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Taxonomic revision of the genus Schaueria (Acanthaceae)

Ana Luiza A. Côrtes^{1,2} · Thomas F. Daniel³ · Alessandro Rapini¹

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Abstract The genus Schaueria (Acanthaceae) has not been comprehensively treated for more than 150 years. Here, we propose a recircumscription of Schaueria based on molecular phylogenetic results and present a taxonomic revision of the genus. We recognise 14 species, which occur mainly in semideciduous montane forests, rain forests, and restingas, from Bahia to Rio Grande do Sul states, Brazil. Three new species are described in the genus—S. hirta, S. pyramidalis, and S. thyrsiflora-and six are excluded from the genus. Four new combinations and two new synonyms are proposed, and five lectotypes are designated. Many species of Schaueria are endangered, critically endangered or vulnerable, and two species are assessed as near threatened because of continuous decline of habitat quality and extent of Atlantic forest. We provide a key to identify the genera of the Tetramerium lineage that occur in South America, and present descriptions, illustrations, and comments for the 14 species of Schaueria, as well as a key to identify them.

Keywords Atlantic forest · Conservation assessment · *Justicia* · Molecular phylogenetics · Morphology

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Ana Luiza A. Côrtes analuiza.cortes@gmail.com

- ¹ Programa de Pós-graduação em Botânica, Universidade Estadual de Feira de Santana, Avenida Transnordestina s/n, Novo Horizonte, Feira de Santana, Bahia 44036-900, Brazil
- ² Faculdade Guanambi, Avenida Governador Nilo Coelho, s/n, São Sebastião, Guanambi, Bahia 46430-000, Brazil
- ³ Department of Botany, California Academy of Sciences, 55 Music Concourse Dr., Golden Gate Park, San Francisco, CA 94118, USA

Introduction

Schaueria Nees (Acanthaceae) is a monophyletic genus endemic to the Brazilian Atlantic forest and occurs from Bahia to Rio Grande do Sul. The genus is poorly known, except for *S. calycotricha* (Link & Otto) Nees, which is cultivated in many botanical gardens around the world. It represents a small clade within the *Tetramerium* lineage (Acanthoideae: Justicieae), comprising perennial herbs and shrubs, mainly in forests of eastern Brazil. The inflorescences possess green or yellow, narrow bracts and yellow or white, small flowers. The genus has not been treated comprehensively since the work of Nees (1847a, b), who recognised about 20 species. Ten of these are accepted in the present treatment, together with three new species and one new combination for the genus.

Nees (1839 ["1838"]) described Schaueria based on Justicia calycotricha Link & Otto, and considered J. calytricha Hook., J. flavicoma Lindl., and J. calycotricha Hook. as synonyms. Almost 10 years later, Nees (1847a) added 13 species to Schaueria, three of them-S. gonyostachya (Nees & Mart.) Nees & Mart., S. maximilianii Nees, and S. humuliflora (Nees & Mart.) Nees & Mart.-were segregated from Justicia. Months later, Nees (1847b) published two other species: S. capitata Nees from Rio Grande do Sul, Brazil, and S. decipiens Nees from "Rio Grande", Mexico. In these treatments, Nees divided Schaueria into two groups: one with broad bracts, comprising S. marginata Nees, S. humuliflora, S. malifolia Nees, and S. hirsuta Nees, and the other with linear-subulate bracts (including the remaining 12 species). He also subdivided this latter group ("Angustibracteata") into three subgroups on the basis of floral characters: "Calycotrichae", with subsessile flowers, long, setaceus calyx lobes and tubulose corollas with short yellow lips; "Thyrsacanthoideae", with pedicels and large flowers, medium to small calyx lobes and tubulose corollas with open lips; and "Lophurae", with medium to small calyx lobes and infundibuliform white corollas with tube and lips unequal.

