



<https://doi.org/10.11646/phytotaxa.584.2.5>

## *Passiflora brauliensis*, a new species of *Passiflora* supersection *Laurifoliae* (*Passifloraceae*) from the volcanic forest of Costa Rica

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### Abstract

A new species from Costa Rica is described following a closer analysis of the *Passiflora nitida* complex. Given that the actual true identification of *Passiflora nitida* typified from Venezuela but distributed throughout South America was rather poorly constrained, the new species presented here was long identified incorrectly as supposedly being a form of *P. nitida*, for it sharing several floral characteristics. Following intense revision of the source literature, supplemented by fieldwork across Central America, the Costa Rican accessions of “*Passiflora nitida*” appeared to be significantly different from its South American counterpart in several morphological and habitational characteristics. While it was found that true *Passiflora nitida* only inhabits non-volcanic terrains, *Passiflora brauliensis* sp. nov. presented in this paper attributes to be the only member of this complex endemic to solely volcanic regions, where it is found in wet lowland to premontane transitional forest on the eastern flanks of Costa Rica’s most active volcanoes. The ecology, distribution, and association with the *Passiflora nitida* complex is highlighted, as well as its relationship with the other species within *Passiflora* supersect. *Laurifoliae* found throughout Latin America.

**Keywords:** Central America, endemism, Granadilla, Maracuja, *Passiflora nitida*, Passionflower

### Introduction

Among the more than 600 species of *Passiflora* Linnaeus (1753: 955) distributed across its wide range of habitats and environments, there have been several species complexes identified concerning the diverse morphological and visual characteristics of species borne from the interactions between plant, pollinator and predator (Knapp & Mallet 1984, Ulmer & MacDougal 2004, Kuethe 2020). Early identifications of species or identifications from subsequent herbarium collections cannot always take this dynamic into full account, and rarely have we seen distinction based on habitational differences that are focused on soil chemistry, distribution and disposition. This often results in a discontinuous lateral distribution; whereby specific constituent species of a complex cannot co-exist as they are not adapted to the same physical properties and soil chemistry borne from the contrast between volcanic- and limestone regions.

This leads to separate narrow endemic species which exhibit multiple subtle differences when studied in living specimen, and it are those that are the most identified in error for a larger overarching complex with a seemingly wide distribution (Knapp & Mallet 1984). It was partially because of such indolence that species such as *Passiflora nitida* Kunth (1817: 130) or *Passiflora ambigua* Hemsley (1902: 128) “appear” much wider distributed and much more variable than what they truly are (Kuethe, pers. comm.). This was very much the case for certain accessions of “*Passiflora nitida*” found in Costa Rica, a species from *Passiflora* supersect. *Laurifoliae* (Killip ex Cervi) Feuillet & MacDougal (2003: 38) naturally endemic to (sub)Amazonian South America, but with seeming scattered populations recorded throughout the Central American isthmus (Estrada & Rodríguez 2009).

For the last two decades, the only member of supersect. *Laurifoliae* deemed native to the Central Americas was believed to be *Passiflora ambigua*, with reportedly *Passiflora nitida* having been introduced (and sometimes even

naturalized) for its popular edible fruit. However, the identity of true *Passiflora nitida* is somewhat poorly constrained, and deviating forms were collectively placed under the *Passiflora nitida* taxon (e.g., *Passiflora coloranigra* Kuethe (2022: 561), *Passiflora fissurosa* Souza (2011: 450)). Targeted fieldwork conducted by the authors in Costa Rica and Panama have yielded little evidence of large-scale commercial planting of “*Passiflora nitida*”, but instead revealed some curious new species that exhibit the general vegetative and floral morphology (5–6 coronal series, erect opercular structure with filaments more than 8 mm), found in the wet volcanic forests of the Central Costa Rican volcanoes. Especially when studied in herbarium only, these may have been easily confused for the overarching *Passiflora nitida* if no further information such as colour, ecology or habitat were provided by the original collectors.

