)
	2	Colombia	Barichara (Santander)
	3	Colombia	Palmira (Valle del Cauca)
Supersection <i>Decaloba</i> (DC.) MacDougal & Feuillet			
Section <i>Decaloba</i> (DC.) Mast			
<i>Passiflora misera</i> Kunth	2	Colombia	Jamundí (Valle del Cauca)
<i>Passiflora trifasciata</i> Lemaire	2	Ecuador	Misahuallí (Napo)
<i>Passiflora alnifolia</i> Kunth	2	Colombia	Manizales (Caldas)
	2	Colombia	Chachagüí (Nariño)
	2	Colombia	Tona (Santander)
<i>Passiflora bogotensis</i> Benth.	2	Colombia	Bogotá (Cundinamarca)
<i>Passiflora biflora</i> Lam.	2	Colombia	Mariquita (Tolima)
	2	Colombia	La Mesa (Cundinamarca)
<i>Passiflora cuspidifolia</i> Harms	1	Colombia	Duitama (Boyacá)

<i>Passiflora erythrophylla</i> Mast.	2	Colombia	Duitama (Boyacá)
<i>Passiflora magdalenae</i> Triana & Planch.	2	Colombia	Victoria (Caldas)
<i>Passiflora sexflora</i> Juss.	2	Colombia	Calarcá (Quindío)
<i>Passiflora trinervia</i> (Juss.) Poir.	2	Colombia	Salento (Quindío)
<i>P. sp. nov</i>	2	Colombia	Pereira (Risaralda)
Section <i>Xerogona</i> (Raf.) Killip			
<i>Passiflora capsularis</i> L.	2	Colombia	Jericó (Antioquia)
	2	Colombia	Barichara (Santander)
	2	Colombia	Cartago (Valle del Cauca)
<i>Passiflora rubra</i> L.	2	Colombia	Manizales (Caldas)
	2	Colombia	Buenavista (Quindío)
Supersection <i>Hahniopathanthus</i> (Harms.) Killip			
<i>Passiflora guatemalensis</i> S. Wats.	2	Colombia	Filadelfia (Caldas)

Subgenus *Passiflora*

Supersection *Passiflora*

Series *Passiflora*

<i>Passiflora cincinnata</i> Mast.	3	Brazil	
	3	Brazil	
<i>Passiflora edulis</i> f. <i>edulis</i> Sims	3	Colombia	Salamina (Caldas)
	2	Colombia	Manizales (Caldas)

<i>Passiflora edulis</i> f. <i>flavicarapa</i> Degener	2	Colombia	Puracé (Cauca)
	1	Peru	
	1	Colombia	Génova (Quindío)
	4	Brazil	
	3	Colombia	La Unión (Valle del Cauca)
	3	Colombia	Rivera (Huila)
	3	Peru	
	3	Peru	
<i>Passiflora incarnata</i> L.	3	Colombia	Anserma (Caldas)
	1	U.S.A	Miami (Florida)
<i>Passiflora bahiensis</i> Klotzsch	3	Brazil	Salvador (Bahia)
Supersection <i>Stipulata</i> Feuillet & MacDougal			
Section <i>Kermesinae</i> (Cervi) Feuillet & MacDougal			
<i>Passiflora lehmanni</i> Mast.	2	Colombia	Buenavista (Quindío)
<i>Passiflora smithii</i> Killip	2	Colombia	Ibagué (Tolima)
Section <i>Granadillastrum</i> Triana & Planch.			
<i>Passiflora caerulea</i> L.	3	France	Montpellier (Herault)
<i>Passiflora subpeltata</i> Ortega	3	Colombia	Santa Marta (Magdalena)
<i>Passiflora gibertii</i> N.E. Brown	2	Brazil	
Section <i>Dysosmia</i> DC.			

