Passiflora
ONLINE JOURNAL

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THIS MONTH'S ISSUE ***Passiflora arborea*****.** ***Passiflora edulis*** **in Ibadan. Colombian** ***Tacsonia*** ***and more....***

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Passiflora 'Star of Bristol'

Contents Issue 10

Genetic Resources of Colombian *Tacsonias* (*Passiflora* supersection *Tacsonia*): A biological treasure still to discover, use and conserve

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History and taxonomy

The first report of *Tacsonia* appeared in 1789 in the book *Genera Plantarum* published by A. L. de Jussieu, who considered the species *P. mixta* and *P. adulterina* described in 1781 by Linnaeus junior (L. f.) sufficiently distinct from previously described species of *Passiflora*, to justify the creation of a new genus within Passifloraceae. *Tacsonia* was maintained as a genus and divided in different sections by de Candolle (1828), Reichenbach (1828), Rafinesque (1838), Roemer (1846), Karsten (1857, 1858), and Master (1872). Later, Triana & Planchon (1873), Harms (1925) and Killip (1938) recognised *Tacsonia* at the subgenus level and the latter described 38 species in his work *The American species of Passifloraceae*. In 1988, Escobar (1988) revised the Colombian species, including new ones, dividing the subgenus *Tacsonia* into 11 sections and three series. More recently, the classification of Feuillet & MacDougal (2003) downgraded *Tacsonia* to the supersection level in subgenus *Passiflora*. The subgenera *Manicata*, *Rathea* and *Tacsoniopsis*, recognized by Escobar (1988, 1989), were integrated as sections of *Tacsonia*. Currently, supersection *Tacsonia* comprises 65 species, including five species described in the 21st century (*P. tarminiana* Coppens & Barney, *P. carrascoensis* P. Jørg. & R. Vasquez, *P. unipetala* P. Jørg., Muchhala & J. M. MacDougal, *P. kuethiana* B. Esquerre, and *P. salpoense* S. Leiva & Tantalean).

Morphology

The species of supersection *Tacsonia* are woody vines, usually climbers with tendrils, axillary stipules and petiolar nectary glands (**Figure 1** pp. 26-27). In addition *Tacsonia* exhibit large, brilliant pink, violet or scarlet red flowers with unique floral features such as, a cylindrical elongate floral tube or hypanthium reaching up to 14 cm long, a corona reduced to short tubercles (ca. 1 mm long) or short filaments, and a limen-operculum system that limits the access to the nectary chamber. Their fruits are smooth, glabrous or pubescent, and have an impressive interspecific variation in size, shape and colors (**Figure 2** and **5** p.29). Although supersection *Tacsonia* (Juss.) Feuillet & J. M. MacDougal constitutes a very young group (Abrahamczyk et al. 2014) and exhibits a high number of common traits, its species display large intraspecific variability in size and colors for many traits, such as leaves and flowers (Ocampo & Coppens d´Eeckenbrugge 2017). However, there are many cases in low level taxa as sections and series, where two or more species are difficult to distinguish (e.g. *P. cremastantha* Harms vs. *P. leptomischa* Harms).

Reproductive biology

Tacsonia species are diploid, with $2n = 18$ (De Melo et al. 2001) and according to Escobar (1985, 1989), self-compatibility is the rule in *Tacsonia* and section *Manicata*, producing seeds and fruits after controlled self-pollination. With cross pollination however, fruit set is increased. (Primot et al. 2005; pers. obs. Gustavo Morales). Out of the 65 species recorded 37 are pollinated primarily by the sword-billed hummingbird, *Ensifera ensifera* Lesson;. (**Figure 3**). The remaining species have smaller sized hypanthiums, i.e. from 1 to 3 cm long, (Abrahamczyk et al. 2014) and are pollinated by several species of short-billed hummingbirds or bats.

Distribution and ecology

The uplifting of the Andes created new habitats and favored local isolation, inducing high speciation rates in many taxa. Supersection *Tacsonia* provides a particularly striking example, with its exclusively South American distribution, from Venezuela to Bolivia (**Figure 4** p. 28), in cloud forests (**Figure 11** pp. 40-41, **Figure 12** pp. 42-43) of the Tropical Andes and the Sierra Nevada de Santa Marta (northeastern Colombia) from 1700 to ca. 4300 m, at the limits of ‘páramo’ and ‘puna’ (Ocampo et al. 2014). The páramo is the ecosystem of the regions of the tropical Andes above the continuous forest line, yet below