However, like the other segregate species from the *Passiflora nitida* complex, the new species show several distinct differences in floral colour, vegetative anatomy, fruit shape and colour, as well as habitational preference, which prompted the authors to further investigate these accessions of this Costa Rican “*Passiflora nitida*”. These segregates are restricted to volcanic, ecologically distinct regions that do not warrant widespread naturalization as per what would be expected for an invasive introduced species. Instead, the plants proposed here as a new species accommodate some of the last remaining remnants of the Central American volcanic primary forest along the Caribbean slopes of the Cordillera Central of Costa Rica, well versed for their high endemism and unique biodiversity. Following additional collections from the Braulio Carrillo National Park, Cancho Negro and La Selva Research Station in Costa Rica, new material of this supposed “*Passiflora nitida*” culminated several distinct morphological differences that allowed to assign *Passiflora brauliensis* sp. nov. Its distribution, habitat, ecology and morphological relation with the other species of supersect. *Laurifoliae* is discussed.

## Material and methods

Targeted fieldwork was conducted by the authors between 2018 and 2022, following reported sightings of a “red *Passiflora nitida*” found in the Braulio Carrillo National Park, Heredia, and at the La Selva Biological Research Station 15 km further north in central-eastern Costa Rica. Both locations are known for their abundance of biodiversity and unique ecology that supports a high level of endemic species. Herbarium material was collected by the second and third author and stored at USJ (herbarium acronym follows Thiers 2022), as well as three flowers and seeds preserved in alcohol and stored at the same herbarium. Additional collections stored at herbaria LSCR, CR, IRVC and MO have been made available and studied in support of this manuscript. Literature studies and assessment of the type specimens and variation seen for *Passiflora nitida* and its nearest related species across the Americas have been undertaken, including additional specimens studied from the herbaria P, INPA, U, USZ, LPB, NY, HUEFS, MO, US and STRI.

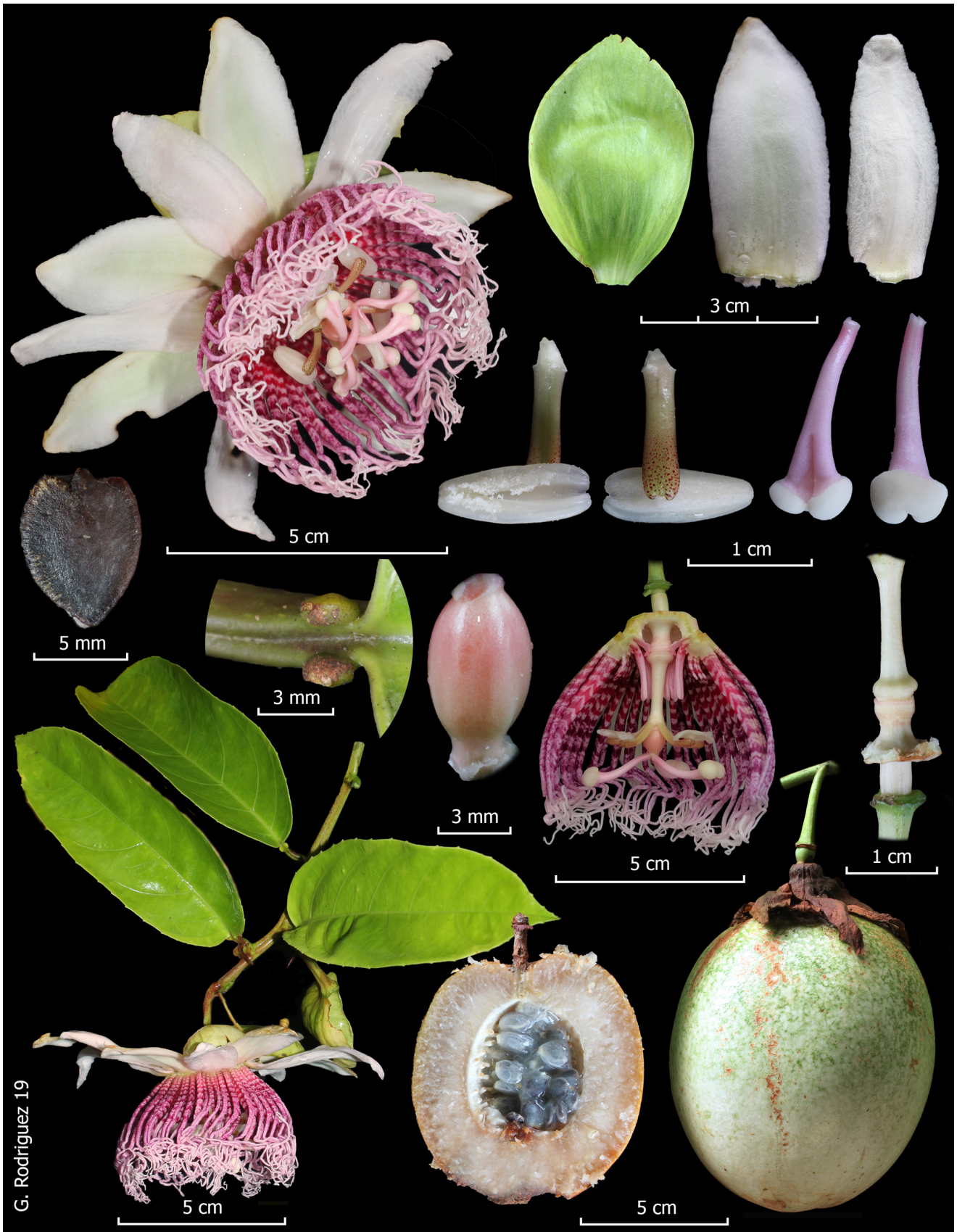
Additional studies of *Passiflora nitida* in Colombia, Bolivia, Brazil, Venezuela and Guyana were used to help identify key differences between this species and the new species proposed in this paper. The species distribution map was elaborated using the ESRI software (ESRI 2011), based on field collections, geological works, herbaria collections and georeferenced photographic material identified as *Passiflora brauliensis* Kuethe, R. Barboza, Alvarez sp. nov. A contemporary conservation status has been assigned using the GeoCat software endorsed by RBG Kew (<http://GeoCAT.kew.org>) and further augmented with the IUCN (2022) categories and criteria.