<i>Passiflora foetida</i> L. var. <i>foetida</i>	2	Colombia	Quibdó (Chocó)
<i>Passiflora vesicaria</i> L. var. <i>vesicaria</i>	3	Colombia	Armero (Tolima)
Supersection <i>Laurifolia</i> (Cervi) Feuillet & MacDougal			
Series <i>Laurifoliae</i> Killip ex Cervi			
<i>Passiflora guazumaefolia</i> Juss.	2	Colombia	Plato (Magdalena)
<i>Passiflora nitida</i> Kunth	1	Colombia	Quibdó (Chocó)
<i>Passiflora popenovii</i> Killip	2	Colombia	Timbío (Cauca)
<i>Passiflora maliformis</i> L.	2	Colombia	Fredonia (Antioquia)
	3	Colombia	Palestina (Caldas)
	2	Colombia	Buga (Valle del Cauca)
	2	Colombia	Calarcá (Quindío)
	2	Colombia	Rivera (Huila)
	3	Colombia	Tuluá (Valle del Cauca)
	1	Colombia	La Unión (Valle del Cauca)
	2	Colombia	Ibagué (Tolima)
Series <i>Quadrangulares</i> Feuillet & MacDougal	2	Colombia	Chachagüí (Nariño)
<i>Passiflora alata</i> Curtis	3	Brazil	
	3	Brazil	
<i>Passiflora quadrangularis</i> L.	3	Colombia	Paicol (Huila)
	2	Colombia	Palmira (Valle del Cauca)

Series *Tiliifolia* Feuillet & MacDougal

<i>Passiflora ligularis</i> Juss.	3	Colombia	Anserma (Caldas)
	1	Colombia	Cuenca (Azuay)
	3	Colombia	Salento (Quindio)
	1	Colombia	Santa Rosa (Risaralda)
	2	Colombia	Génova (Quindio)
<i>Passiflora serrulata</i> Jacq.	2	Colombia	Plato (Magdalena)
<i>Passiflora tiliifolia</i> L.	2	Colombia	El Cerrito (Valle del Cauca)
<i>Passiflora serratodigitata</i> L.	2	Brazil	

Supersection *Distephana* (DC.) Feuillet & MacDougal

<i>Passiflora vitifolia</i> Kunth	2	Colombia	Victoria (Caldas)
	2	Colombia	Ibagué (Tolima)
	1	Colombia	El Cerrito (Valle del Cauca)

Supersetion *Tacsonia* (Juss.) Feuillet & MacDougal

Section *Colombiana* Escobar

Series *Leptomischae* Escobar

<i>Passiflora antioquiensis</i> Karst.	2	Colombia	Sta. Rosa Osos (Antioquia)
	2	Colombia	Manizales (Caldas)
<i>Passiflora flexipes</i> Triana & Planch.	2	Colombia	Salento (Quindío)
<i>Passiflora tenerifensis</i> L.K. Escobar	2	Colombia	El Cerrito (Valle del Cauca)

	1	Colombia	El Cerrito (Valle del Cauca)
Series <i>Colombianae</i> Escobar			
<i>Passiflora adulterina</i> L.f.	2	Colombia	Duitama (Boyacá)
<i>Passiflora lanata</i> (Juss.) Poir.	2	Colombia	Duitama (Boyacá)
Series <i>Quindiensae</i> Escobar			
<i>Passiflora linearistipula</i> L.K. Escobar	2	Colombia	Manizales (Caldas)
Section <i>Elkea</i> Feuillet & MacDougal			
<i>Passiflora cumbalensis</i> var. <i>cumbalensis</i> (H. Karst.) Harms	2	Ecuador	Tulcán (Carchi)
	1	Colombia	Pasto (Nariño)
<i>Passiflora luzmarina</i> Jorgensen	1	Ecuador	Loja (Loja)
	1	Ecuador	Loja (Loja)
<i>Passiflora tarminiana</i> Coppens & Barney	3	Argentina	Castellar
	2	Colombia	Boyacá
	2	Colombia	Silvia (Cauca)
	4	Ecuador	Baños (Tungurahua)
	1	Peru	
<i>Passiflora tripartita</i> var. <i>mollissima</i> Holm-Nielsen & Jørgensen	3	Colombia	El Cerrito (Valle del Cauca)
	3	Venezuela	Táchira
	4	Colombia	Cundinamarca
	1	Ecuador	Baños (Tungurahua)

