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Stigmatodon enigmaticus (Bromeliaceae, Tillandsioideae), a new lithophytic species from the Campos Rupestres within the Brazilian Atlantic Forest

DAYVID R. COUTO^{1,*}, PAULO M. GONELLA^{1,2} & ANDREA F. COSTA³

¹Instituto Nacional da Mata Atlântica (INMA), Av. José Ruschi, 4, 29650-000, Santa Teresa, Espírito Santo, Brazil

✉ dayvidcouthotmail.com; <https://orcid.org/0000-0002-9563-8001>

²Universidade Federal de São João del-Rei, Campus Sete Lagoas, Rodovia MG 424, km 47, Sete Lagoas, Minas Gerais, 35701-970, Brazil

✉ pmgonella@gmail.com; <https://orcid.org/0000-0001-8332-5326>

³Departamento de Botânica, Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, São Cristóvão, Rio de Janeiro, 20949-040, Brazil

✉ afcosta@acd.ufrj.br; <https://orcid.org/0000-0002-9200-4222>

*Author for correspondence

Abstract

Stigmatodon enigmaticus is described and illustrated as a new lithophytic taxon from the quartzitic Campos Rupestres within the biodiversity hotspot of the Atlantic Forest, in Minas Gerais state, Southeastern Brazil. This puzzling new species presents floral features that are unique in the genus as they are associated with ornithophily, as in most *Vriesea*, contrasting with the chiropterous features of all previously known *Stigmatodon* species. It is assigned to the “*S. limae* group”, being most similar to *S. vexatus*, with which it is compared. *Stigmatodon enigmaticus* is a microendemic species and is here assessed as Critically Endangered due to its restricted habitat, reduced population size, and threats from invasive species. This finding adds to several others that reinforce the relevance of the currently unprotected Serra do Padre Ângelo as a priority for conservation.

Keywords: Brazilian Flora, bromeliads, conservation, rocky outcrops, Vrieseinae

Introduction

The Atlantic Forest is the most diverse Brazilian phytogeographic domain regarding its flora and is considered a hotspot for biodiversity conservation (Myers *et al.* 2000, BFG 2021). Also, it is one of the main centers of diversity of Bromeliaceae in the world, with many genera endemic to this domain (see Martinelli *et al.* 2008). Species of Bromeliaceae subfamily Tillandsioideae Harms (1930: 115) are relevant for diversity in different Atlantic ecosystems. In forest ecosystems, for example, epiphytic species of the genus *Vriesea* Lindley (1843: 11) predominate (Freitas *et al.* 2016). In contrast, for non-forested open ecosystems, such as rocky outcrops, species from the genera *Alcantarea* (É. Morren ex Mez) Harms (1929: 802), *Stigmatodon* Leme, G.K. Brown & Barfuss (Barfuss *et al.* 2016: 56), and *Waltillia* Leme, Barfuss & Halbritter (Leme *et al.* 2017a: 29) are predominant (Kessous *et al.* 2020).

The genus *Stigmatodon* currently comprises 34 species (including the new species described here) that are endemic to eastern Brazil, where they can be found on granitic/gneissic inselbergs within the Atlantic Forest, but also on the Quartzitic Campos Rupestres of the Espinhaço Range (Barfuss *et al.* 2016; Couto *et al.* 2022; Leme *et al.* 2022a). According to Couto *et al.* (2022), two informal groups are recognized within the genus: *Stigmatodon* s.str. (*sensu* Barfuss *et al.* 2016), and the “*Stigmatodon limae* (Smith 1970: 181) D.R. Couto & A.F. Costa in Couto *et al.* (2022: 354) group”. *Stigmatodon* s.str. is characterized by the presence of semixeromorphic to xeromorphic coriaceous leaves, leaf blades with truncate margins, stamens arranged three on each side of the corolla at anthesis, and tubo-laciniate stigma type (Barfuss *et al.* 2016). This group includes 21 epilithic species, *i.e.*, they grow exclusively on vertical rock wall habitats on inselbergs from southeastern Brazil (states of Bahia, Espírito Santo, Minas Gerais, and Rio de Janeiro) (Couto *et al.* 2022; Leme *et al.* 2022a).