## Taxonomy

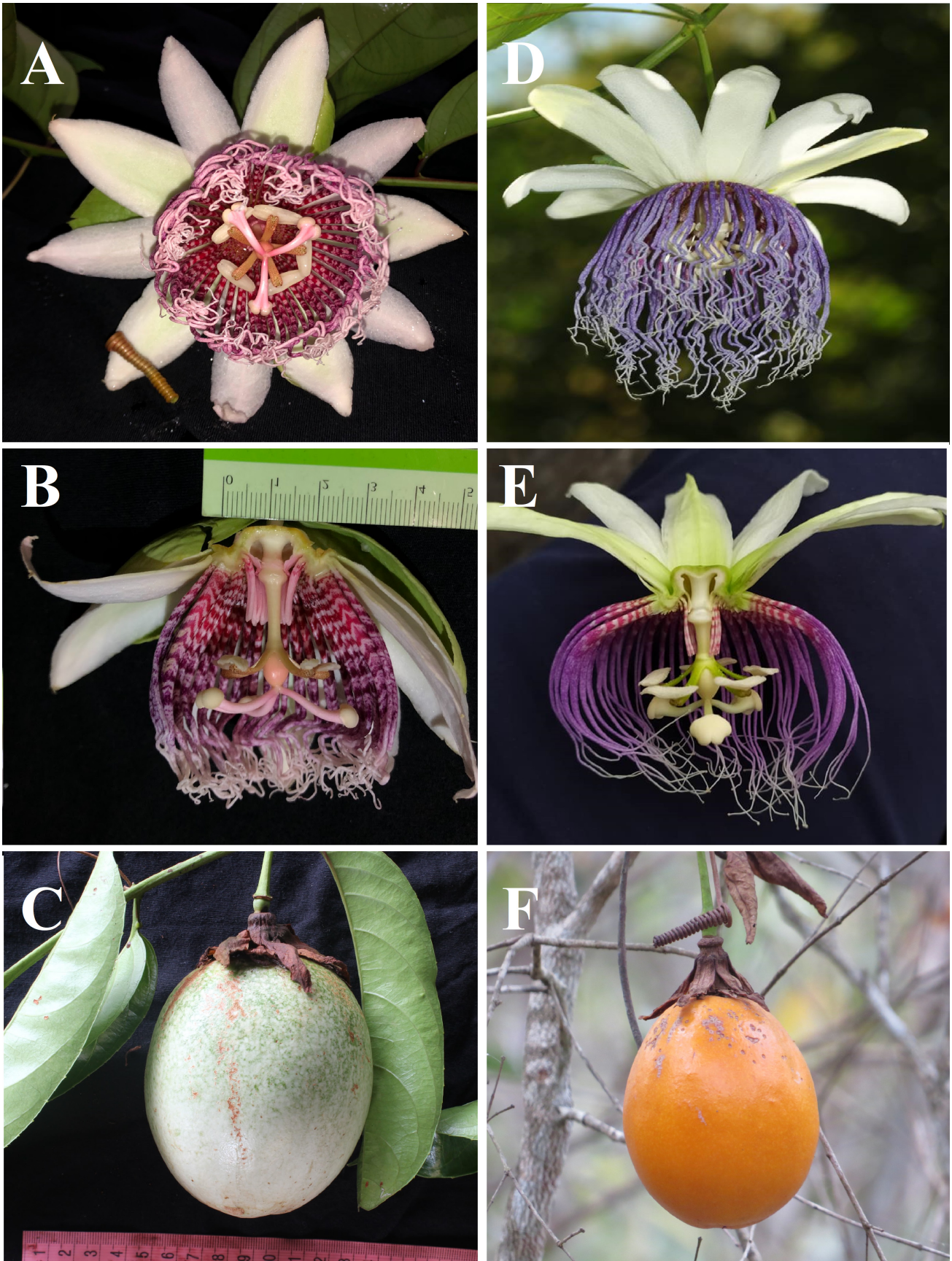
*Passiflora brauliensis* Kuethe, R. Barboza, L. Alvarez sp. nov. (Figures 1, 2 (A–C), 3)