	2	Colombia	Pasto (Nariño)
	1	Peru	
	3	Colombia	El Cerrito (Valle del Cauca)
	1	Venezuela	Táchira
<i>Passiflora tripartita</i> var. <i>tripartita</i> Holm-Nielsen & Jørgensen	2	Ecuador	Ambato (Tungurahua)
Section <i>Parritana</i> Escobar			
<i>Passiflora jardinensis</i> L.K. Escobar	2	Colombia	Jardín (Antioquia)
<i>Passiflora parirtae</i> (Mast.) L.H Bailey	2	Colombia	Herveo (Tolima)
Section <i>Insignes</i> Feuillet & MacDougal			
<i>Passiflora pinnatistipula</i> Cav.	1	Colombia	Boyacá
<i>Passiflora</i> x <i>rosea</i> (H.Karst.) Killip	1	Ecuador	Tuta (Boyacá)
Section <i>Tacsonia</i>			
<i>Passiflora mathewsii</i> (Mast.) Killip	1	Ecuador	Cuenca (Azuay)
<i>Passiflora mixta</i> L.f.	2	Colombia	El Cerrito (Valle del Cauca)
	3	Colombia	El Cerrito (Valle del Cauca)
	3	Colombia	El Cerrito (Valle del Cauca)
	1	Colombia	El Cerrito (Valle del Cauca)
	1	Colombia	El Cerrito (Valle del Cauca)
Section <i>Manicata</i> (Harms) Feuillet & MacDougal			
<i>Passiflora manicata</i> (Juss.) Pers.	1	Ecuador	Baños (Tungurahua)

2	Colombia	Santander
2	Colombia	Santander
2	Colombia	Santander

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

Organ	Qualitative characters (84)	Code	Quantitative characters (43)	Code
Stem	Habit	STHA	Diameter	STDI
	Shape	STSH	Internode length	STIN
	Pubescence	STPU		
	Anthocyanin	STAN		
Tendrill	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
	Pubescence – 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		
	Hypanthium 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		

Table 3 Mean values and coefficients of variation for all the descriptors per subgenera according to Killip's and Feuillet & M

Organ	Factor	Level	Feuillet & MacDougal's				
			<i>Passiflora</i>				
			Killip's classific				
			<i>Passiflora</i>	<i>Distephana</i>	<i>Dysosmia</i>	<i>Tacsonia</i>	<i>Manicata</i>
	Descriptors	<i>n</i>	504	20	25	340	35
Stem	STEDI	Mean	44.01	35.00	15.00	30.00	30.00
		CV	0.15	0.00	0.00	0.00	0.00
	STIN	Mean	321.40	61.30	40.04	285.54	321.63
		CV	0.55	0.14	0.14	0.52	0.31
	SPLE	Mean	14.45	6.20	2.70	8.69	11.65
		CV	0.73	0.17	0.26	0.55	0.12
	SPWI	Mean	5.98	1.00	5.35	7.48	18.64
		CV	1.24	0.00	0.10	0.87	0.12
	SPTA	Mean	0.13	0.00	6.22	2.72	3.87
		CV	5.77	-	0.04	0.94	0.19
Leaf	LEMS	Mean	4.26	6.10	5.00	6.81	8.63
		CV	0.81	0.05	0.00	0.29	0.06
	LEAB	Mean	58.09	77.90	92.24	105.42	116.74
		CV	1.17	0.10	0.03	0.40	0.07
	LELC	Mean	120.92	115.10	73.22	96.95	112.82
		CV	0.26	0.09	0.04	0.21	0.24
	LERL	Mean	51.21	96.30	45.47	83.91	117.99
		CV	1.06	0.13	0.04	0.41	0.27
	LECL	Mean	75.49	49.30	42.16	37.59	52.39
		CV	0.56	0.11	0.05	0.39	0.23
	LESS	Mean	15.37	44.00	41.05	21.72	41.35
		CV	1.16	0.02	0.08	0.55	0.22
	LELA	Mean	0.00	0.00	0.00	0.00	0.00
		CV	-	-	-	-	-
	LENN	Mean	0.00	7.00	0.00	0.00	0.00
		CV	-	0.15	-	-	-
	PELE	Mean	44.24	30.85	21.92	22.57	28.63
		CV	0.58	0.18	0.16	0.34	0.21
	PEDG	Mean	23.91	0.50	0.00	9.25	7.89
		CV	0.75	0.00	-	0.57	0.36
	PENM	Mean	2.90	2.00	0.00	6.09	9.20
		CV	0.58	0.00	-	0.37	0.29
Bract	BRLE	Mean	33.91	26.70	20.92	36.30	42.97
		CV	0.50	0.19	0.11	0.29	0.10
	BRWI	Mean	21.50	8.70	16.20	15.70	26.04
		CV	0.47	0.18	0.27	0.36	0.09
	PDLE	Mean	44.50	46.85	49.39	86.71	65.70
		CV	0.45	0.13	0.16	1.43	0.25
	PDDI	Mean	2.66	2.50	1.50	2.50	2.50
		CV	0.12	0.00	0.00	0.00	0.00
	PDPL	Mean	8.63	4.92	2.60	8.93	13.70