Torrey (1859) described Schaueria parvifolia Torr. and S. linearifolia Torr. from Mexico; both are currently treated in Carlowrightia A.Gray, a classification that was confirmed by phylogenetic studies (Daniel et al. 2008). Grisebach (1879) published S. caduciflora Griseb. from Argentina, but this species was recently transferred to Thyrsacanthus Moric. (Côrtes et al. 2010). Clarke (1900) described S. populifolia from Africa, but molecular data (McDade and Darbyshire personal comm.) suggest its inclusion in the lineage Isoglossinae-Justicieae, and not in Tetramerium lineage. Rusby (1927) described S. azaleiflora Rusby from Bolivia, a species that is being transferred to Pachystachys Nees (Côrtes et al. 2015). Finally, Hilsenbeck and Marshall (1983) described S. calycobractea Hilsenb. & D.L.Marshall from Mexico, a species included in the synonymy of S. parviflora (Leonard) T.F.Daniel (Daniel 1990).

Nees (1847b) treated *Schaueria* in the tribe Gendarussae, section "Genuinae part A", delimited by bilocular anthers lacking appendices. The tribe was distinguished by the 4- or 5-lobed calyx, bilabiate corolla, androecium with 4 or 2 stamens, staminodes absent or 2, unilocular (section 1: "Pseudo-Aphelandreae") or bilocular (section 2: "Genuinae part A and B") anthers, with parallel to divergent loci that either lack appendages (part A) or bear appendages (part B), and unguiculate capsules with 4 or rarely many seeds.

Bentham (1876) recognized *Schaueria* in the tribe Justicieae, subtribe "Eujusticieae", and in a group of genera characterized by androecia lacking staminodes and having two stamens with equal and parallel thecae, and bearing bithecous anthers that lack or have very short basal appendages. In *Schaueria*, he listed only eight of Nees's Brazilian species, and highlighted the significant difference between *S. parvifolia* and *S. linearifolia*, both now treated in *Carlowrightia*, when compared to the other species of the genus.

In Lindau's (1895) treatment of Acanthaceae, *Schaueria* was placed in the tribe Odontonemeae, subtribe Odontoneminae (Acanthoideae, Imbricatae). The tribe was characterized by narrow and short bracts and bracteoles, (2)4- or 5-lobed calyx, 2(4) stamens, staminodes absent or 2, anthers fused at different or at the same height, and "Spangenpollen" (i.e., 3-aperturate, 6-pseudocolpate pollen). His delimitation of Odontoneminae was similar to those of Nees (1847b) and Bentham (1876), but its com-

position was largely different, mainly because of the exclusion of several genera currently treated under *Justicia* and the inclusion of others. Bremekamp (1965) included this tribe and five other tribes of Lindau in his Justicieae.

Molecular phylogenetics (McDade et al. 2000, 2005, 2008; Kiel et al. 2006; Daniel et al. 2008) clarified several taxonomic divergences in Acanthaceae, showing *Schaueria* and related genera emerging within the *Tetramerium* lineage of Justicieae (McDade et al. 2000; Daniel et al. 2008). This lineage shares symplesiomorphic characteristics of the tribe Justicieae: 3-colporate, 6-pseudocolpate pollen grains with reticulate exine, androecia with 2 stamens and no staminodes, bilocular anthers with parallel thecae that lack appendages, and a chromosome number of n = 18 (although this number is not known for the entire lineage).

The lack of clear morphological synapomorphies for the Tetramerium lineage might be the cause of divergent circumscriptions. In Daniel et al. (2008), Schaueria appears to form a basal grade of a clade including Pachystachys and Streblacanthus, forming together the likely sister group of a broad clade with Thyrsacanthus plus a Mexican clade [Justicia gonzalezii (Greenm.) Henrickson & Hiriart, Yeatesia mabryi Hilsenb., and Mirandea hyssopus (Nees) T.F.Daniel]. Phylogenetic analyses (Côrtes et al. 2015; Fig. 1) confirmed Schaueria as monophyletic, within the Tetramerium lineage, providing that S. azaleiflora, S. hirsuta, S. humuliflora, S. malifolia, and S. parviflora are excluded from the genus. This work presents the taxonomic revision of Schaueria under this new circumscription and assesses the conservation status of each species according to the IUCN (2014) guidelines.