TYPE:—COSTA RICA. Heredia province: Sarapiquí, comunidad de Cacho Negro, 350 m, 10°14'23" N, 83°58'06" W, 3 October 2022 (fl., fr.), Gared Rodríguez-Barboza & L. Alvarez 19 (holotype USJ!; isotype CR!).

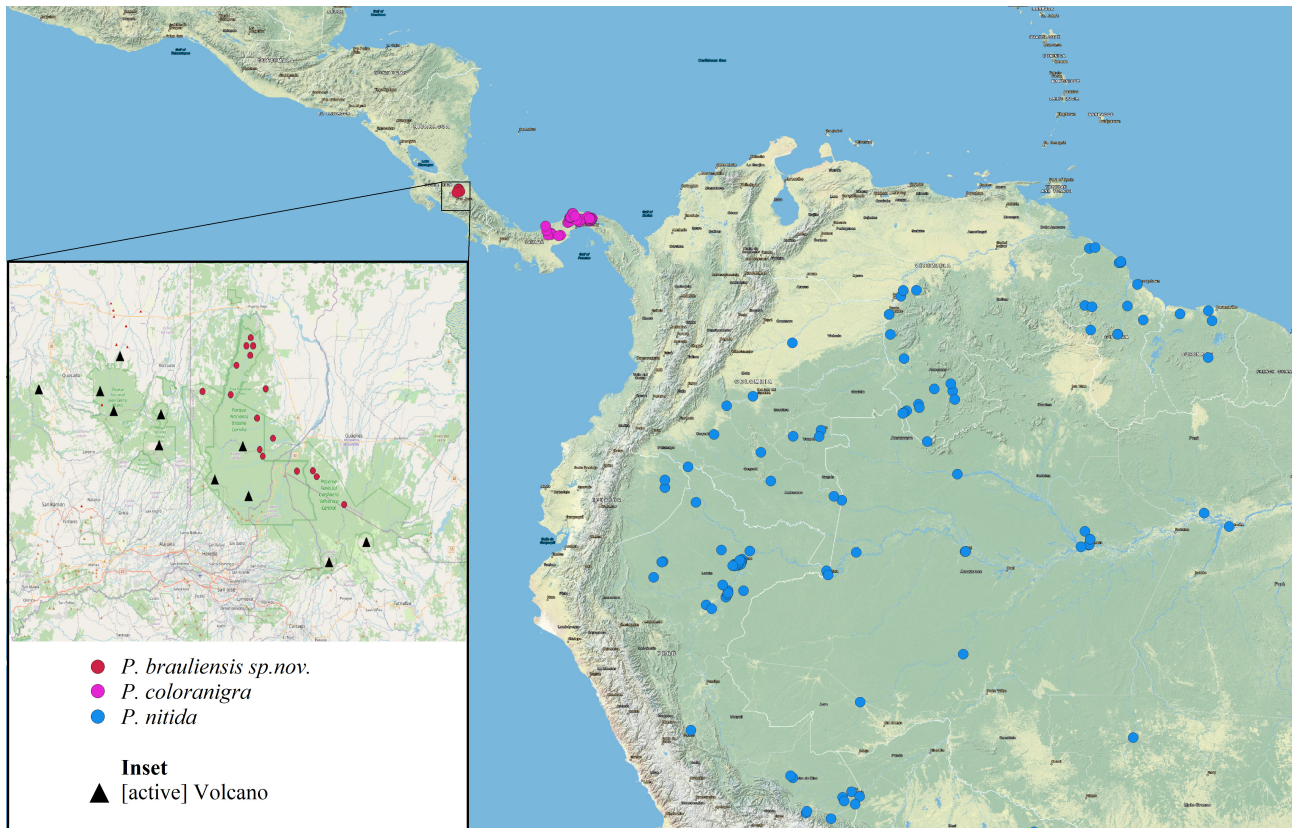
**Diagnosis:**—This new species is similar to *Passiflora nitida* and *Passiflora fissurosa*, from which it differs by the deep pink colour of the corona and operculum (vs. blue-with-white in *P. nitida* or purple in *P. fissurosa*), the reduction of glands on the bracts (vs. glandular in *P. nitida*), and the texture of the older stems (sub-fissurose opposed to woody in *P. nitida* or deeply fissurose in *P. fissurosa*). This species is further distinct by its distribution being restricted to the volcanic forest of Costa Rica (vs. Amazonian regions for *P. nitida* and *P. fissurosa*).