On the other hand, the “*Stigmatodon limae* group” is morphologically characterized by small-sized, night-blooming species, with inflorescences usually simple (Couto *et al.* 2022; Leme *et al.* 2022a), and with three different stigma

types: tubo-lacinate type II, convolute-blade (the vriseoid type II), and convolute-blade type III (stigmatontoid type III) (Leme *et al.* 2022a). This group includes 13 generalist species, in terms of habitat [epilithic, saxicolous, and rarely epiphytic on trunks of *Vellozia* (Velloziaceae)], inhabiting different rocky outcrops types (inselbergs and quartzite outcrops), on different rock inclinations, in southeast (Espírito Santo, Minas Gerais) and northeast Brazil (Alagoas, Bahia, and Pernambuco) (Leme & Siqueira Filho 2006a; Couto *et al.* 2022). Seven of the 13 species are endemic to the inselbergs and six are restricted to Campos Rupestres (including the new species described here).

Within the Atlantic Forest, the quartzitic Campos Rupestres occupy a smaller area (Mello-Silva 2018). The “Atlantic Campos Rupestres” are found in the oriental and southernmost Espinhaço Range, in the Iron Quadrangle (Carmo & Jacobi 2013), in isolated mountains connecting the Espinhaço Range to the Mantiqueira Range, such as Serra de São José (Alves & Kolbek 2009, Vasconcelos 2011), and in the Serra do Ibitipoca and Serra Negra, part of the Mantiqueira Range (Abreu *et al.* 2011, Forzza *et al.* 2013). It was not until very recently that areas of Campos Rupestres were identified in easternmost Minas Gerais, in the quartzitic João Pinto Formation, namely the Serra do Padre Ângelo (Gonella *et al.* 2015, Mello-Silva 2018), Pico da Aliança (Lopes *et al.* 2016), and Serra da Onça (this one included in the Sete Salões State Park; Siniscalchi *et al.* 2016).

In the past decade, at least 31 new plant species have been described for these easternmost Campos Rupestres and associated vegetation. These new taxa belong to different angiosperm lineages, including Asteraceae (Siniscalchi *et al.* 2016, Loeuille & Pirani 2016, Loeuille & Pirani 2019, Antar *et al.* 2021b, Oliveira *et al.* 2022), Begoniaceae (Kollmann 2020, Kollmann & Gonella 2021), Droseraceae (Gonella *et al.* 2015), Eriocaulaceae (Andrino & Gonella 2021), Lamiaceae (Antar *et al.* 2021a), Lythraceae (Cavalcanti *et al.* 2022), Melastomataceae (Goldenberg *et al.* 2022), Orchidaceae (Miranda 1999, Campacci 2014, 2015, Harding & Bohnke 2015), and Passifloraceae (Mezzonato-Pires *et al.* 2021). Among the families with novelties described for these mountains, Bromeliaceae stands out, with nine species described so far: *Aechmea timida* Leme (Leme *et al.* 2014: 67), *Alcantarea occulta* Leme (Leme & Kollmann 2013: 10), *A. nana* Leme (Leme *et al.* 2014: 72), *Krenakanthus roseolilacinus* (Leme, 2015: 284) Leme, Zizka & Paule *in* Leme *et al.* (2022b: 145), *Orthocryptanthus arcanus* (Leme *et al.* 2020: 191) Leme, Zizka & Paule *in* Leme *et al.* (2022b: 147), *O. santaritensis* (Leme, S. Heller & Zizka *in* Leme *et al.* 2017b: 78) Leme, Zizka & Paule *in* Leme *et al.* (2022a: 147), *O. vasconcelosianus* (Leme, 2015: 287) Leme, Zizka & Paule *in* Leme *et al.* (2022b: 148), *Vriesea sanctaparecidae* Leme *in* Leme & Kollmann 2013: 35), and *Stigmatodon vexatus* (Leme, 2016: 137) Leme & D.R. Couto *in* Leme *et al.* (2022a: 13). Such a high number of newly described taxa in this historically neglected region reinforces the importance of floristic studies for biodiversity prospecting, as well as highlights the easternmost campos rupestres as a region of extreme biological importance, being a priority for the creation of a Protected Area.

During field expeditions related to the project “Rupicolous Ecosystems of the Atlantic Forest”, of the National Institute of the Atlantic Forest (INMA—Santa Teresa, Espírito Santo, Brazil), a puzzling new species of rupicolous bromeliad was found, here assigned to *Stigmatodon*. This taxon is endemic to quartzitic rocky outcrops (Campos Rupestres) areas within Atlantic Forest, located in Serra do Padre Ângelo, Conselheiro Pena municipality, eastern Minas Gerais state. In this work, this new taxon is described, illustrated, has its conservation status assessed, and its taxonomic affinities with *Stigmatodon vexatus* are discussed.