Materials and methods

This revision is based on literature, analysis of approximately 280 specimens from herbaria (including types and images), field observations, and phylogenetic results both published and in preparation. Herbarium material was consulted at B, BM, BR, CAS, CEN, CEPEC, CGE, CUZ, ESA, G, GOET, GUA, GZU, HUEFS, INPA, K, M, MBM, MG, NY, OXF, P, R, RB, SP, SPF, UB, UC, UEC, UFG, US, USM, USZ, W (the acronymons follow Thiers 2015) and the private herbarium of Wied-Neuwied (in Germany). Field studies in South America, mainly Brazil and Bolivia, were undertaken between 2009 and 2011; voucher specimens from fieldwork are deposited at HUEFS.

The species are arranged according to their phylogenetic affinities (Fig. 1). Measurements, colors, and other details are based mostly on herbarium specimens, but also on Fig. 1 Summary cladogram based on phylogenetic analysis with six plastid (*trnL*–F, *trnT*– L, *trnS*–G, *rpS*16, *ndhF*–*rp*132– *trnL*, *trnH*–*psbA*) and one nuclear (ITS) DNA regions (Côrtes et al. 2015), showing the position of *Schaueria* species in Justicieae. All branches are supported by \geq 95 % (PP) except for those indicated with an *arrow* (\leq 95 % PP); names in *bold* are those discussed in the text



living plants and field observations. Measurements refer to mature structures and terminology used to describe inflorescences follows Daniel (1999). Pollen grains, calyx indumentum, and seed surfaces were analysed with scanning electron microscopy (SEM); pollen grains, portions of calyces, and seeds were mounted directly on stubs and covered with gold to be analysed with SEM LEO 1430 VP–Carl Zeiss. The pollen and seed terminology follows Punt et al. (2007), whereas that of trichomes follows Payne (1978). Species conservation status is based on IUCN (2014) criteria. The extent of occurrence (EOO) or area of occupancy (AOO) were utilizied as measures of the spatial area occupied by each taxon based on geographical distribution IUCN (2014). The specimens examined are listed in the Appendix.

Results

The 14 species of *Schaueria* are distributed in the Atlantic forest of Brazil (Fig. 2), a floristic domain characterized by high levels of endemism and substantial habitat loss and fragmentation (Myers et al. 2000; Ribeiro et al. 2009; Martins 2011). The domain consists of several vegetation types based on altitudinal gradient, climate and the distance from the sea (Oliveira-Filho and Fontes 2000; Ribeiro et al. 2009). Species of *Schaueria* occur in dense rain forests, semideciduous forests, and *restingas*, between 80 and 700 m, with species mostly concentrated in Rio de Janeiro and Bahia states. The southernmost distributional limits are in Rio Grande do Sul (*S. capitata*), Santa Catarina and Paraná (*S. paranaensis*) (Fig. 3d). Most species are narrowly

Fig. 2 Map of eastern Brazil showing delimitation of Atlantic forest in gray and the geographic distribution of *Schaueria* (abbreviations of States Brazilian: *BA* Bahia, *MG* Minas Gerais, *SP* São Paulo, *ES* Espírito Santo, *RJ* Rio de Janeiro, *PR* Paraná, *SC* Santa Catarina, *RS* Rio Grande do Sul)



distributed; only *S. capitata* is widely distributed (Fig. 3). *Schaueria marginata, S. gonatistachya, S. hirta, S. pyramidalis,* and *S. maximilianii* occur in Bahia, but the range of *S. hirta* extends to northern Espírito Santo (Fig. 3a). The other species of *Schaueria (S. lachnostachya* Nees, *S. litoralis* (including *S. lophura* and *S. virginea*), *S. macrophylla*, and *S. calytricha*) occur mainly in Rio de Janeiro and southern Espírito Santo, although the range of *S. litoralis* extends as far south as São Paulo, with one syntype of *S. lophura* collected in Porto Seguro, Bahia (Fig. 3b, c).