Flower	PDLF	CV	0.41	0.07	0.00	0.40	0.12
		Mean	0.00	0.00	0.00	0.00	0.00
	PDBS	CV	-	-	-	-	-
		Mean	0.00	0.00	0.00	0.00	0.00
	FLNS	CV	-	-	-	-	-
		Mean	5.00	2.00	4.20	1.40	5.00
	FLOG	CV	0.00	0.00	0.84	0.80	0.00
		Mean	114.94	110.00	142.00	10.99	158.00
	FLPL	CV	0.45	0.42	0.23	2.02	0.14
		Mean	34.58	56.25	18.90	44.28	42.27
	FLPW	CV	0.28	0.06	0.14	0.25	0.08
		Mean	10.36	13.58	7.92	19.39	14.65
	FLSL	CV	0.43	0.20	0.13	0.23	0.09
		Mean	36.15	59.60	19.47	46.91	44.36
	FLSW	CV	0.26	0.05	0.11	0.24	0.08
		Mean	14.71	16.60	7.22	18.65	14.17
	FLNC	CV	0.34	0.07	0.12	0.28	0.13
		Mean	13.32	13.90	8.32	15.07	15.85
	FLHD	CV	0.26	0.13	0.05	0.17	0.09
		Mean	13.04	11.90	8.40	10.21	10.93
	DHS	CV	0.30	0.15	0.05	0.23	0.07
		Mean	17.39	12.75	8.40	12.00	14.64
	FLHS	CV	0.29	0.06	0.05	0.21	0.11
		Mean	27.00	55.75	12.88	103.36	42.44
	FLLE	CV	0.23	0.07	0.08	0.17	0.07
		Mean	11.97	12.07	8.35	71.01	13.03
	FLCN	CV	0.31	0.09	0.10	0.28	0.24
		Mean	5.56	6.10	2.48	10.17	8.58
	FLFL	CV	0.32	0.26	0.06	0.25	0.08
		Mean	35.39	24.10	11.20	2.10	5.82
	FLSF	CV	0.44	0.05	0.33	0.80	0.23
		Mean	11.08	14.20	4.60	14.86	12.19
	FLOL	CV	0.25	0.12	0.13	0.32	0.12
		Mean	8.30	10.76	3.71	11.60	8.20
	FLSL	CV	0.30	0.06	0.20	0.17	0.10
		Mean	11.11	13.20	6.44	13.61	12.14
	FLGL	CV	0.25	0.06	0.09	0.24	0.12
		Mean	1.91	2.72	1.00	4.37	2.70
	FLAL	CV	0.58	0.09	0.02	0.67	0.19
		Mean	11.36	42.08	8.46	82.69	29.11
	FLOP	CV	0.29	0.08	0.11	0.21	0.09
		Mean	2.75	10.00	2.32	6.61	10.37
	FLLL	CV	0.46	0.06	0.07	0.24	0.08
		Mean	1.65	3.55	1.40	1.53	1.25
		CV	0.64	0.14	0.07	0.36	0.16
	PEDG/PELE	Mean	0.56	0.02	0.00	0.41	0.28
		CV	0.53	0.22	-	0.45	0.32
	LECL/LELC	Mean	0.59	0.43	0.58	0.39	0.47
		CV	0.37	0.11	0.04	0.30	0.14
	BRWI/BRLE	Mean	0.64	0.34	0.78	0.43	0.61
		CV	0.22	0.32	0.28	0.25	0.07
	FLPW/FLPL	Mean	0.30	0.24	0.42	0.44	0.35