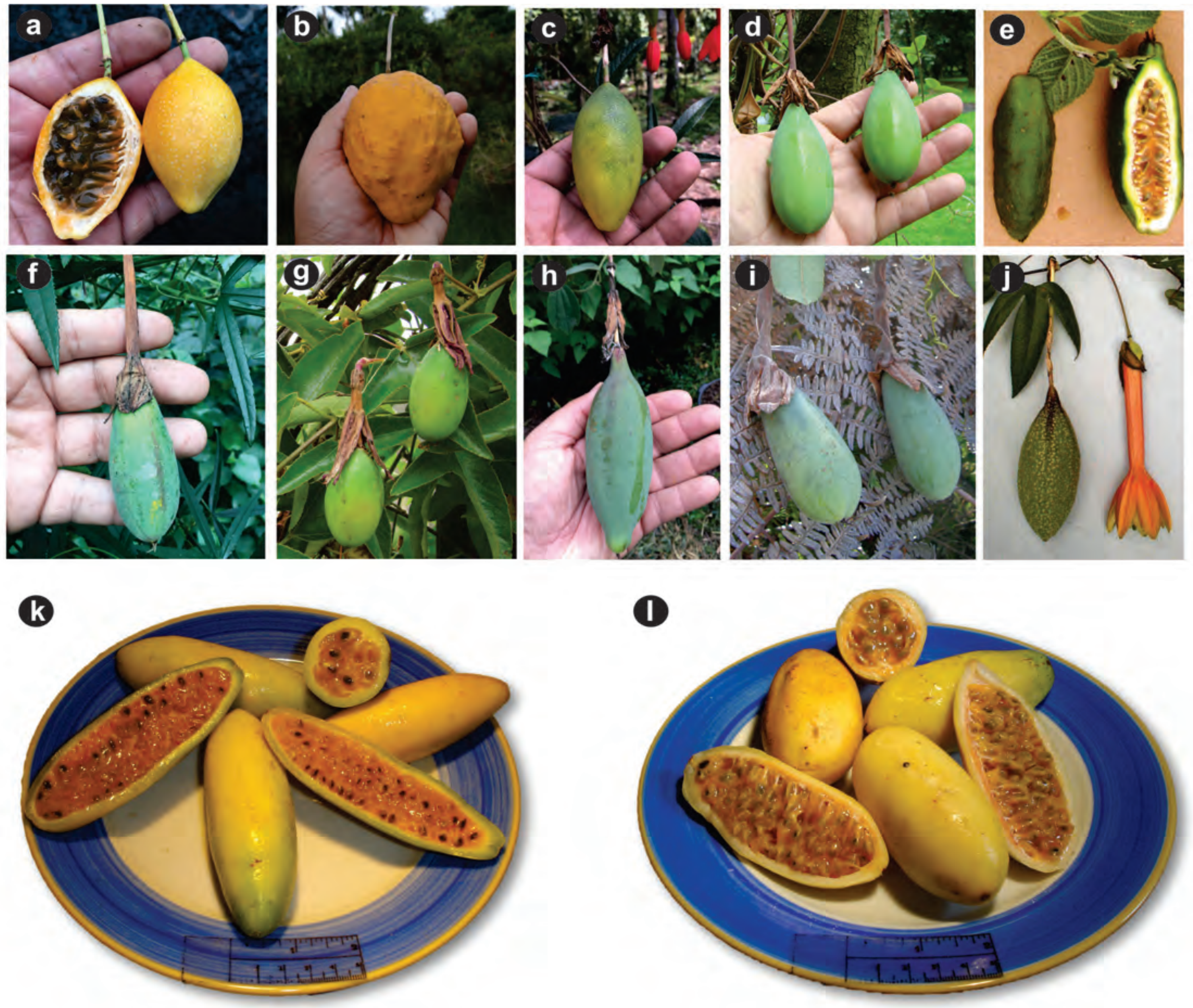


Figure 2. Fruit variability. a *P. adulterina*, b *P. parritae*, c *P. rugosa* var. *rugosa*, d *P. cumbalensis*, e *P. teneriferensis*, f *P. tripartita* var. *tripartita*, g *P. manicata*, h *P. antioquiensis*, i *P. mixta*, j *P. linearistipula*, k *P. tarminiana*, l *P. tripartita* var. *mollissima*. © John Ocampo.