Schaueria usually has terminal and axillary inflorescences, which may be thyrses, racemes or spikes. The basic unit of the inflorescence is a dichasium composed of a main axis and two lateral ones, with a bract and two bracteoles below the central flower. In most species, the dichasia have 3–7 flowers, but they can be reduced to a single one in some species. Dichasia may be pedunculate with pedicellate flowers (thyrses), sessile with pedicellate flowers (dichasiate racemes) or sessile with sessile flowers (dichasiate spikes) (Daniel 1999). The hypothesis of dichasia reduced to a single flower in Acanthaceae has been confirmed in *Ruellia speciosa* Mart. ex Nees, which can produce both solitary flowers and flowers in dichasia (Tripp 2010), and in species of *Herpetacanthus* Nees ex Moric., which may present a transition between spike and thyrse, with dichasia appearing only in some nodes (Indriunas 2011).

In *Schaueria*, the flowers are essentially bilabiate. The corolla tube is usually cylindrical or expands gradually towards the mouth in some species. The upper lip is shortly bilobed or entire, recoiled, recurved, incurved or straight;



Fig. 3 Geographic distribution of *Schaueria* species. In *gray* is the delimitation of Atlantic forest (abbreviations of States Brazilian: *BA* Bahia, *MG* Minas Gerais, *SP* São Paulo, *ES* Espírito Santo, *RJ* Rio de Janeiro, *PR* Paraná, *SC* Santa Catarina, *RS* Rio Grande do Sul)

the lower lip is 3-lobed, recoiled, recurved or straight. Most species have a short (1–2 cm long) and white (or rarely yellow) corolla, but in three species (*S. calytricha, S. pyramidalis*, and *S. sulfurea*), corollas are larger (4–4.5 cm long) and yellow. The flowers are nototribic or sternotribic. The nototribic flowers are the most common in *Schaueria*, as in most angiosperms. They have dorsal style and anthers and deposit pollen grains on the back of floral visitors. The sternotribic flowers are found only in *S. litoralis*. They have ventral style and anthers and deposit pollen grains on the visitor's ventral side (Willmer 1953). Sternotribic flowers were considered a possible synapomorphy of the *Tetramerium* lineage core group (Daniel et al. 2008) because they had not been detected in other clades.

Schaueria shows considerable variation in the type of indumentum present in inflorescences, including bracts, bracteoles and calyces. In most species, inflorescences are hispidulous to sparsely hispidulous with eglandular, unicellular trichomes 0.06-0.3 mm long. These trichomes may have smooth surfaces or surfaces with protuberances (Fig. 4b-1). Sessile or shortly stalked glandular trichomes with a multicellular head are common on the adaxial surface of calyces whereas stalked glandular multicellular trichomes are common on the margins of calyx lobes of some species (Fig. 4). Schaueria lachnostachya is easily recognised by the calyx ciliate with eglandular, flexuous trichomes that may reach approximately 1-1.2 mm long and are composed of seven or eight cells (Fig. 4c). Schaueria capitata bears stalked glandular trichomes 1-1.5 mm long on bracts, bracteoles, and calyx (Fig. 4e, f) and S. sulfurea bears strigose indumentum, with smooth, appressed eglandular trichomes (Fig. 4g, h). The presence of stalked glandular trichomes on calvees may vary in S. calytricha and S. litoralis. Although the two species were originally described as lacking these trichomes, specimens of both species can have stalked glandular trichomes ca. 0.5 mm long (rare in S. calytricha) (Figs. 4a-l, 5).