Shape relation

	CV	0.24	0.14	0.08	0.16	0.10
FLSW/FLSL	Mean	0.41	0.28	0.37	0.41	0.32
	CV	0.24	0.11	0.09	0.23	0.16
FLNC/FLHD	Mean	1.04	1.17	0.99	1.53	1.46
	CV	0.13	0.05	0.03	0.23	0.10
FLLE/FLHL	Mean	2.33	4.64	1.56	1.54	3.42
	CV	0.21	0.08	0.17	0.26	0.21
FLCN/FLHL	Mean	0.47	0.50	0.30	0.15	0.69
	CV	0.22	0.22	0.10	0.34	0.22
FLAL/FLHL	Mean	1.01	3.50	1.03	1.23	2.35
	CV	0.35	0.08	0.19	0.32	0.24
PDDI/PDPL	Mean	0.08	0.05	0.03	0.08	0.04
	CV	0.77	0.13	0.16	0.70	0.27
PDPL/PDLE	Mean	0.23	0.11	0.05	0.29	0.22
	CV	0.63	0.15	0.16	0.77	0.27
BRLE/FLHL	Mean	2.89	2.25	2.55	0.54	3.52
	CV	0.47	0.27	0.22	0.39	0.28
FLGL/FLAL	Mean	0.18	0.06	0.12	0.06	0.09
	CV	0.68	0.06	0.12	1.49	0.23
LECL/LECL	Mean	0.58	0.47	0.58	0.39	0.50
	CV	0.44	0.14	0.04	0.30	0.12

acDougal's classification

classification (2003)

	<i>Decaloba</i>	<i>Astrophea</i>	<i>Deidamioides</i>		
ation (1938)					
	<i>Decaloba</i>	<i>Psilanthus</i>	<i>Astrophea</i>	<i>Thryphostematoides</i>	Total sample
	310	10	50	10	1304
	10.81	9.60	230.00	5.00	37.96
	0.24	0.05	0.25	0.00	1.11
	98.50	50.80	54.67	22.91	235.09
	1.05	0.04	0.32	0.10	0.76
	5.34	8.70	4.45	0.46	9.82
	0.47	0.08	0.16	0.61	0.83
	2.46	1.00	2.86	0.25	5.59
	1.88	0.00	0.29	0.21	1.22
	0.18	0.00	0.00	0.00	1.03
	3.40	-	-	-	1.96
	0.21	0.00	0.00	0.00	3.89
	3.50	-	-	-	0.92
	80.38	33.10	0.00	0.00	75.40
	0.39	0.08	-	-	0.75
	59.80	116.50	247.27	32.11	103.05
	0.38	0.01	0.26	0.38	0.46
	65.31	92.70	0.00	0.00	63.42
	0.35	0.03	-	-	0.72
	33.50	18.70	123.49	22.38	54.96
	0.53	0.08	0.31	0.15	0.69
	45.76	89.40	0.00	0.00	25.74
	0.38	0.01	-	-	0.83
	4.09	6.00	0.00	0.00	1.02
	1.10	0.00	-	-	2.79
	0.00	0.00	0.00	0.00	0.11
	-	-	-	-	8.10
	25.26	24.70	26.20	19.09	31.99
	0.69	0.05	0.36	0.14	0.66
	15.25	0.00	26.38	19.09	16.65
	1.18	-	0.37	0.14	0.98
	0.81	0.00	2.00	2.00	3.27
	1.22	-	0.00	0.00	0.85
	2.63	8.60	2.10	1.00	25.31
	1.68	0.10	0.10	0.00	0.75
	1.28	2.70	1.30	0.50	13.93
	2.73	0.18	0.00	0.00	0.81
	19.74	99.30	17.88	23.86	49.56
	0.63	0.01	0.35	0.10	1.41
	1.51	1.11	2.92	0.80	2.30
	0.02	0.05	0.11	0.00	0.24
	4.42	3.30	13.44	8.24	7.81