Methods

Fieldwork to Serra do Padre Ângelo has been carried out since 2013. Specimens were collected, herborized, and deposited in the herbaria MBML and R (acronyms according to Thiers, continuously updated). The morphological data were obtained through analysis of herbarium specimens and field observations of its population. The description and illustrations of the new taxon followed the usual botanical terminology (Stearn 1973, Radford 1986), and for the family (Smith & Downs 1977, Scharf & Gouda 2008).

The conservation status was applied according to the IUCN Red List criteria (IUCN 2012), where the extent of occurrence (EOO) and area of occupancy (AOO) analysis were obtained with the GeoCat tool (Bachman *et al.* 2011).

Taxonomy

Stigmatodon enigmaticus D.R. Couto, Gonella & A.F. Costa, *sp. nov.* (Figures 1–2)

Stigmatodon enigmaticus differs from *S. vexatus* by the more numerous leaves (15–25 vs. 10–12 in number), distinctly smaller leaf blade ($6\text{--}8.5 \times 1.5\text{--}2.3$ cm vs. $13\text{--}14 \times 2.8\text{--}3.7$ cm), with acuminate apex (vs. caudate), floral bracts red (vs. green), flowers with diurnal anthesis (vs. nocturnal), greenish-yellow sepals (vs. green), yellow petals (vs. greenish-yellow), and stamens and stigma exceeding the corolla (vs. shorter than the corolla).

Type:—BRAZIL. Minas Gerais: Conselheiro Pena, Serra do Padre Ângelo, Serra do Pinhão, campo rupestre, 1,300 m elevation, 2 May 2021 (flowered in cultivation in November 2021), *P.M. Gonella 2965, D.P. Cordeiro, G.A. da Silva, P.R. Bartholomay, J.C. Ribeiro & L. Medeiros* (holotype MBML!).

Description:—*Plant* rupicolous, heliophytic, 21–35.5 cm tall when flowering, propagating by basal axillary shoots. *Leaves* 15–25, forming a utriculiform rosette; *sheath* ovate to elliptic, $6\text{--}8.5 \times 4\text{--}5.5$ cm, purplish to purplish-green distally, castaneous at the base, densely lepidote on both sides, chartaceous; *blade* narrowly triangular, $6\text{--}8.5$ cm long, $1.5\text{--}2.3$ cm wide at the base, green to dark reddish, densely lepidote on both sides, forming white crossbands on adaxial surface, suberect to spreading-recurved, revolute along the margins (under water stress), apex acuminate. *Peduncle* suberect or curved at the base, (16-)23–30 cm long, 1.2–1.8 mm in diameter, green, glabrous; *peduncle bracts* erect, exceeding the internodes, imbricate, elliptic, apex rounded then acuminate to caudate, $1.7\text{--}3 \times 1.4$ cm, the lower ones subfoliaceous, green, the upper ones red, lepidote on both sides, more sparsely lepidote near the margins, densely white lepidote near the apex. *Inflorescence* simple, 4–12 cm long, suberect, with apical sterile bracts, 3–7 flowered; *main axis* slightly geniculate, 2.8–3 mm in diameter, green, glabrous, internodes 5–9(-16) mm; *floral bracts* suborbicular, apex broadly obtuse, $1.7\text{--}2.2 \times 1.0\text{--}1.7$ cm, ecarinate, secund with the flowers at anthesis, red, exceeded by the sepals, densely lepidote abaxially, adaxially glabrous, coriaceous. *Flowers* distichous, secund at anthesis, diurnal, 4.0–5.5 cm long; *pedicel* green, 4.5–7.2 mm long; *sepals* elliptic, apex obtuse, $20\text{--}23 \times 10\text{--}11$ mm, greenish-yellow, ecarinate, glabrous, coriaceous, free; *petals* linear-oblong, $3.0\text{--}3.5 \times 0.5\text{--}0.8$ cm, apex rounded to emarginate, suberect with spreading apex, yellow, glabrous, connate at the base to 0.9–1.5 mm, forming a prevailing tubular corolla; *petal appendages* $6\text{--}7.6 \times 2\text{--}2.5$ mm, spatulate, apex rounded, distally free for 2.5–3.2 mm; *stamens* exerted for 2–3.8 mm; *anthers* oblong in outline, 4–5 mm long, obtuse, dorsifixed near the base; *filaments* complanate, 25–31 mm long, pale yellow, adnate to the petals for 4.3–5 mm; *ovary* superior, 4.2–5.4 mm long; *style* 30–35 mm long; *stigma* convolute blade type (the vriseoid type II), exceeding the corolla for 8–9 mm, green, *ca.* 1.4 mm in diameter. *Capsules* unknown.