Pollen grains in Schaueria are typical of the Tetramerium lineage and other members of Justicieae. They are homogenous, being isopolar, 3-colporate, 6-pseudocolpate (only 3-colporate in S. sulfurea). Their form varies from prolate to subprolate (polar axis longer than equatorial axis). The exine is usually reticulate and heterobrochate (Fig. 6a-h, l-r), except in S. sulfurea, in which the exine is microechinate with some pollen grains also microreticulate (Fig. 6i-k). The membrane of the colpori is usually covered with microverrucae or rugulae (S. gonatistachya). Syncolpate, syncolporate, and parasyncolporate pollen grains, may be rarely found (e.g., Fig. 6n). Pollen grains with different types of sculptural features, such as in S. sulfurea, can also be found in species of the Mirandea Rzed. clade and in other lineages of Acanthaceae (Daniel 1998; Daniel et al. 2008). The 2-colporate pollen grains with reticulate exine and 7–9 areoles per colpori observed in *S. hirsuta* (Fig. 6s, t; Daniel 1998) confirm the position of this species among the New World Justicioids rather than in the *Tetramerium* lineage.

Most seeds in *Schaueria* are lenticular, except those of *S. paranaensis*, which are obovoid and not compressed. The seed base is notched where it is inserted on the septum of the capsule. Seeds are 2.5–7 mm wide, usually white when immature becoming brown when mature. The most important seed character is surface ornamentation (Figs. 7a–v, 8). The seed surface varies from reticulate to slightly reticulate (*S. marginata*; Fig. 7u, v) or reticulate with sinuous walls and reduced lumina (*S. paranaensis*; Fig. 7j, k). Reticulum walls (muri) can be granulate or not (Fig. 7k, r, t). In some species, there are papillae in the axils of the muri (Fig. 7e, t, v). Seeds are usually tuberculate (Fig. 7a–q, t); tubercles may be present or not on the border of seeds (Fig. 7a–v).

Taxonomic treatment

Key to the South American genera of *Tetramerium* lineage

1a.	Bracts 6–18 mm wide 2
1b.	Bracts 0.5–2 mm wide
2a.	Corolla >3 cm long
	Pachystachys s.s. (except P. badiospica)
2b.	Corolla <2 cm long Fittonia
3a.	Corolla 1–1.2 cm long, white Schaueria
3b.	Corolla 3-4 cm long, red, purple, pink or yellow
4a.	Corolla pink or purple, tube 1.5–2.5 cm long, not expanded distally into a throat 1–1.5 mm diam
4b.	Corolla red or vellow, tube 2–4.7 cm long, gradually
	expanded distally into a throat 4–8 mm diam 5
5a.	Corolla red; seasonally dry vegetation
	Thyrsacanthus
5b.	Corolla red or yellow; Amazonian and Atlantic forests
6a.	Bracts brownish-red or green, lanceolate-narrowly
	lanceolate; corolla red; Peru Pachystachys
6b.	Bracts yellow-green, linear-triangular; corolla yel-
7.	Iow, Blazil alla Bollvia
/a.	Antantic forest of Brazil Schauerta
/D.	Amazonian forest of Bolivia
	Schaueria ("Pachystachys") azaleiflora

Schaueria Nees, Del. Sem. Hort. Vratisl.: 3. 1839 ["1838"], **nom. cons.**—TYPE: *S. calycotricha* (Link & Otto) Nees (*Justicia calycotricha* Link & Otto). [= *Schaueria calytricha* (Hook.) A.L.A.Côrtes] non *Schauera*



Fig. 4 SEM micrographs of indumentum and trichomes on the calyx of *Schaueria. S. calytricha (Santos 391)*: **a** slightly hispidulous adaxial surface; **b** eglandular trichome with protuberance. **c** *S. lachnostachya (Cortes 154)*: adaxial surface showing margin ciliate with long eglandular trichomes. **d** *S. litoralis (Cortes 193)*: adaxial surface showing sessile glandular trichomes. *S. capitata (Cortes 200)*: **e** stalked glandular trichome abaxial surface; **f** slightly hispidulous adaxial surface, composed of trichomes and sessile glandular trichomes, and stalked glandular trichomes on margin. *S. sulfurea*