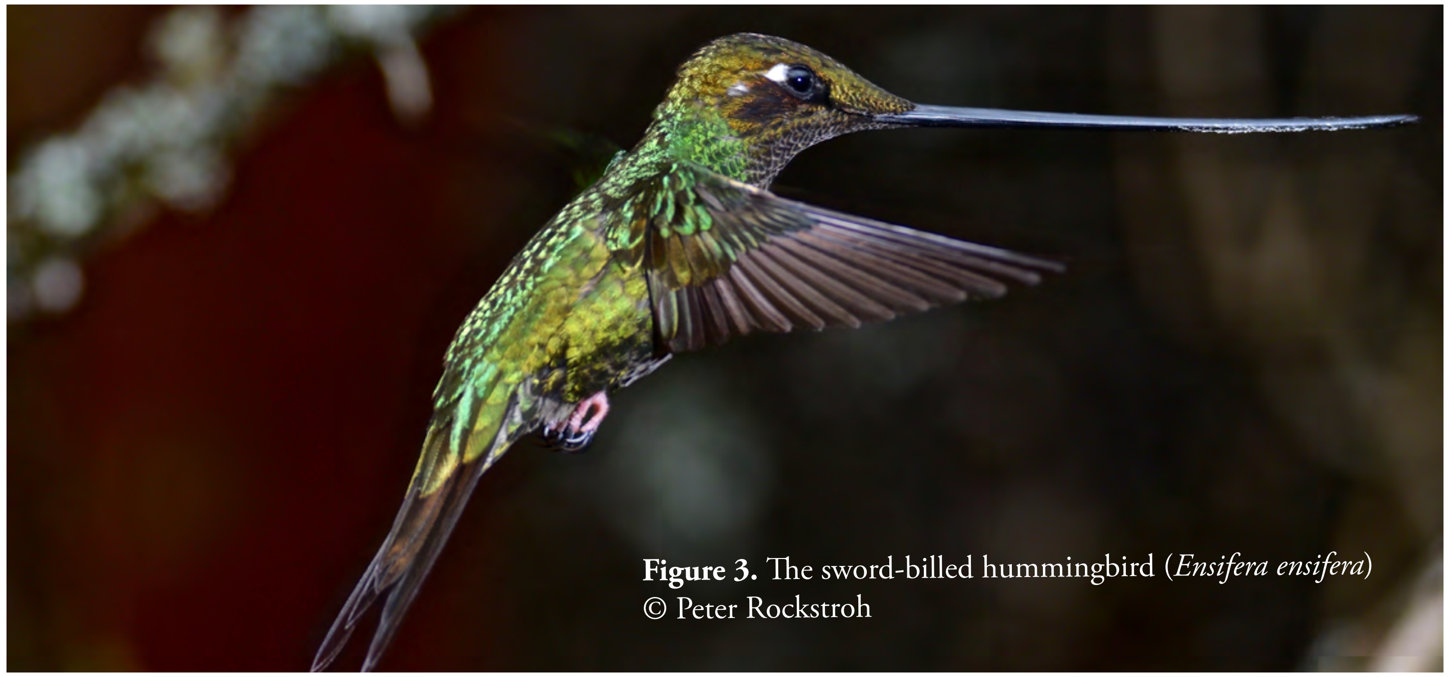


Figure 3. The sword-billed hummingbird (*Ensifera ensifera*) © Peter Rockstroh

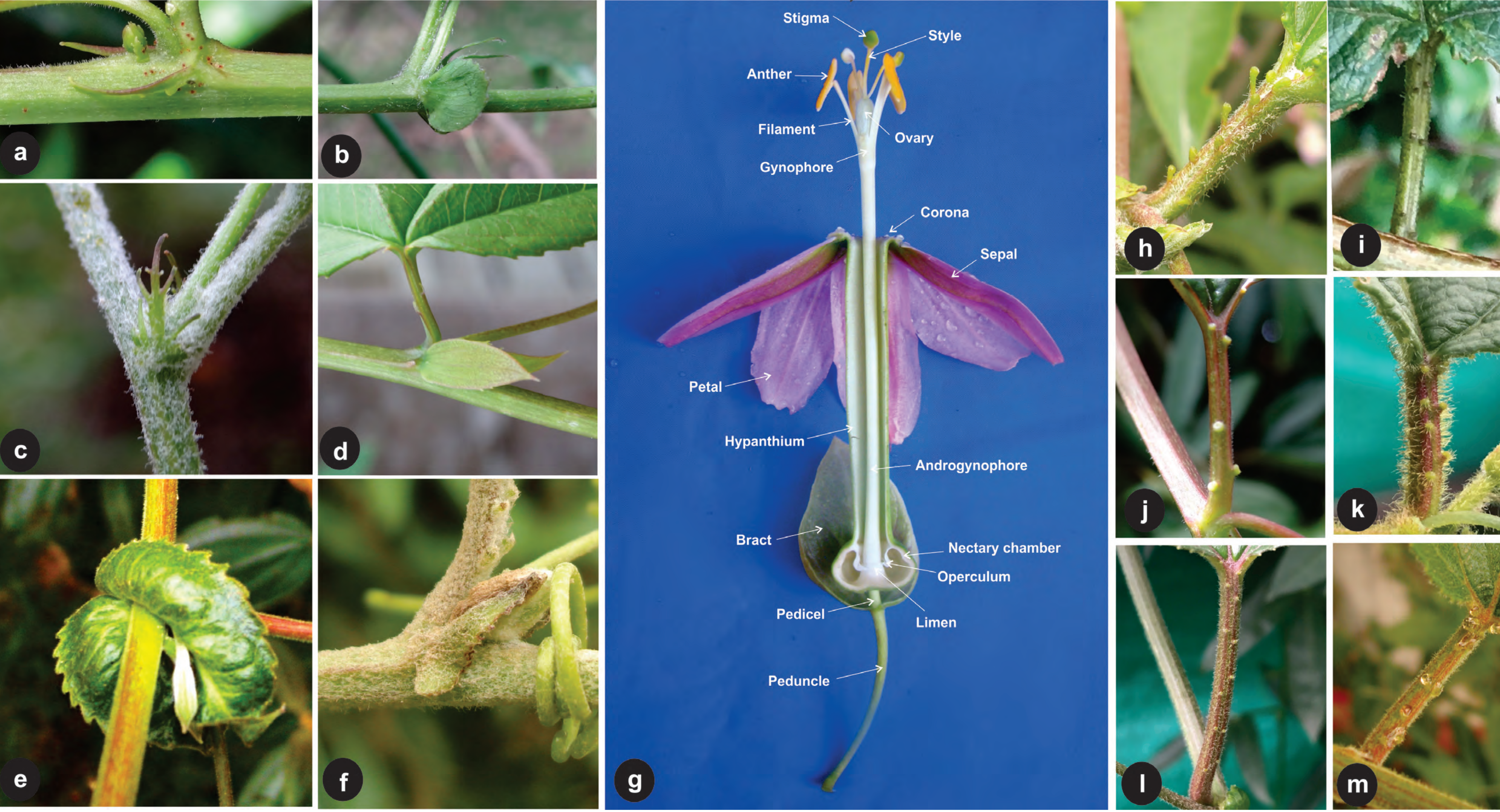


Figure 1. Morphological variability in the supersection *Tacsonia*. (a, j) *P. parritae*, (b, i) *P. tripartita* var. *tripartita*, (c) *P. pinnatistipula*, (d) *P. colombiana*, (e, h) *P. mixta*, (f) *P. crispolanata*, (g) *P. tarminiana*, (i) *P. cremastantha*, (k) *P. rugosa* var. *rugosa*, (m) *P. antioquiensis.* © John Ocampo.

the permanent snowline and the puna are the grasslands within that area.

This group of 65 inventoried species shows a marked adaptation to growing in forests on highland slopes with abundant everyday rainfall (2000 to 3000 mm on average per year) and temperatures range from 0 to 15 ºC (Schwerdtfeger 2004). The *Tacsonia* group is monophyletic and diverged from the remaining *Passiflora* approximately 10.7 Ma ago (underwent radiation at 9–8 Ma), during a major uplifting phase of the northern Andes (Abrahamczyk et al. 2014).

Economic importance

Many of the *Tacsonia* species are of economic importance because of their fruit quality, their adaptability for cultivation as ornamental vines, or their medicinal properties (Coppens d´Eeckenbrugge 2003; Zucolotto et al. 2011). Among these species, 22 are reported as having edible fruits and two (*P. tarminiana* and *P. tripartita* var. *mollissima* (Kunth) Holm-Nielsen & Jørgensen) have been cultivated for centuries by the indigenous people of the Andean region under different names such as *tacsos, curubas* or *puru puru* (Ulmer & MacDougal 2004; Ocampo et al. 2014). These *tacsos* or *curubas* are represented in almost all the tropical Andes and are found escaped in the wild in Mexico, La Réunion Island (France), East Africa, Hawaii (U.S.A), New Zealand, and even in the Canary Islands (Schwerdtfeger, 2004), particularly *P. tarminiana*, which is known as *banana passion fruit* or *banana poka*. The fruits of these species (**Figure 5**) are consumed as fresh fruit and are used in preparations as juices, cocktails, ice cream and other desserts. The nutritional information content on these species is scarce and there are only few reports of *P. tripartita* var. *mollissima*, which stands out for its high Vitamin A and C, and mineral content.

Colombian curubas

Colombia's location and variety of ecosystems places the country in second place only to Brazil with regard to biodiversity, but it is in first place measured per square kilometer. (Myers et al. 2000). The country has a complex topography and is divided into six main biogeographic regions (Amazonia, Andes, Caribbean, Orinoquia, Pacific and Insular), covering an area of 1,141,748 km^2. The Andean region has a highly varied topography with a wide range of altitudes (from 100 to 5400 m), and three long mountain ranges separating two main inter-Andean valleys from the other regions. Colombia is the region richest in *Passiflora* with 174 recorded species mainly distributed in the Andean region (84%) between 1000 to 3000 m, with the most common ones thriving in disturbed habitats, such as roadsides, cultivated land, and secondary forests (Ocampo et al. 2007, 2010). Among the species reported, 71% are threatened to some degree and three are considered extinct. The genus *Passiflora* is considered as an indicator of biodiversity in Colombia as its species have ecological

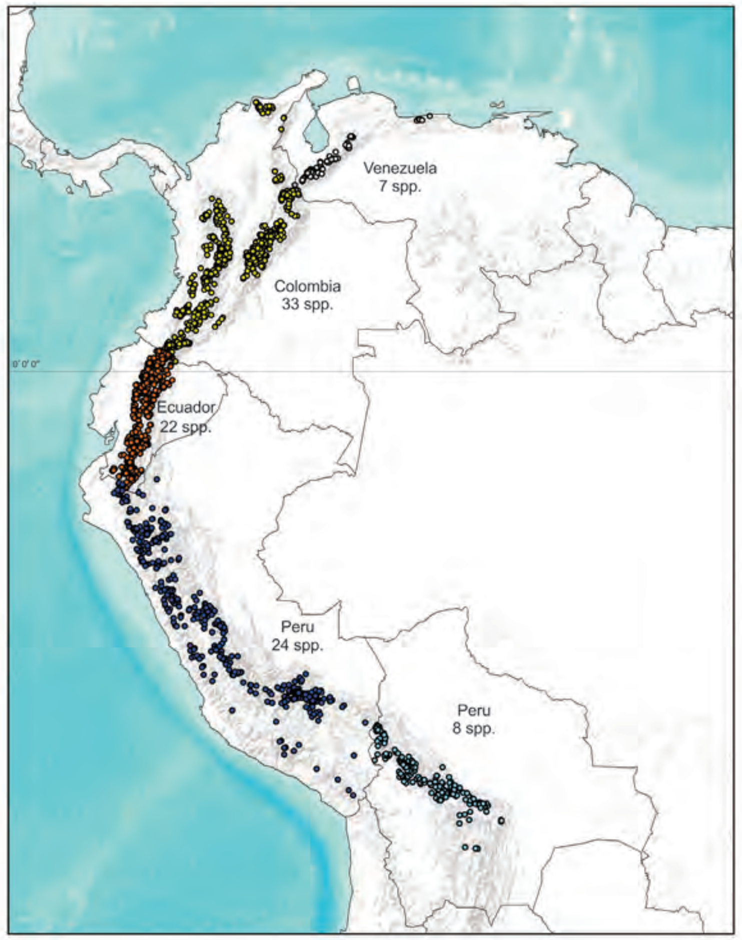


Figure 4. Spatial distribution of the species of supersection *Tacsonia*.

interactions with many organisms, comprising herbivores (particularly *Heliconius* spp. butterflies), protective ants, pollinators, and the plant communities providing them physical support and access to sunlight (Escobar 1988; Holm-Nielsen et al. 1988; Ocampo et al. 2010).).