Phenology:—Collected with flowers in October (*in situ*), and in November and December (in cultivation).

Distribution and ecology:—*Stigmatodon enigmaticus* is a lithophyte on quartzitic rocky outcrops (Fig. 1C) within the Atlantic Forest, in the municipality of Conselheiro Pena, eastern Minas Gerais state, Brazil. So far, the species is only known from the type locality at Serra do Pinhão (above 1,250 m elevation), part of Serra do Padre Ângelo (Fig. 1A). At the type locality, the species forms a small and sparse population, exposed to full sunlight, growing in crevices or fissures, or directly on bare rock, usually on horizontal or inclined quartzitic rocky outcrops (Fig. 1), surrounded by herbaceous and shrubby vegetation (Fig. 1B, C). The floral characteristics of this species, i.e., floral bracts red, flowers with diurnal anthesis, yellow petals, and stamens and stigma exceeding the corolla (Fig. 1F–H), allows us to suggest that it is possibly pollinated by hummingbirds (Neves *et al.* 2020), an unusual characteristic for the genus *Stigmatodon* (its species have nocturnal flowers and bat-pollination). This observation raises new and promising perspectives for evolutionary, morphological, and taxonomic studies in *Stigmatodon*.

Preliminary conservation status:—Critically Endangered (CR): B2ab(iii). *Stigmatodon enigmaticus* is a microendemic species with an Area of Occupancy (AOO) of 4 km², found only in Serra do Pinhão (Fig. 1 A–B). While the rock outcrop where it is found is relatively protected from fires by the irregular topography, the surroundings have been severely transformed in the past decades, from the original matrix of Semideciduous Seasonal Forest to pastures for cattle farming. Fires for pasture renovation are regular in the area, as is the active conversion of the few remnants of secondary forest into pastures, with the use of fire, one of such observed during one of the expeditions to the area in October 2022. Similar criminal fires resulted in a wildfire of great proportions that affected the neighboring Pico do Padre Ângelo in September 2020, affecting many of its endemics (Andrino & Gonella 2021, Kollmann & Gonella 2021, Gonella *et al.* 2022). The frequent fires in the area facilitated the invasion of the rocky outcrops by alien grass species, such as *Melinis minutiflora* Beauvois (1812: 54), which can be found on the rocky outcrop that *S. enigmaticus* inhabits. The area where the species is found is not protected by any sort of Protected Area but should be recognized

as a priority for conservation given the exceptional biodiversity and the relevance of the ecosystem services provided by the mountainous relief and native vegetation of Serra do Padre Ângelo, such as water cycle, climate balance, and pollinators, among others. Finally, less than 20 mature individuals could be located in the area, suggesting that the population is relatively small, as is common with microendemic species from the Campos Rupestres (Conceição *et al.* 2007). Given the aforementioned characteristics and threats, we have preliminarily assessed *S. enigmaticus* as Critically Endangered based on the categories and criteria of IUCN (2012).



FIGURE 1. *Stigmatodon enigmaticus*. **A.** General view of the landscape of campos rupestres and forests at type locality at Serra do Pinhão, part of Serra do Padre Ângelo (Conselheiro Pena, MG). **B.** Quartzitic rocky outcrops, habitat of *S. enigmaticus*. **C.** Habit of *S. enigmaticus*. **D.** Flowering specimen of *S. enigmaticus* (specimen Couto *et al.* 6625, paratype). **E.** Detail of leaves and bracts of the base of the inflorescence. **F.** Side view of the inflorescence of a cultivated specimen (specimen Gonella *et al.* 2965, holotype), showing the red bracts and yellow perianth. **G.** Lateral view of the flower. **H.** Front view of the flower, showing the position of stamens and stigma. (Photos: A–C, E, G, H by PMG; F by DRC; D by Lucian Medeiros).