(*Frigoletto 20*): **g** strigose adaxial surface; **h** smooth eglandular trichome. **i** *S. hirta* (*Forzza 5104*): adaxial surface showing margin with trichomes with protuberance. **j** *S. pyramidalis* (*Oliveira 747*): adaxial surface with short stalked glandular trichomes. *S. marginata* (*Côrtes 231*): **k** abaxial surface showing stalked glandular trichome on margin; **l** adaxial surface showing smooth eglandular trichomes. *Bars* **a**, **f** 50 µm; **b**, **h**–**j** 10 µm; **c** 500 µm; **d**, **e**, **g**, **k** 100 µm; **l** 20 µm; *gl* glands



Fig. 5 Diagram of calyx trichome types in Schaueria

Nees ex Lindley (1836) **nom. rej.**, non *Schaueria* Hassk. (1842), **nom. illeg.** (Art. 5.3).

= Flavicoma Raf., Fl. Tellur. 4: 63. 1838 **nom. rej.**— TYPE: *Flavicoma capitata* Raf. (*Justicia flavicoma* Lindl.).

Erect perennial herbs to shrubs with cystoliths and often with conspicuously multicelullar trichomes; trichomes usually white and concentrated in two decussate lines along internodes. Leaves opposite, petiolate; blades usually membranaceous, margin repand to crenate. Inflorescences terminal and axillary thyrses (pedunculate dichasia and pedicellate flowers), dichasiate spikes (sessile dichasia and flowers) or dichasiate racemes (sessile dichasia and pedicellate flowers); dichasia decussate, 1-5-flowered, sessile or pedunculate, subtended by a bract; bracts opposite, green or vellow, relatively short, narrow, usually linear-triangular or triangular (rarely lanceolate), margin entire; bracteoles 2, sessile or pedicellate. Calyx green or yellow, deeply 5-lobed, often acrescent in fruit, lobes equal to unequal in length; corolla nototribic, rarely sternotribic, yellow or white, tube cylindrical or gradually expanded distally into a throat, narrow proximal portion (if distinct) shorter than throat, throat (if present) obconic, limb 2-labiate, upper lip bilobed or entire, recoiled, recurved, incurved or straight, lower lip 3-lobed, lobes straight, recoiled or recurved; stamens 2, exerted from corolla mouth, inserted near the base of corolla or at base of the throat, filaments white, generally hispidulous, anthers 2-thecous, glabrous, white, thecae parallel or slightly oblique, oblong, dehiscing longitudinally, staminodes absent; pollen grains prolate to subprolate, usually 3-colporate, 6-pseudocolpate, exine reticulate; style exerted from corolla mouth, white, stigma bilobate. Capsules stipitate, head clavate, retinacula present, septa with retinacula remaining attached to inner wall of mature capsule; seeds 4, lenticular to obovoid, brown when mature, usually reticulate, tuberculate, margin with tubercles present or absent.

Notes: Schaueria is conserved against *Schauera* Nees ex Lindley (1836; Lauraceae) with *S. calycotricha* (Link & Fig. 6 SEM micrographs of pollen grains of *Schaueria* (including Schaueria hirsuta = Justicia ilhensis). **a** *S.* calytricha (Santos 391): equatorial view. **b**, **c** *S.* lachnostachya (Côrtes 154): equatorial and polar views. **d** *S.* litoralis (Côrtes 193): equatorial view. **e** *S.* macrophylla (Brade 19899): equatorial view. **f** *S.* capitata (Côrtes 200): equatorial view. **g** *S.* paranaensis (Côrtes 266): equatorial view. **h** *S.* spicata (Schott 4723): equatorial view. *S.* sulfurea (Frigoletto 20): **i**, **j** equatorial and polar views; **k** detail of exine sculpture. **l** *S.* thyrsiflora (Braz 333): equatorial view. **m**, **n** *S.* gonatistachya (Côrtes 239): equatorial and polar views. **o** *S.* hirta (Amorim 6814): equatorial view. **p**, **q** *S.* marginata (Côrtes 231): equatorial and polar views. **r** *S.* pyramidalis (Oliveira 747): equatorial view. **s**, **t** *J.* ilhensis (Stapf 349): equatorial and polar views. Bars 10 µm, except **g**, **j**, **q** (=5 µm) and **k** (=2 µm)