Supersection *Tacsonia* displays the highest *Passiflora* species richness and endemism in Colombia with 33 reported species (**Figure 6** p. 30) that are divided into nine sections (Ocampo et al. 2014) and distributed from 1700 to 3840 m. (**Table 1** p. 48-49). Among them, 22 are endemic to Colombia and most have a restricted distribution to only one department (e.g. *P. cremastantha*, *P. formosa* T. Ulmer, *P. jardinensis* L. K. Escobar, *P. pamplonensis* Planch. & Linden ex Triana & Planch, *P. quindiensis* Killip, *P. tenerifensis* L. K. Escobar and *P. uribei* L. K. Escobar). The most important reference works that documented all species of *Tacsonia* and described nine new species between the years 1986 to 1992 were carried out by Linda K. Albert de Escobar (1988, 1989). Additionally, Escobar proposed sections *Colombiana*, *Parritana* and *Fimbriatistipula*, whose species are mostly distributed in Colombia. Section *Colombiana*, distributed in the center of the cordilleras, and from the northeast and up to the Venezuelan Andes, is often characterized by a very long peduncle and linear-lanceolate stipules. In addition to this important taxonomical work, several collaborative projects have focused on Passifloraceae, within the frame

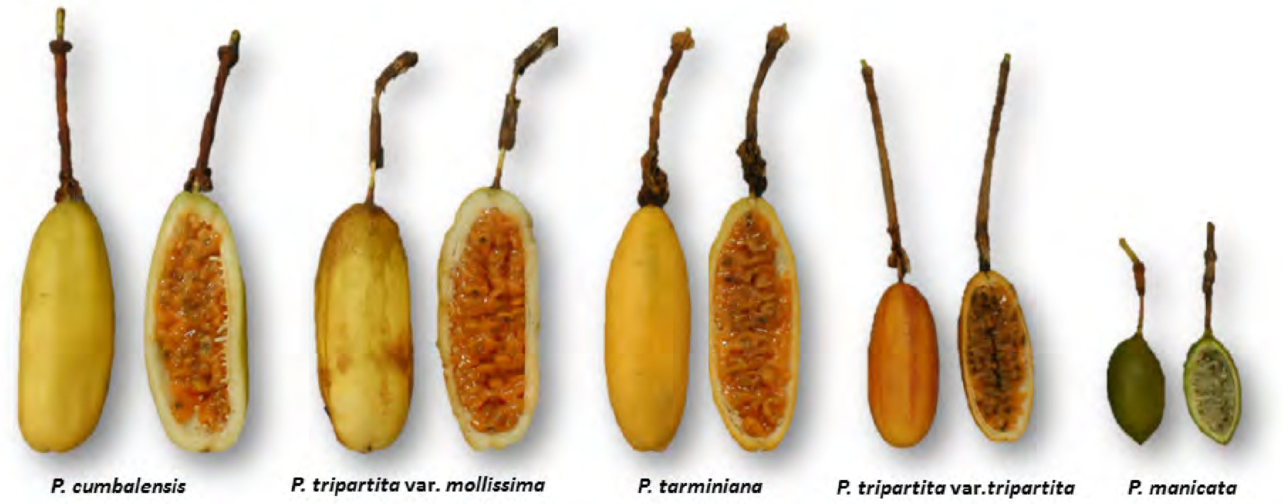


Figure 5. Examples of *Tacsonia* fruit © John Ocampo

of regional projects, supported by institutions such as Bioversity International, Colciencias, International Center for Tropical Agriculture (CIAT), Corpoica, Universidad de Caldas and the Ministry of Environment (MADS). They have generated a considerable amount of information such as the identification of species (*P. tarminiana*), new to science or to the country, and the study of the genetic resources of these species (Coppens d´Eeckenbrugge et al. 2001; Segura et al. 2002, 2003, 2005; Ocampo et al. 2004; Primot et al. 2005).

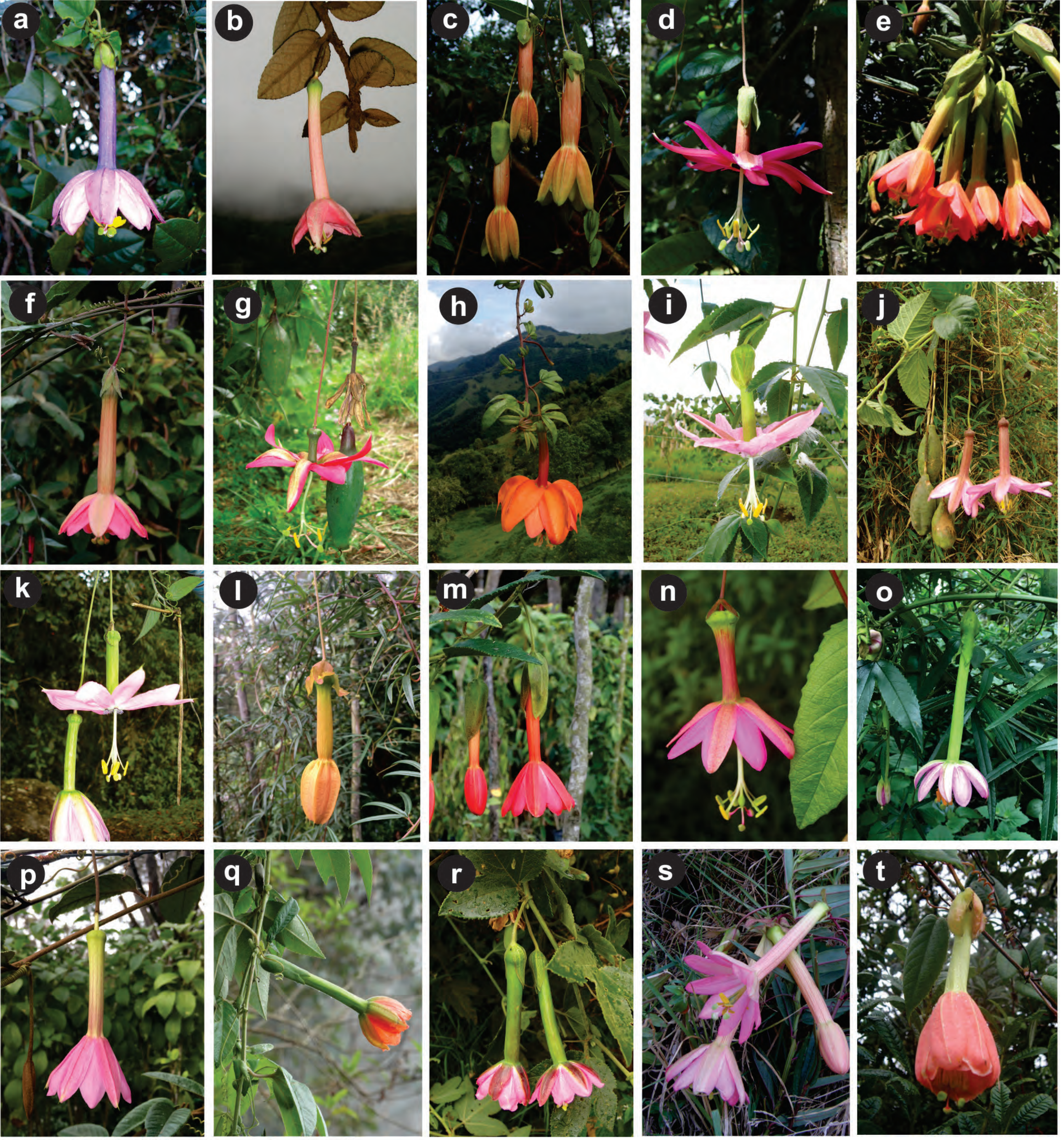
Several authors have reported easy interspecific hybridization in supersection *Tacsonia*, involving cultivated as well as wild materials (Escobar 1985, Primot et al. 2005). The interspecific hybrids may be viable and fertile or exhibit serious anomalies for several generations, as in the case of *P. tripartita* var. *mollissima* x *P. cumbalensis* (H. Karst.) Harms (Schöeniger 1986). Spontaneous hybridizations in the wild may have led to some over classification in this supersection. For instance, of the 33 species reported for Colombia, five (*P. cremastantha*, *P. formosa*, *P. pamplonensis*, and *P. purdiei* Killip) are known only from the type material. Whether this is due to high endemism, ancient extinction or atypical specimens resulting from hybridization, cannot be ascertained unless a second specimen is recorded, as could be done for *P. linearistipula* (Ocampo et al. 2007).