**FIGURE 1.** *Passiflora brauliensis* sp.nov. Compilation of floral and vegetative morphology. Here deduced from Rodríguez-Barboza & L. Alvarez 19.



**FIGURE 2.** Direct comparison between *Passiflora brauliensis* (A–C) and *Passiflora nitida* (D–F). The material for *Passiflora nitida* taken from near the Type location in Venezuela. The material for *P. brauliensis* taken from Cacho Necho—Costa Rica. Photo courtesy of Miguel Molinari, Martin Wettges, Leonardo Alvarez Alcazar and Gared Rodriguez-Barboza.



**FIGURE 3.** Distribution of the *Passiflora nitida* complex. Featuring *P. brauliensis* (Red); *P. coloranigra* (Purple); and *P. nitida* (Blue).

**Description:**—*Plant* large woody liana with tendrils, glabrous throughout; *stems* becoming woody to sub-fissurose when mature, terete, green, younger shoots green, occasionally reddish; *stipules* linear, 1–1.5 cm long, glandular towards the apex, soon deciduous, green; *petioles* 1–2 cm long, green-reddish, reddish above, slightly ribbed, with a single pair of ovate, sessile, green glands positioned 3/4<sup>th</sup> the length to near of the base of the leaf, occasionally slightly closer towards the middle of the petiole, glands 1.6–2.1 mm wide, non-producing; *leaves* simple, ovate-lanceolate to ovate-elliptic, 8–17.5 × 3–6 cm, obtuse at the base, acute to acuminate at the apex, penninerved with a 8–10 pairs of secondary veins, foliar margins glandular serrate, glabrous throughout, mildly coriaceous to membranous, green and glossy on both the adaxial and abaxial surface, most notable at younger stems; *inflorescence* solitary, borne at the younger stems, pendulous, 6–11 cm long; *peduncles* solitary, terete, 2.2–5.3 cm long, green or sometimes reddish in colour, pendent; *pedicel* white, terete, 0.5–1 cm long; *bracts* 3, persistent, light green, broadly elliptic to obovate, 3–5.7 × 2.1–4.5 cm, margin smooth, eglandular or with few small greenish glands towards the apex, slightly concave; *flowers* very showy, 10–13.5 cm in diameter, white with red to pinkish red, very sweetly scented with a citrus-like fragrance; hypanthium campanulate, white, about 1.2–1.5 cm high, 2–2.4 cm wide, glabrous; *sepals* white, rather fleshy in texture, oblong-ovate, 4.3–5.6 × 1.6–2.1 cm, obtuse at apex, dorsally corniculate just below apex with a hooked awn 3–5 mm long; *petals* subequal to sepals, white, narrowly oblong-ovate, 4.1–5.3 × 1.1–1.8 cm, acute-obtuse apex, membranous; *corona* filaments in 5–6 series, reddish pink with multiple white bands; the outer two series the most prominent, stout at the base becoming wavy in upper half, ligulate, 4–6 cm long, reddish-pink proximally becoming more reddish-purple to whitish distally, presenting 4–6 of lighter pinkish to whitish bands in lower half, second series subequal in length and size to the outer series, conspicuously more intense in colour than the outer series, third to fifth series filiform, 0.3–0.8 cm long, reddish-pink with few white bands, slightly curved outwards; operculum filamentose, intense pink, erect-linear or slightly inclined towards the androgynophore, noticeably longer than preceding filaments, 0.7–1.3 cm long, becoming very slightly darker in colour towards the base, inner operculum membranous, becoming slightly filamentose towards the apex, lighter pink, 3–4.5 mm long; limen membranous, recurved, 2–3 mm high, white; androgynophore white to whitish-pink without speckles, 12–15 mm long; *staminal filaments* greenish brown, mottled with red dots distally, 0.9–1.2 cm long; *anthers* white, 1.1 cm long; *ovary* ovoid to ellipsoid, whitish pink, glabrous, ellipsoid to obovoid, 0.5–0.7 cm long; *styles* pink, 0.9–1.2 cm long; *stigma* white, 0.4–0.5 cm; *fruit* obovoid, 8–10.3 cm long, green with white shades when immature, completely yellow to yellowish green when mature, edible; *seeds*

black, triangular-ovate, base truncate, apex acute, inconspicuously striated,  $0.8 \times 1.1$  cm, covered with a transparent aril.

**Phenology:**—This new species has been observed with flowers in July, March and October and with fruits from September to July.

**Distribution and habitat:**—*Passiflora brauliensis* is known only from the Caribbean slope of the Cordillera Volcánica Central in Costa Rica, where it is found primarily within the Heredia and north-western Limón provinces. This large species grows in primary and secondary forest, at an altitude between 50 and 550 meters of elevation. According to Holdridge (1967), this species occurs in two different life zones, which are tropical wet forest (bmh-t) dominated by *Pentaclethra macroleoba* (Willd.) Kuntze (1891: 201) and transitional to premontane volcanic forest with cloud forest-like conditions. Notable populations have been sighted in the La Selva Biological Station and environs, as well as from various transitional regions where it was found in the premontane wet forest within the protectorate of the Braulio Carrillo National Park. This species was observed reaching maturity from subcanopy to canopy in the forest, with the flowers appearing mostly high up within the canopy. It was also found growing along the forest edges and roadsides, but most of the observations came from plants growing near rivers.

**Etymology:**—This species is named after the Braulio Carrillo National Park in Costa Rica, location where it was first sighted.

**Conservation notes:**—This new species is presently known from 15 collections (10 of which recorded from herbarium), which plot to an Area of Occupancy (AOO) of about 28 km<sup>2</sup> and an Extent of Occurrence (EOO) of 251 km<sup>2</sup>. This scales *Passiflora brauliensis* EN (Endangered) under criteria B1ab(i, iii) and B2a(ii) of the IUCN (2022). Its restricted and endemic distribution to the Caribbean slope of the Cordillera Volcánica Central in Costa Rica, and the extensive loss of habitat due to the rapid change of land use from mostly the period between 1950 to 1990 (Sader & Joyce 1988, Evans 2010), fully testifies this outcome. Although the species is present in land which is currently part of the protected San Juan-La Selva Biological Corridor, there remains high levels of ongoing illegal logging within in the area and the populations presently reported are scattered and discontinuous or fragmented.