Otto) Nees as the type (Rickett and Stafleu 1960) and *Flavicoma* Raf.

Key to the species of Schaueria

- 1a. Inflorescences thyrses (peduncles and pedicels present) 2 1b. 2a. Bracts 7–11 mm long; calyx 1.1–2.2 cm long; corolla with upper lip recoiled S. calytricha 2b. Bracts 1-2 mm long; calyx 3-7 mm long; corolla with upper lip incurved or slightly incurved 3 Subshrubs; calyx 3-4 mm long; corolla yellow, 3a. 4-4.5 cm long, upper lip incurved S. sulfurea Herbs; calyx 6-7 mm long; corolla white, ca. 1 cm 3b. long, upper lip slightly incurved S. thyrsiflora 4a. 4b. Dichasiate racemes; dichasia 1-7-flowered9 5a. Corolla yellow, 3.8-5 cm long, tube expanded into a throat: filaments of stamens muricate Corolla white, 1.1-1.2 cm long, tube not expanded 5b. into a throat; filaments of stamens glabrous or 6a. Herbs; young stems hirsute with trichomes 1-1.7 mm long; leaf blade hirsute, with eglandular trichomes 1-1.7 mm long, margin hirsute-ciliate with trichomes 1-1.7 mm long S. hirta 6b. Subshrubs or shrubs; young stems glabrous or pubescent with trichomes 0.2-0.3 mm long; leaf blade glabrous or pubescent with eglandular trichomes 0.3-0.4 mm long, margin glabrous or strigose-pubescent with trichomes 0.08-0.3 mm
- 7a. Bracts 1.5–2 mm long; calyx 1.5–2 mm long; corolla tube 6–7.5 mm long S. gonatistachya





Fig. 7 SEM micrographs of seed of species of *Schaueria*; coat sculpture and detail of surface: *S. calytricha* (*Côrtes 160*): **a** lenticular seed; **b** surface reticulate and tuberculate; *S. lachnostachya* (*Côrtes 154*): **c** lenticular seed; **d** surface reticulate and tuberculate; **e** detail of surface with papillae in axils of muri; *S. litoralis* (*Carauta 4932*): **f** lenticular seed; **g** surface reticulate and tuberculate; *S. capitata* (*Côrtes 187*): **h** lenticular seed; **i** surface reticulate and tuberculate; *S. capitata* (*Côrtes 187*): **h** lenticular seed; **i** surface reticulate and tuberculate; **k** surface reticulate with sinuous muri and reduced lumina, reticulum and muri

granulate; *S. thyrsiflora (Braz 333)*: l lenticular seed; m surface reticulate and tuberculate; *S. gonatistachya (Kameyama 67)*: n lenticular seed; o surface reticulate and tuberculate; *S. hirta (Forzza 5104)*: p lenticular seed; q surface reticulate and tuberculate; r granules on reticulum; *S. pyramidalis (Fiaschi 1094)*: s lenticular seed; t surface reticulate with papillae in axils of muri; *S. marginata (Côrtes 231)*: u lenticular seed; v surface slightly reticulate with papillae in axils of muri and tuberculate. *Bars* a, c, n, p, s 1 mm, b 100 µm; d, e, g, i, m, o, q, t, v 50 µm; f, h, j, l, r, u 500 µm; e, k 10 µm





- Young stems not striate, hispidulous; calyx linear– triangular; flowers nototribic S. maximilianii

- 13b. Bracts $5-7 \times 2-2.5$ mm; corolla externally puberulous from the mouth to the apex of lobes, internally puberulous on tube with eglandular and glandular trichomes; stamens ca. 7 mm long ... *S. marginata*.