0.71	0.15	0.42	0.05	0.54
0.00	0.00	23.30	26.50	1.10
-	-	0.21	0.06	4.64
0.00	0.00	23.30	16.50	1.02
-	-	0.21	0.10	4.68
2.00	1.00	1.00	2.00	3.10
1.10	0.00	0.00	0.00	0.91
72.73	172.50	135.00	0.00	73.71
0.96	0.03	0.20	-	0.94
7.98	11.20	24.08	13.54	30.28
0.76	0.08	0.19	0.19	0.55
2.76	4.90	8.44	3.56	10.86
0.93	0.06	0.35	0.27	0.66
14.62	39.10	24.47	14.51	33.51
0.38	0.02	0.16	0.29	0.46
5.62	7.00	9.36	5.51	13.11
0.39	0.13	0.27	0.34	0.50
8.55	10.00	7.59	7.10	12.33
0.34	0.08	0.17	0.14	0.32
8.73	8.70	7.55	6.81	10.82
0.36	0.06	0.17	0.14	0.34
9.59	7.50	8.28	6.81	13.30
0.36	0.07	0.21	0.14	0.39
11.52	162.00	23.24	8.30	44.56
0.31	0.02	0.18	0.11	0.88
6.32	112.90	5.82	4.96	26.47
2.29	0.02	0.25	0.16	1.16
3.64	29.30	4.92	3.80	6.48
0.34	0.07	0.11	0.18	0.57
7.68	2.90	13.39	5.83	17.37
0.40	0.25	0.19	0.11	1.02
4.26	8.30	6.36	2.46	10.13
0.34	0.06	0.14	0.15	0.50
3.45	11.90	4.98	2.85	7.81
0.40	0.06	0.14	0.07	0.47
4.62	5.10	6.76	3.63	9.92
0.31	0.14	0.33	0.07	0.43
0.93	9.20	1.00	0.51	2.34
0.26	0.11	0.00	0.06	0.94
6.25	150.50	12.40	4.86	30.69
0.36	0.01	0.30	0.04	1.14
2.12	4.20	1.84	0.84	3.88
0.49	0.10	0.17	0.06	0.67
0.87	0.00	0.60	0.65	1.38
0.70	-	0.34	0.08	0.65
0.60	0.00	1.01	1.00	0.52
0.67	-	0.03	0.00	0.64
0.58	0.16	0.50	0.76	0.52
0.44	0.08	0.12	0.26	0.42
0.18	0.32	0.62	0.50	0.47
1.41	0.24	0.07	0.00	0.53
0.24	0.44	0.34	0.26	0.33

0.82	0.11	0.23	0.16	0.42
0.42	0.18	0.38	0.38	0.40
0.38	0.13	0.25	0.17	0.28
0.99	1.16	1.01	1.05	1.17
0.08	0.14	0.03	0.13	0.26
5.85	1.44	4.25	1.70	3.07
0.71	0.03	0.30	0.16	0.87
1.89	0.26	0.89	0.77	0.74
0.78	0.08	0.24	0.12	1.32
3.36	1.33	2.21	1.00	1.75
0.79	0.02	0.31	0.12	0.95
0.11	0.01	0.18	0.03	0.09
0.65	0.05	0.25	0.11	0.75
0.40	0.03	0.76	0.35	0.30
1.36	0.15	0.43	0.10	1.10
0.92	0.08	0.38	0.21	1.67
1.28	0.10	0.21	0.15	0.92
0.17	0.06	0.09	0.11	0.14
0.41	0.12	0.39	0.08	0.80
0.59	0.43	0.76	0.16	0.52
0.37	0.11	0.26	0.08	0.42

Table 4 Factor loadings from the principal component analysis (varimax normalized rotation) carried out

Descriptors	Principal components				
	1	2	3	4	5
STDI	-0.088	0.215	-0.892	-0.023	0.041
LEAB	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
PENN	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
FLHL	0.824	0.208	0.026	-0.080	-0.137
FLCN	-0.521	0.723	0.034	-0.007	-0.329
FLFL	0.529	0.651	0.082	0.097	0.171
FLSF	0.677	0.658	0.076	0.061	-0.049
FLOL	0.454	0.693	0.067	0.073	0.263
FLSL	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
% total variance	46.028	16.999	11.138	4.913	3.986