It is important to note that *P. formosa* was described as a new species from the same specimen considered as an atypical specimen of *P. lanata* (Juss.) by Escobar (1988). Over classification 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, which seems to represent just an isolated population. Likewise, in several cases, experts or *Passiflora* enthusiasts may have underestimated intraspecific variation in widely distributed and highly polymorphic species, or even intra-individual variation, splitting well known species in several new species only distinguished by a few quantitative or color traits (Ocampo & Coppens d´Eeckenbrugge 2017). For instance, a revision of field, herbarium and literature data leads us to consider that three species reported for Colombia in 2016 (*P. quinonesiae*, *P. splendida* and *P. creuci-caetanoae*) are likely synonyms for *P. cuatrecasasii*, *P. cremastantha*, and *P. rugosa* var. *rugosa*, respectively.

Most endemic species of *Tacsonia* were found in highlands difficult to access, and it is reasonable to expect more species to be described from currently poorly explored areas, such as the South of Huila, Tolima, Santander and Norte de Santander departments. The limited number of explorations in these regions of the northern Andes raises expectations that Colombia may harbor many yet unknown species, and future studies should encompass new regions, including protected and conflict areas (Ocampo et al. 2010).

Commercial and cultivated species

The most popular species are called *curubas* in Colombia and *tacsos* in Ecuador and Perú. The two most important curuba taxa are *P. tripartita* var. *mollissima* and *P. tarminiana* (**Figure 2** p. 25 **and Figure 5** p. 29). Both of them can escape from cultivation in man-disturbed habitats, and populations originating in the wild have been rarely observed (Ocampo et al., 2007). *P. tarminiana* however may present serious problems as an invasive species, as in Hawaii and New Zealand. These two curubas are mostly used to prepare refreshing beverages as juices. Their cultivation is ancient, and they were semi domesticated by the indigenous people of South America well before the Spanish conquest (National Research Council 1989). Their intensive commercial exploitation is quite recent however, dating from the 1950's. Pérez-Arbeláez (1956), in his work *Useful Plants of Colombia*, mentioned *curubas* as a promising species due to their easy growth and abundant fructification. In the same decade, Jaramillo (1957) published the results of the first agronomical trial



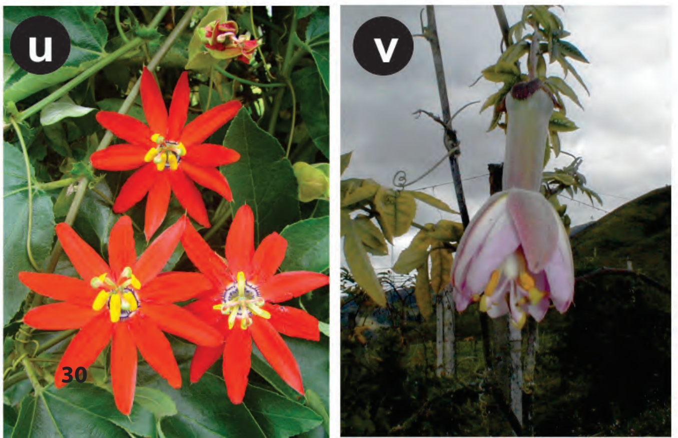


Figure 6. Species diversity of the supersection *Tacsonia* distributed in Colombia: (a) *P. cumbalensis*, (b) *P. lanata*, (c) *P . linearistipula*, (d) *P. cremastantha*, (e) *P. crispolanata*, (f) *P. adulterina*, (g) *P. antioquiensis*, (h) *P. parritae*, (i) *P. tarminiana*, (j) *P. tenerifensis*, (k) *P. flexipes*, (l) *P. jardinensis*, (m) *P. rugosa* var. *rugosa*, (n) *P. truxilensis*, (o) *P. tripartita* var. *tripartita*, (p) *P. cuatrecasasii*, (q) *P. mixta*, (r) *P. tripartita* var. *mollissima*, (s) *P. trianae*, (t) *P. fimbriatistipula*, (u) *P. manicata* and (v) *P. pinnatistipula*. © John Ocampo (a, b, c, d, f, g, h, i, j, k, l, m, o, p, q, r, u, v), Gustavo Morales (s, t), Miguel Molinari (n) and Sebastián Rendón (e).

Figure 7. *Passiflora mixta*
© John Ocampo

of commercial cultivation of *curuba* in Colombia. Since then, other studies have followed. Thus, Campos (1992, 2001) includes important contributions regarding the main agricultural practices (pruning, irrigation, among others), and a description of the curuba de Castilla (*P. tripartita* var. *mollissima*) and the curuba India (*P. tarminiana*). More research is required to allow higher yields and chemical treatment aimed at tackling different phytosanitary problems, mostly related to fungi, flies, and nematodes.

Today, Colombia is the country with the widest commercial cultivation of curubas (*P. tripartita* var. *mollissima* and *P. tarminiana*) along its three cordilleras, above 1800 m, mainly in the departments of Boyacá, Cundinamarca, Nariño and Tolima. These fruit crops are a useful source of income for small-scale farmers, thanks to their long production season, and have contributed to farmer stability in the Colombian countryside. National statistics do not differentiate between these two species and for the last years 1556 hectares have been reported with an average production of 10 tons per hectare, and a total yearly production of 23,000 tons (Agronet 2017). Additionally, curuba de Castilla is being exported to Germany, Hong Kong and Netherlands, but volumes are not significant regarding the potential these species have.

P. tripartita var. *mollissima*

The curuba de Castilla o tumbo is a vigorous vine with a useful life of up to ten years and even more under favorable phytosanitary conditions. Its flowers are pendant with a green hypanthium and a campanulate corolla of a dark magenta pink color (rarely white color). The fruit (**Figure 2** p. 24**, Figure 5** p. 29 and **Figure 8**) is pale yellow, oblong, rounded at both ends, 9-15.5 x 3.5-5 cm, with an average weight of 90 g. The orange pulp makes up for 60% of the fruit, it has a pH of 3.0 to 3.5, °Brix of 8 to 9 and more than 100 seeds (Campos & Quintero 2012). The main phytosanitary problems are anthracnose (*Colletotrichum gloerosporoides* Penz Sacc.) that mostly attacks fruits, and nematodes of genus *Meloidogyne* spp. and *Fusarium* sp. affecting roots, and And the worm of the *Pyrausta perelegans* Hampson (moth) boreing the flower buds (Campos 2001).

P. tarminiana

The curuba India or curuba Quiteña, (**Figure 9** p. 34-35) is very similar to curuba de Castilla, with pendulous flowers and reflex corolla of a light rose pink color (rarlely white color). The fruit (**Figure 2** p. 24**, Figure 5** p. 29 and **Figure 10** p. 36-37) is elongated and fusiform, 8-11 x 3-4 cm, it has a deeper yellow color, sometimes tinted with reddish orange, with an average weight of 80 g. The pulp is of a paler orange color and less astringent, as compared to de Castilla, and makes 58% of the fruit weight; °Brix is

Figure 8. *P. tripartita* var. *mollissima* fruit and juice © John Ocampo

Figure 9. *Passiflora tarminiana*
© John Ocampo

Figure 10. *P. tarminiana* flower and fruit © John Ocampo

10 to 11 and pH 2.5 (Campos & Quintero 2012).