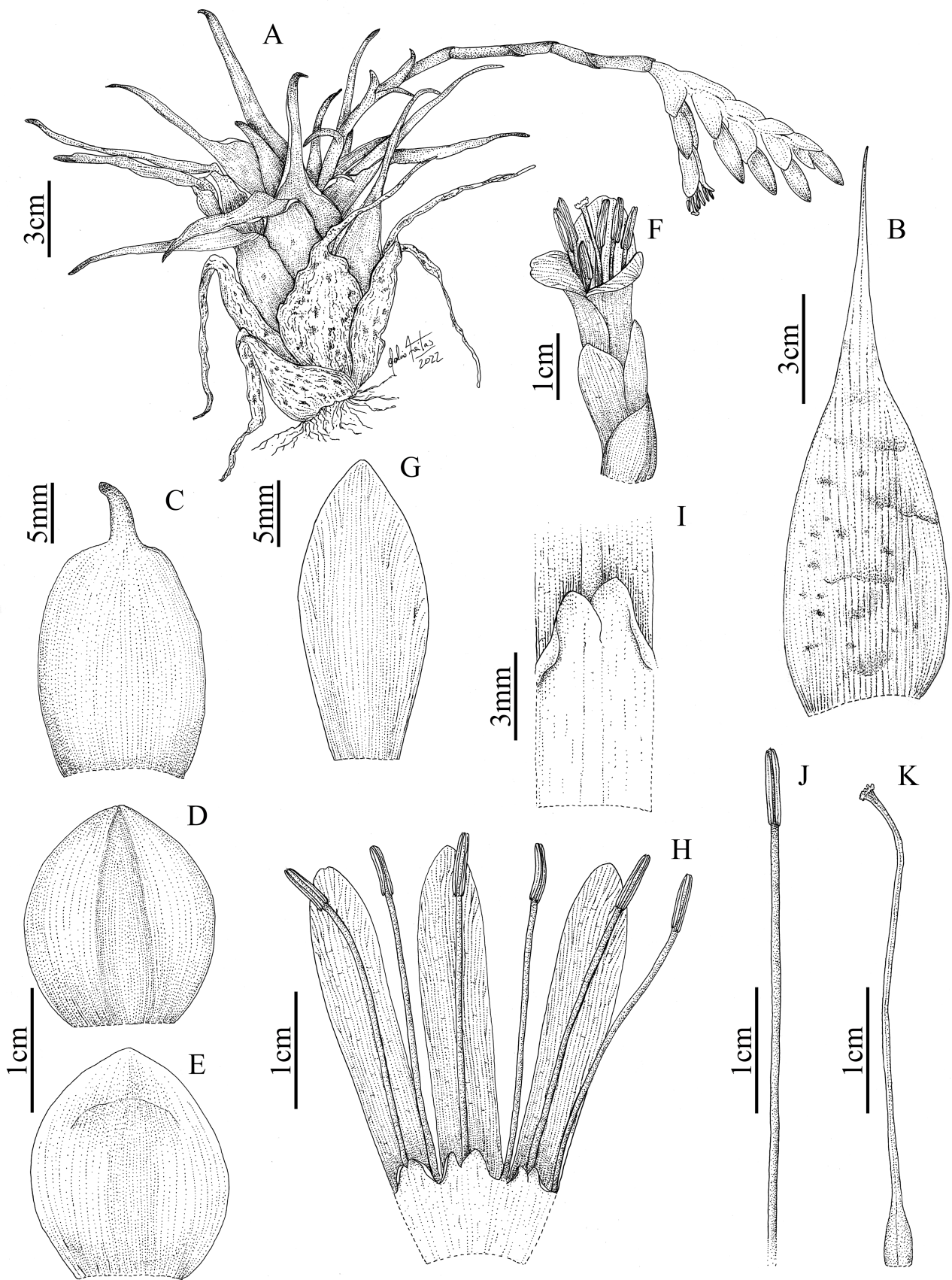


FIGURE 2. *Stigmatodon enigmaticus*. A. Habit. B. Leaf. C. Peduncle bract. D. Floral bract, adaxial surface. E. Floral bract, abaxial surface. F. Flower. G. Sepal. H. Petals, stamens and appendages at the base. I. Details of basal petal appendages. J. Filament and anther. K. Pistil. Drawing by Joelcio Freitas based on the holotype *P.M. Gonella 2965* (MBML).

Etymology:—This new species was discovered in May 2021, when only sterile specimens were observed, and its vegetative characteristics pointed to *Stigmatodon*. However, when in flower, its red bracts and yellow sepals and petals, common in *Vriesea* and so far not reported for *Stigmatodon*, raised the question of its generic placement. This puzzling combination inspired the epithet, from the Greek *aenigma*, meaning “riddle”, or “enigma”.