**Paratypes:**—COSTA RICA. Heredia: Sarapiquí, Finca La Selva, 15 September 1980, *James mallet* 6 (CR); Heredia: Sarapiquí, Horquetas, 400 m, 28 November 1983 (fr.), *N. Zamora* 409 (CR); Heredia: Sarapiquí, Reserva Ecológica Gavián Blanco. 26 November 2004 (fr.), *O. Vargas* 1127 (LSCR); Heredia: Finca La Selva, the OTS Field Station on the Río Puerto Viejo, just E of its junction with the Río Sarapiquí, 100 m. 7 April 1982, *Hammel* 11602 (MO); Heredia: Puerto Viejo de Sarapiquí, La Selva Field Station, central trail line 3000. 10°25'N, 84°00'W, July 12 1979, *John smiley* 10 (IRCV); Heredia: Sarapiquí, Near Puerto Viejo, March 1979, *L. E. Gilbert* s.n. (TEX); Heredia: Sarapiquí, Finca La Selva, The OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, banks of El Salto, 2800 line of S boundary, elevation just about 100 m, 14 april 1981 (fr.), *James Folsom* 9763 (DUKE); Limón: Pococí, Guápiles, PN. Braulio Carrillo, Sector Quebrada González, 500 m, 10°10'0"N, 79°27'00.0"W, 26 May 2001 (fr.), *A. Estrada* 3025 (CR); Limón: Pococí, Guápiles, Área no protegida, Teleférico del Bosque Lluvioso, 500 m, 10°11'0"N, 83°55'0"W, 28 May 2001 (fr.), *A. Estrada* 3030 (CR).

## Discussion

According to the current taxonomic classification, *Passiflora brauliensis* should be placed within subgenus *Passiflora*, supersection *Laurifolia*, for it having filiform linear stipules, ovate to ovate-oblong unlobed leaves, a single pair of opposite petiolar glands, free bracts and pendent flowers with a conspicuous corona (Feuillet & MacDougal 2003). Within this group, *Passiflora brauliensis* closely resembles *Passiflora nitida*, *Passiflora coloranigra* and *Passiflora fissurosa* in vegetative and morphological traits, which led to these species commonly being misidentified for the overarching *Passiflora nitida*. All the above-mentioned species share the large, pendent inflorescence; having flowers with 5–8 coronal series of which the outer two are subequal in length; and an operculum that stands about 8–10 mm tall. Within this alliance, however, *Passiflora brauliensis* and *Passiflora nitida* both have fleshy white petals and sepals, while in *Passiflora fissurosa* and *Passiflora coloranigra* the petals and sepals are a deep purple. Vegetatively, all these four species are extremely similar, showing only minor differences in vestiture of the bark, size and location of the petiolar nectaries, and serration of the foliar margin (see Table 1).

Aside from the morphological differences outlined in the table below and elaborated in Figure 2, what truly marked the final decision to describe *Passiflora brauliensis* over *Passiflora nitida* or its variants, was the uniqueness of its distribution and habitat. Fruiting accessions of a "*Passiflora aff. nitida*" have been collected by *O. Vargas*

1127 and stored at LSCR, who tentatively questioned the authenticity of this being true *Passiflora nitida*. This was further implicated by the fact that all the specimens stored at the abovementioned herbaria were either in sterile state or presented a fruiting specimen. The absence of distinct flowers in any of the herbarium vouchers studied made the distinction between *P. nitida* and the new *P. brauliensis* greatly difficult. The only specimens filed under “*Passiflora nitida*” displayed on databases such as Tropicos or SpeciesLink all hail from this one area in the Heredia province, which further questions the legitimacy of *Passiflora nitida* having been “naturalized” from an introduced source. Instead, this focused distribution suggests rather a narrow natural distribution that is restricted to the premontane eastern flanks of the central Costa Rican volcanoes. This would also explain its complete absence (or the apparent absence of “*P. nitida*” for that matter) in the territories outside of this restricted distribution, as this habitat isn’t contiguous and being flanked by the flat and marshy plains of the llanuras de San Carlos north of Volcán Arenal going into Nicaragua; or by the non-volcanic limestone hills of the Talamanca mountains going south into neighboring Panama (see Figure 3).