This species is hardier than *P. tripartita* var. *mollissima*, more resistant to anthracnose, and adapted to a wider environmental range. Thus, it can be cultivated as low as 2000 m, where curuba de Castilla does not grow, although it produces smaller fruits in these conditions.

P. tripartita var. *tripartita* and *P. tripartita* var. *azuayensis*

P. tripartita var. *tripartita* and *P. tripartita* var. *azuayensis* are found in the southern part of Colombia, in Ecuador and in northern Perú in the wild state or in home-gardens. These curubas can be differentiated from their *P. tripartita* var. *mollissima* sister taxon by the less abundant pubescence in their vegetative parts their deeper leaf lobulation. These two botanical varieties produce fruits that are generally smaller with a more colorful pericarp, between yellow and reddish orange (**Figure 5** p. 29), particularly in the intercarpelar zones. Its pulp is less abundant, sweeter and tastier than the ones of curuba de Castilla and curuba India. However, these varieties are less vigorous and less productive.

P. mixta

P. mixta commonly known as curubito de Indio, tumbo, and xamppajrrai (quechua), is the most widely distributed species in super-section *Tacsonia*, all along the Andes, from Venezuela to Perú and Bolivia where it grows from 1700 to 3700 m. Its morphology is similar to that of *P. tripartita*, but it is distinguished by its more rigid peduncles that maintain its flowers in a more or less horizontal to erect position (**Figure 7**. p. 31). In the type that is most common in Colombia and in the northern part of Ecuador, the mature fruit is relatively small (4-8 x 2-4 cm), a hard, green pericarp, a yellow tint at maturity; the pulp is greyish or greenish, rarely yellow, with a not so pleasant taste. Most plants with yellow fruit pulp originated from spontaneous introgressions with *P. tripartita* var. *mollissima*. In northeastern Colombia, Venezuela, and Perú, we have observed types of *P. mixta* with larger fruits, hard pale yellow skin and orange and sweet pulp. In Ecuador, some fruits present a soft, yellowish green pericarp, similar to that of *P. tripartita* var. *mollissima*, with orange pulp. In certain cases, fruits of *P. mixta* are sold in rural markets but its cultivation is rare. The species main interest lies in its affinity and sexual compatibility with *P. tripartita* var. *mollissima*, its hardiness, and its adaptability to more variable conditions, in particular to relatively warmer and drier climates at lower altitudes. It has a reputation of being resistant to fungi, such as *Colletotrichum* sp., *Oidium* sp., *Alternaria passiflorae* J.H. Simmonds, and nematodes *Meloidogyne* spp. (Sañudo & Jurado 1990). We have however often observed accessions susceptible to the first two of these pathogens, indicating that there are also variations in these characters.

P. cumbalensis var. *goudotiana*

P. cumbalensis var. *goudotiana*, curuba bogotana, chupadora, or the rosy passionfruit is cultivated near Bogotá, (**Figure 14** p. 47) in home-gardens between 1800 and 3000 m, and produces an obovoid curuba similar to the commercial curuba, but with a bright red skin. Some types produce big yellow fruits with abundant, aromatic and sweet pulp (**Figure 5** p. 29), and are consumed the same way as *P. tripartita* var. *mollissima*. Eleven botanical varieties of *P. cumbalensis* have been described in the countries where these curubas grow (Escobar 1988; Holm-Nielsen et al. 1988), based on flower color variations, leaf shape, nectariferous glands and leaf pilosity. Fruit size is 5-11 x 2-5 cm (Escobar 1988). Some wild types give very good fruits but their phenology is very distinct compared to *P. tripartita* var. *mollissima* and they do not adapt well to cultivation. According to Schoëniger (1986) *P. cumbalensis* is allogamous and may show inbreeding depression. According to Sañudo & Jurado (1990), *P. cumbalensis* var. *cumbalensis* is resistant to the fungal diseases (*Oidium* sp., *C. gloerosporoides*, *A. passiflorae*) that affect curuba de Castilla.

P. pinnatistipula

P. pinnatistipula Cav. is called gulupa (Colombia), tacso or puru puru (Ecuador, Perú), or tin-tin (Perú). It is native to Perú, Bolivia and Chile and is cultivated in home-gardens from Chile to Colombia between 2500 to 3800 m. Its fruits are round or subglobose, 4 to 6 cm in diameter, with a greyish green to yellow pericarp, which is thin and coriaceous, but brittle. The pulp is greyish to yellowish, sweet or slightly acid and very scented. It can be consumed directly or in preparations, but its yield is low because the seeds are relatively thick and hard. Plants fruit several times a year (Escobar 1981) with a limited yield and resistance to pathogen fungi (Sañudo & Jurado 1990).

P. x *rosea*

P. x *rosea* is a natural hybrid from *P. pinnatistipula* and *P. tripartita* var. *mollissima*. It is produced easily when the two species are cultivated in the same area. Moreover, it is very similar to *P. pinnatistipula* and is distinguished by the length of its anthers and its anomalous androgynophore; the stipules are more foliaceous and the bracts are coalescent at their base. Fruit ovoid, 8 x 2.5 cm in diameter with pubescent pericap. Generally, the anthers are petaloid and sterile. Like *P. pinnatistipula* it is also resistant to *A. passiflorae* (Sañudo & Jurado 1990), but its fruit production is normally very limited, which seems to be due to the relative incompatibility of the parental genomes.

P. antioquiensis

Curuba antioqueña (*P. antioquiensis* Karst.) is characterized by having a shorter hypanthium, as compared to other tacsos, and a reduced corona of thin filaments (**Figure 6** p. 30). It is distributed along the Central and Western Cordilleras of Colombia, between 1800 and 2700 m. The tradition regarding its cultivation has been lost and it has become a rare habitant of home-gardens. It seems to need particular microclimatic conditions to thrive and it can be difficult to obtain regular production of flowers and fruits. It has been naturalized in New Zealand (Heenan & Sykes 2003); reports of wide cultivation, there or in Australia, have never been documented (the Atlas of Living Australia only mentions 19 specimens from New Zealand and one from Papua New Guinea). Its spectacular crimson red flower that hangs off an extremely long peduncle (30-50 cm) has made it appreciated as ornamental. Its fruits are fusiform, of 5-9 x 2-3 cm (**Figure 2** p. 35), with a yellowish green pericarp, fragile and greyish to orange arils that reminding the taste of a *maracuyá*, but sweeter. According to Sañudo & Jurado (1990), *P. antioquiensis* is resistant to fungal diseases.

Inter-specific hybridizations and breeding

The most important commercial species are susceptible to several pests and diseases with considerable negative effects on production. Thanks to the number of species and botanical varieties producing edible fruits of commercial size, supersection *Tacsonia* has a high potential for crop diversification and economic development. This has induced research institutions in Andean countries to prioritize their characterization and the evaluation of wild and cultivated populations (National Research Council 1989), and develop strategies for conservation and improvement of these genetic resources. Indeed, the breeding potential of cultivars for curuba or tacsos is not restricted to *P. tripartita* var. *mollissima* or *P. tarminiana* (Coppens d´Eeckenbrugge 2003).