on 24 quantitative des

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

Feuilleit & MacDougal (2003)	<i>Astrophea</i>		<i>Decaloba</i>		<i>Passiflora</i>						<i>Deidamioides</i>	
Killip (1938), Escobar (1988), MacDougal (1994)	<i>Astrophea</i>		<i>Decaloba</i>		<i>Psilanthus</i>	<i>Passiflora</i>	<i>Distephana</i>	<i>Dyosmia</i>	<i>Tacsonia</i>	<i>Manicata</i>	<i>Tryphostemmatoides</i>	
Species/accesion 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	2n = 24		2n = 12, 22, 24, 36		2n = 12	2n = 18	2n = 18	2n = 18, 20, 22	2n = 18	2n = 18	2n = 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	vine	
Stem section	irregular	terete/angular		angular	terete/angular/winged	terete	terete	terete	terete/angular	angular	terete	
Secondary xylema	present	absent		absent	absent	absent	absent	absent	absent	absent	absent	
Tendrill position	absent	axillary		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	setaceous	
Stipule nectaries (conspicuous)	absent	absent		absent	absent/present (<i>P. maliformis</i>)	present	present	absent	absent	absent	absent	
Leaf lobation	one	three		three	one/three/more	three	three	one/three	three	three	one	
Leaf base	cuneate-rounded	cuneate-rounded/cordate/ peltate (<i>P. coriacea</i> and <i>P. guatemalensis</i>)		cordate	cuneate-rounded/cordate	cordate	cordate	cuneate-rounded/cordate	cordate	cordate	rounded	
Leaf apex	obtuse/acute	rounded/obtus/acute		acute/very acute	rounded to very acute	acute	acute	acute/very acute		obtus to very acute	retuse	
Leaf margin	entire	entire/serrate (<i>P. adenopoda</i>)		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 (<i>P. adenopoda</i>)		absent	absent/sinus	sinus	absent	absent/sinus (<i>P. jardinensis</i>)		absent	leaf base	
Petiolar nectaries	absent	absent/orbicular (<i>P. adenopoda</i>)/ cylindrical (<i>P. coriaceae</i> and <i>P. suberosa</i>) /auriculate (<i>P. auriculata</i>)		absent	lateral lobe (<i>P. edulis</i> f. <i>edulis</i>) 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 (<i>P. sexflora</i>)		absent	absent	absent	absent	absent		absent	present	
Bract shape	linear	setaceous/linear/ foliaceous (<i>P. adenopoda</i> , <i>P. guatemalensis</i>) /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, linear		filamentous	filamentous	
Corona filaments	sickle-sword-shaped	linear		linear	linear	linear	linear	filamentous, linear		linear	linear	
Corona filaments number	free	free		free	free	fused at base	free	free		free	free	
	uniseriate	biseriate/ uniseriate (<i>P. guatemalensis</i> and <i>P. adenopoda</i>)/ triseriate (<i>P. magdalenae</i> and <i>P. sp. nv</i>)		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 (<i>P. guatemalensis</i>)		white	purple white (<i>P. guazumaefolia</i>)	red	purple	purple white (<i>P. jardinensis</i>)		purple	white	
Petals	present	present/ absent (<i>P. coriaceae</i> and <i>P. suberosa</i>)		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	campanulate	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 (<i>P. rubra</i> and <i>P. capsularis</i>)		elongate	globose/ elongate (<i>P. quadrangularis</i>)	globose	globose	elongate/ globose (<i>P. pinnatistipula</i>)		elongate	globose	
Categorized (from quantitatives traits)												
Stem diameter	≥ 120 mm	≤ 20 mm		≤ 20 mm	≥ 30 mm	≥ 30 mm	≤ 20 mm	≥ 30 mm		≥ 30 mm	≤ 20 mm	
Leaf length	> 215 mm / < 190 mm (<i>P. sphaerocarpa</i>)	< 190 mm		< 190 mm	< 60 mm < 190 mm	< 60 mm < 190 mm	< 190 mm	< 60 mm < 190 mm		< 190 mm	< 190 mm	
Sepal length	≤ 30 mm	≤ 30 mm		> 30 mm	> 30 mm	> 30 mm	≤ 30 mm	> 30 mm / ≤ 30 mm (<i>P. lucmarina</i> and <i>P. mathewsii</i>)		> 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*^a, *P. rubra*^{b*}, *P. suberosa*^{b*}, *P. sexflora*^b, *P. guatemalensis*^b, *P. bahiensis*^a, *P. edulis* f. *edulis*^a, *P. guazumaefolia*^a, *P. smithii*^a, *P. subpeltata*^a, *P. serrulata*^a



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Cali, July 06, 2016

Plant Systematic and Evolution
Scientific Committee

Dear Scientific Committee,

We hereby submit the paper with the title **Morphological characterization in the genus *Passiflora* L.: an approach to understanding its complex variability** to Plant Systematic and Evolution. Our research brings new information on the genus *Passiflora* as there are no currently published works on its morphological variability. 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 material (Ocampo et al. 2007; 2010), a wide species sample could be gathered. However, practical limitations allowed describing accessions of only 51 of the 171 reported species from eight subgenera for the genus in the country. A few non-native species were added extending the sample to 61 species. 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 populations.

The manuscript's main text has 7059 words.

Best Regards,

John Ocampo
Geo Coppens d'Eeckenbrugge

- Ocampo, J.A., Coppens d'Eeckenbrugge, G., Restrepo, M., Salazar, M., and Jarvis, A. 2007. Diversity of Colombian Passifloraceae: biogeography and an updated list for conservation. *Biota Colombiana* 8(1): 1-45.
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