This also poses one final, interesting observation regarding the species from the *Passiflora nitida* complex: that being that *Passiflora brauliensis* is the only member of this unofficial group that inhabits volcanic terrains. This is important as volcanic areas tend to have a distinct soil chemistry, being markedly more acidic and allophane enriched, especially when supplemented with the periodic addition of fresh tephra’s (Delmelle *et al.* 2015). Limestone areas, however, tend to have more alkaline soils enriched with calcium-carbonates and fine clays. Studying the wide distribution of *Passiflora nitida* and its allies, they were primarily collected from non-volcanic regions, including: the Amazonian regions, the Guyanan regions, the Brazilian Cerrado and the premontane transitional (non-volcanic) ranges of the Andean-Amazon metamorphic belt (Tropicos 2022). *Passiflora coloranigra*, the only other member of this alliance also present in the Central American isthmus, can only be found across the limestone hills and lowlands of Panama, well away from the country’s only active volcano: Volcán Barú. This would fully explain why true *Passiflora nitida* cannot be present in the Braulio Carillo National Park and indicates that, as per the physical and chemical attributes of the habitat, *Passiflora brauliensis* is distinctly different from *Passiflora nitida*.

**TABLE 1.** Comparison between the nearest related species of *Passiflora brauliensis* sp. nov.

	<i>P. nitida</i> Kunth	<i>P. brauliensis</i> sp. nov.	<i>P. fissurosa</i> Souza	<i>P. coloranigra</i> Kuethe & Meerman
Distribution	Amazonian and Cerradan South America	Central Volcanic Mountain Range of Costa Rica	Central Amazonas, Brazil	Central Panama
Habitat	Amazon and premontane Andes	Volcanic transitional forest	Riparian rainforest, brookforest	Limestone hills and lowland rainforest
Mature stem	Wooded	Sub-fissurose	Thick-fissurose	Wooded
Leaf	Oblong-ovate	Ovate-lanceolate to ovate-elliptic	Lanceolate-ovate	Ovate
Petiole nectaries	Top of petiole, auriculate	¾th above the middle of petiole, globose	Top of petiole, globose	Middle of petiole, globose to subglobose
Bracts	Green, coriaceous, margins glandular serrate	Light green, sub-coriaceous to membranous, margins smooth	Green, coriaceous, margins smooth to slightly serrate	Red, coriaceous, margins glandular to glandular serrate
Petal colour	White	White	Purple	Purplish-red
Corolla colour	Blue to purple	Pink to red	Purple	Dark purple-red
Ovarian colour	Greenish-yellow	Pink	Whitish-green	Red
Opercular structure	Erect, singular, white	Erect, double, pink to reddish	Erect, double, vinaceous to white	Erect, singular, dark reddish-purple
Fruit and pericarp	Deep yellow to orange, thin.	White to light greenish-yellow, thick	Green to greenish-yellow, thick	Deep purple to red, thin.

Although *Passiflora nitida* is found to be variable within its natural distribution, featuring various colour intensities for its corona, shape and size of the bracts or foliar characteristics, the members of this alliance from within the Central American isthmus show little to no intermediate forms. This further amplifies that we consider three well-delineated concepts within this alliance that do not progressively change. These being: *Passiflora nitida* for (sub)Amazonian/Guyanese South America; *P. coloranigra* for the central limestone regions of Panama; and *P. brauliensis* for the eastern volcanic rain forests of Costa Rica. The distribution of these species is greatly allopatric, severely doubting the presence of contiguous genetic interchange between these species but rather suggesting an extreme case of parallel evolution under a common pollinator. It would be interesting to further experiment with this possible genetic incompatibility by growing all three constituents within a single collection under controlled conditions and study the F2 hybridized products between these three.

## Acknowledgements

We would like to thank John Messley, Andy Jones and Randy Hendersson for taking photographs of the species and bringing this to our attention. We are sincerely thankful to Eva Benavides, who so passionately joined me to Costa Rica, throughout many dirt roads and long forest hikes, searching for this species in the Braulio Carrillo National Park. We thank the curators from the Costa Rican National Herbarium and Dr. Luis A. Fournier Origgi for kindly giving us access to the herbarium collections that were of particular importance for this study. We would also like to thank the other curators of the herbaria listed for providing access to the collections for studying the specimens on file, or digitizing the vouchers so we could study the material remotely. We also like to thank Cornelis Yacha for accommodating us at the Ecolodge in the park during our time in the field, and providing additional information and notes on the conservation and population of the species and Travis Fabián Fernández for the help in the field work. As always, we would like to thank the reviewers for their expertise and suggestions to help improve this manuscript.

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