Colombia could focus its efforts in exploring and studying different types of curubas as it is the country with the highest diversity of species and the best home market for curubas. In this way, these curubas (*P. cumbalensis*, *P. antioquiensis*, *P. leptomischa*, *P. flexipes* Tr. & Planch., *P. cremastantha* and *P. parritae*) are just as tasty as granadillas and could be developed for direct consumption (Quintero 2009; Ocampo et al. 2007). In the first place, the criteria to obtain new curuba cultivars involve the selection of ideotypes with higher yielding plants with larger fruits, good post-harvesting behavior and that are resistant to *C. gloerosporioides* so they can respond to market requirements.

Spontaneous interspecific hybrids that involve both wild and cultivated forms have been regularly observed by producers and have been reported by numerous authors, suggesting weak interspecific barriers in supersection *Tacsonia*. Escobar (1981) reported cases of spontaneous hybrids between *P. tripartita* var. *mollissima*, *P. cumbalensis*, *P. mixta*, *P. mathewsii* and *P. fimbriatistipula* Harms, remarkable for their vigor, their larger leaves, stipules, bracts and flowers compared to their parental species, with a similar or superior pollen viability. Escobar (1981) also observed hybridizations between *P. tripartita* var. *mollissima* (female parent) and a range of species including *P. ampullacea*, *P. pinnatistipula*, *P. mixta*, *P. mathewsii* and *P. tripartita* var. *tripartita*, which had superior fertility to that of intraspecific crosses and spontaneous self-pollinations.

Studies conducted by Schoëniger (1986) show that interspecific barriers cannot be underestimated in supersection *Tacsonia*. According to this author, spontaneous hybrids between *P. tripartita* var. *mollissima* (female) and *P. mixta* (male) show tolerance to the fungi *Oidium* sp. and *C. gloerosporoides*. The F2 obtained through self-fertilization showed a considerable variation with many transgressive segregation cases, and a high proportion of these hybrids showed an abundant flowering but little or no fructification. Regarding hybridizations of *P. cumbalensis* x *P. tripartita* var. *mollissima*, Schoëniger (1986) reported that the F_1 showed morphological affinity with the male parent. However, the fruits were more similar in shape to the ones of *P. cumbalensis*, but with a high variability in weight (30 to 90 g), a little resistant pericarp, many seeds, and slightly acid and less succulent arils than in *P. tripartita* var. *mollissima*. The F2 obtained through self-fertilization and the R1 (back-cross onto *P. tripartita* var. *mollissima*) showed low germination, high diversity in fruit shape, and its production varied from three to more than 100 fruit per plant.

Sañudo and Zuñiga (1991) also pollinated *P. tripartita* var. *mollissima* with pollen from *P. pinnatistipula*, *P. tripartita* var. *tripartita*, *P. cumbalensis* and *P. mixta*. The hybrids obtained with *P. tripartita* var. *tripartita* showed a higher hybrid vigor and a better juice quality than *P. tripartita* var. *tripartita*; the ones obtained from *P. cumbalensis* showed an increase in fruit size; and the ones from *P. mixta* gave less enduring fruits with an excellent pulp but with many seeds and little juice. All these hybrids inherited resistance to *C. gloerosporioides* anthracnose from one of their parents.

Studies carried out by Quintero (2000) produced cultivars from high yielding plants of *P. tripartita* var. *mollissima* called `Ruizquin´ 1 and 2 that were obtained through *in vitro* propagation with good consumer acceptance in Colombian markets. In high rainfall periods however, they showed high susceptibility to *C. gloerosporioides*. The same author and his son (Quintero 2009) obtained interspecific hybrids between *P. tripartita* var. *mollissima* x *P. mixta* called `Momix´, a cultivar that responds to market expectations

Figure 11. Cloud forest in Cundinamarca (Silvania) © John Ocampo

Figure 12. Habitat disturbed in the Colombian Andes (Genova, Quindío) © John Ocampo

Figure 13. Gustavo Morales conservationist of Colombian species of the supersection *Tacsonia* (*P. rugosa* var. *rugosa*). © John Ocampo.

Figure 14. Enthusiasts, Miguel Molinari (right) and Hernán D. Bernal (left) collecting and photographing *P. cumbalensis* var. *goudotiana* in Cundinarmarca (Sibaté) © John Ocampo

with an excellent yield and good fruit size. It also shows tolerance to *C. gloerosporioides*, and it can be consumed directly and in juice, with either water or with milk due to its higher ºBrix (12-13º). Interspecific compatibility among the most common species of supersection *Tacsonia* (*P. tripartita* var. *mollissima*, *P. tarminana* and *P. mixta*) has also been reported by Primot et al. (2005). The easy hybridization as well as the vegetative fertility and vigor of the hybrids confirm prior observations of spontaneous and experimental hybrids in *Tacsonia.*

P. manicata

Another member of the supersection *Tacsonia* that has been assessed with regard to curuba breeding is *P. manicata* (Juss.) Pers. This species is distributed along the Andes from Venezuela until the north of Perú, between 1500 and 3000 meters, with a shorter floral tube and a complex filamentous corona (**Figure 6** p. 30). The fruit is ovoid, of 3-6 x 3-4 cm with a green coriaceous pericarp when mature (**Figure 5** p. 29), greyish arils, slightly succulent and with a sweetish taste. However, its fruit cannot be considered as edible, as its mature state cannot be clearly distinguished from its immature state, during which the fruits can have toxic and psychotropic effects (hence the name "diablito" in Ecuador (Yockteng et al. 2011)). The interest of this species lays in its hardiness, and its adaptation to warmer and drier environments, and its cross ability with curubas: *P. antioquiensis* (Martín & Nakasone 1970), *P. tripartita* var. *mollissima* (in both crossing directions) and *P. edulis* (as the male parent). The fertility of these two hybridizations are half of the fertility after intraspecific pollination (Escobar 1985; Ocampo et al. 2016). *P. manicata* is resistant to nematodes and fungal diseases (*C. gloerosporoides*, *Oidium* sp. and *A. passiflorae*) and can be used as rootstock for *P. tripartita* var. *mollissima* (Campos 2001).

Breeding priorities

Supersection *Tacsonia* offers good options to improve and diversify the curubas that are currently being commercialized. The first priority would be to better explore the resistance characters present in *P. tripartita* var. *tripartita* and *P. tripartita* var. *azuayensis*, *P. mixta*, *P. schlimiana*, *P. mathewsii* and in the types of *P. cumbalensis* that have yellow fruit in benefit of *P. tripartita* var. *mollissima* and *P. tarminiana*. The second priority would be to reevaluate the red curuba *P. cumbalensis*; doing this, we would be rescuing this domesticated curuba before it becomes extinct. Likewise, the semi domesticated forms of *P. antioquiensis* should be rescued, and, resources being available, *P. leptomischa*, *P. flexipes* and *P. cremastantha.* This could define another focus for commercial fruits (if fruit quality is adequate) or from plants used as ornamentals. *P. pinnatistipula* could also contribute if there were selections with less seed size and better pulp yield.