Additional specimens examined (paratypes):— BRAZIL. Minas Gerais: Conselheiro Pena, Serra do Padre Ângelo, Serra do Sossego, campo rupestre, 1,250 m elevation, 15 October 2022, (fl.), D.R. Couto 6625, P.M. Gonella, L. Medeiros, D. Cordeiro & L. Magalhães (R!); *ibidem*, 1,350 m elevation, 13 May 2022, P.M. Gonella 3521, E.P. Fernandez, G. Crispin, G.A. Queiroz & J.C. Ribeiro (MBML!).

Discussion:—*Stigmatodon enigmaticus*, resembles the small rupicolous species of “*Stigmatodon limae* group” (Fig. 1 C), from which it is easily distinguished by its red floral bracts, as well as by the yellow and linear-oblong petals, and the exerted stamens and stigma.

Among the species of the *S. limae* group, this new species is morphologically most similar to *S. vexatus*, which is endemic to the Pico da Aliança, an emblematic quartzitic mountain distant about 20 km from the type locality of *S. enigmaticus*, in the neighboring municipality of Alvarenga. *Stigmatodon enigmaticus* can be distinguished from *S. vexatus* by its ovate to elliptic leaf sheaths (*vs.* broadly ovate), which are purplish to purplish-green toward the apex and castaneous at the base (*vs.* vinaceous brown adaxially), leaf blade with revolute margins (under water stress *vs.* flat to involute), peduncle longer (up to 30 cm *vs.* up to 13 cm), larger flowers (4.0–5.5 cm *vs.* ca. 3.2 cm), and obovate to elliptic sepals (*vs.* oblong-elliptic; data on *S. vexatus* from Leme 2016).

For the *Stigmatodon limae* group, three stigma types have been recognized recently (see Leme *et al.* 2022a), which are relevant to the *Stigmatodon* taxonomy: tubo-laciniate type II, observed in *S. rosulatus* (Leme 2012: 10) Leme, G.K. Br. & Barfuss (*in* Barfuss *et al.* 2016: 58) and *S. ilhanus* Leme & D.R. Couto (*in* Leme *et al.* 2022a: 7); (ii) convolute-blade (the vriseoid type II), observed in *S. freicanecanus* (Siqueira & Leme, 2006a: 377) D.R.Couto & A.F.Costa (*in* Couto *et al.* 2022: 352), *S. oliganthus* (Baker, 1887: 345) D.R.Couto & A.F.Costa (*in* Couto *et al.* 2022: 354), *S. vellozicolus* (Leme & Siqueira 2006b: 406) D.R.Couto & A.F.Costa (*in* Couto *et al.* 2022: 354), *S. vexatus* and *S. enigmaticus*; and (iii) convolute-blade type III (stigmatodontoid type III), observed in *S. andaraiensis* (Leme 2012: 16) D.R.Couto & A.F.Costa (*in* Couto *et al.* 2022: 352), *S. itamarajuensis* Leme, D.R. Couto & L. Kollmann (*in* Leme *et al.* 2022a: 9), *S. limae* (Smith 1970: 181) D.R.Couto & A.F.Costa (*in* Couto *et al.* 2022: 354), and *S. zonatus* (Siqueira & Leme 2006a: 374) D.R.Couto & A.F.Costa (*in* Couto *et al.* 2022: 354).

The floral features of *S. enigmaticus*, i.e., red bracts and yellow perianth, exerted stamens and stigma, and diurnal anthesis, are unique in the genus *Stigmatodon* but common in *Vriesea* (Costa *et al.* 2014, Neves *et al.* 2020, Couto *et al.* 2022). These characteristics, associated with hummingbird pollination syndrome (ornithophily), seem to be the ancestral state among bromeliads, while bat pollination (chiropterophily) originated multiple times in the family as a whole (Aguillar-Rodríguez *et al.* 2019), as well as in *Vriesea* (Kessler *et al.* 2020; Neves *et al.* 2020), and is supported as an ancestral state in *Stigmatodon* species (Couto *et al.* 2022). All the 33 previously known species of *Stigmatodon* bear chiropterophilous flowers, therefore the floral features of *S. enigmaticus* could result from the retention of the ancestral state or a reversion to it, a hypothesis that needs to be tested with molecular phylogeny.

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