Conservation status

Colombia has 22 endemic *Tacsonia* species inventoried with a narrow distribution, implying a high extinction risk. The country has undergone recent transformation of large portions of its natural ecosystems, in particular in the Andean region due to agricultural development (e.g. coffee, sugar cane, rice, bananas and potato plantations) and extensive livestock production (pastures), mining, hydroelectric generation complexes (dams), and illicit crop plantations. Indeed, the extinction of *Tacsonia* species would entail the loss of interdependent organisms such as nectar feeding bats and hummingbirds. In this context, most of the 33 Colombian *Tacsonia* species (57%) are under some degree of threat according to the IUCN criteria (Ocampo et al. 2007, 2014), and one is considered probably extinct - EX. (**Table 1** p. 51). Thus, 10% are under the criteria Critically Endangered (CR), 35% Endangered (EN), and 12% Vulnerable (VU), which clearly illustrates the alarming situation for the supersection.

Tacsonia in Colombia

Conservation or restoration efforts for *Passiflora* supersection *Tacsonia* habitats must be integrated in a more general management strategy at the landscape level (**Figure 12** p. 42-43). The latter can be ensured by coordinating existing actions for watershed protection, management of private and low-level public reserves, creation of environmental corridors, and improvement of agricultural practices that integrate the landscape. *Ex situ* conservation in botanical gardens and seed banks (e.g. cryopreservation, González-Benito et al. (2009)) is another strategy that must be implemented when critical habitats are destroyed. This strategy has begun to be implemented in the Botanical Garden of Bogotá "José Celestino Mutis" for some time now by Gustavo Morales (**Figure 13** p. 44-45), who has led expeditions to collect many species of *Tacsonia* in Colombia (**Figure 14** p. 45-46). He established living collections and began with seed preservation of the most endangered species, such as *P. adulterina*, *P. antioquiensis*, *P. colombiana*, *P. cremastantha*, *P. crispolanata*, *P. cuatrecasasii*, *P. cumbalensis*, *P. jardinensis*, *P. formosa*, *P. parritae*, *P. pinnatistipula*, *P. manicata*, *P. mixta*, *P. rugosa* var. *rugosa*, *P. trianae*, *P. tarminiana*, *P. tripartita* var. *mollissima/tripartita* and *P. uribei*. This example of conservation must be followed by other governmental institutions such as universities and research centers in the Andean countries so that future generations can enjoy this biological wealth.

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Table 1 Official species of the supersection *Tacsonia* inventoried for Colombia. Asterisk (*) indicates endemic species.

Species	Elevation (m.a.s.l.)	IUCN	Synonymous
Section *Colombiana*			
Series *Colombianae*			
Passiflora adulterina L.f.,1781 *	2600 - 3600	NT	*T. adulterina* (L. f.) Juss., 1781
Passiflora crispolanata L.Uribe, 1954 *	2500 - 3500	NT	*P. boyacana* Killip, 1960
Passiflora cuatrecasasii Killip, 1960 *	2200 - 3500	NT	*P. quinonesiae* Bonilla et al. 2016
Passiflora formosa T. Ulmer, 1999 *	3000 - 3100	EN	
Passiflora lanata (Juss.) Poir., 1811 *	2200 - 3500	VU	*T. lanata* Juss., 1805
Passiflora pamplonensis Planch.& Linden ex Triana & Planch., 1873 *	2000 - 3000	CR	
Passiflora rugosa var. *rugosa* (Mast.) Triana & Planch., 1873 *	3000 - 3500	EN	*P. eriocaula* Harms, 1922; *P. creuci-caetanoae* Bonilla et al., 2016
Passiflora rugosa var. *venezolana* L.K. Escobar, 1986	2500 - 3500	EN	
Passiflora trianae Killip, 1938 *	3000 . 3500	EN	*P. trisecta* Planch. & Linden ex Triana & Planch., 1873; *P. rigidifolia* Killip, 1960
Passiflora truxillensis Planch. & Linden, 1873	1800 - 3000	EN	
Series *Leptomischae*			
Passiflora antioquiensis H. Karst., 1859 *	1800 - 2700	NT	*P. antioquiensis* var. *trisecta* H. Karst., 1859; *P. vanvolxemii* (Hook.) Triana & Planch., 1873
Passiflora coactilis (Mast.) Killip	2700	EN	*P. mariae* (Sodiro) Harms, 1925
Passiflora cremastantha Harms, 1922 *	2000 - 2500	CR	*P. splendida* Bonilla et al. 2016
Passiflora flexipes Triana & Planch., 1873 *	2500 - 3380	VU	*T. flexipes* Triana & Planch., 1883
Passiflora leptomischa Harms, 1922 *	2000 - 2800	NT	
Passiflora tenerifensis L.K. Escobar, 1988 *	2800 - 3100	CR	
Series *Quindiensae*			
Passiflora linearistipula L.K. Escobar, 1988 *	2650 - 3170	EN	
Passiflora quindiensis Killip, 1938 *	2900 - 3100	EN	*P. elegans* Triana & Planch., 1873
Section *Elkea*			
Passiflora cumbalensis var. *caucana* L. K. Escobar, 1988	2300 - 2800	LC	
Passiflora cumbalensis var. *cumbalensis* (H. Kast.) Harms, 1894	3000 - 3800	NT	
Passiflora cumbalensis var. *goudotiana* (Triana & Planch.) L.K. Escobar, 1987	1950 - 3000	LC	
Passiflora tarminiana Coppens & Barney, 2001	2000 - 2900	VU	
Passiflora tripartita var. *tripartita* (Juss.) Poir., 1811	3000 -3100	VU	*P. psilantha* (Sodiro) Killip, 1924
Passiflora tripartita var. *azuayensis* Holm-Nielsen & Jørgensen, 1988	2000 - 2650	NT	
Passiflora tripartita var. *mollissima* (Kunth) Holm-Nielsen & Jørgensen, 1988	2200 - 3500	LC	*P. tomentosa* var. *mollissima* (Kunth) Triana & Planch, 1873
Section *Fimbriatistipula*			
Passiflora fimbriatistipula Harms, 1894 *	2130 - 3240	EN	
Passiflora uribei L.K. Escobar, 1988 *	2500 - 2700	EN	
Section *Insignes*			
Passiflora pinnatistipula Cav.,1799	2000 - 3600	NT	*P. pennipes* Sm., 1819 nom. Illeg.; *P. chilensis* Miers, 1826
Section *Manicata*			
Passiflora manicata (Juss.) Pers., 1807	1500 - 2700	LC	*P. manicata* var. *communis* Kunth, 1817; *P. meridensis* H. Karst.,1859
Section *Parritana*			
Passiflora jardinensis L.K. Escobar, 1988 *	2750 - 3000	EN	
Passiflora parritae (Mast.) L.H. Bailey, 1916 *	2500 - 3020	EN	*P. salmonea* Harms, 1894
Section *Tacsonia*			
Passiflora mixta L. f., 1781	1700 - 3700	LC	*P. longiflora* Lam., 1789; *P. brachychlamys* Harms, 1929
Passiflora schlimiana Triana & Planch., 1873 *	2400 - 3220	EN	
Section *Tacsoniopsis*			
Passiflora bracteosa Planch. & Linden, 1873	2200 - 3000	EN	*T. infundibularis* Mast., 1883
Passiflora purdiei Killip, 1938 *	2008 - 2505	EX	
Section *Rathea*			
Passiflora andina Killip, 1938	2800	CR	*P. floribunda* (H. Karst.) Triana & Planch. ex Harms , 1925
Passiflora colombiana L.K. Escobar, 1986 *	2000 - 2500	CR	
Section x *Inkea*			
Passiflora x *rosea* (H. Karst.) Killip, 1938	2500 - 3500	VU	*Poggendorffia* × *rosea* H.Karst., 1857; *T.* × *rosea* (H.Karst.) Sodiro, 1903