1. Schaueria calytricha (Hook.) A.L.A.Côrtes, comb. nov. \equiv Justicia calytricha Hook., Exot. Fl. 3(34): t. 212. 1826.—TYPE: cultivated in Botanical Garden of Liverpool, s.d., s.col. [lectotype **designated here**: illustration in Exot. Fl. 3(34): t. 212. 1826]. (Figs. 3c, 4a, b, 5, 6a, 7a, b, 8, 9a–e; see also photos 23 and 24 in Côrtes 2013).

= Justicia calycotricha Link & Otto, Icon. Pl. Select. 9: 113, t. 53. 1826. \equiv Schaueria calycotricha (Link & Otto) Nees, Del. Sem. Hort. Vrastisl.: 3. 1839 ["1838"].— TYPE: Brazil. Rio de Janeiro, 1823, Beyrich s.n. (holotype: B destroyed; lectotype **designated here**: illustration in Icon. Pl. Select. 9: 113, t. 53. 1826).

= Justicia flavicoma Lindl., Bot. Reg. 12: t. 1027. 1827. \equiv Flavicoma capitata Raf., Fl. Tellur. 5: 63. 1838. \equiv Schaueria flavicoma (Lindl.) N.E.Br., Gard. Chron., n.s., 19: 14. 1883.—TYPE: cultivated in Kent, England (lecto-type **designated here**: illustration in Bot. Reg. 12: t. 1027. 1827).

= Justicia calycotricha Hook., Bot. Mag. 55: t. 2816. 1828, nom. illeg. (hom. post., non *Justicia calycotricha* Link & Otto). *Flavicoma paniculata* Raf., Fl. Tellur. 5: 63. 1838. nom. superfl.—TYPE: cultivated in Botanical Garden of Liverpool, *s.d.*, *s.col.* (lectotype **designated here**: illustration in Bot. Mag. 55: t. 2816. 1828).

Shrubs 0.8–1.5 m tall; young stems subquadrate, glabrous or hirsute with eglandular trichomes 0.2–0.5 mm long concentrated in 2 lines. Petiole 1–8.5 cm long; blade $8-18.5 \times 2.7-8$ cm, ovate to lanceolate or rarely oblong, cuneate to cordate or rarely rounded at base, acute to attenuate



Fig. 9 *Schaueria calytricha*: **a** branch with inflorescence; **b** inflorescence; **c** bracteoles and flower; **d** fruit with seeds; **e** seed (drawn from *Côrtes 160*); *S. lachnostachya*: **f** branch with inflorescence;

g inflorescence; h bract, bracteole and calyx; i flower (drawn from *Côrtes 154*). Drawing by Carla Lima

at apex, membranaceous, surfaces glabrous or with eglandular trichomes (usually restricted to major veins, at least on adaxial surface) 0.1-0.5 mm long, margin repand with appressed eglandular trichomes 0.08-0.2 mm long. Thyrses terminal, 5-9 cm long, rachis quadrate, puberulous to pilose with flexuous eglandular trichomes 0.2-0.3 mm long, rarely with glandular trichomes 0.5–0.7 mm long; dichasia 3–5-flowered, peduncles 3–7 mm long; bracts yellow, 7–11 \times ca. 1 mm, linear-triangular, adaxially hispidulous usually with eglandular trichomes 0.06-0.07 mm long, margin with eglandular trichomes, rarely with glandular trichomes 0.5–0.7 mm long; secondary peduncles ca. 3 mm long; bracteoles yellow, $8-10 \times 0.5$ –0.7 mm, linear-triangular, indumentum like that of bracts; pedicels 1-3.5 cm long. Calyx yellow, 1.1-2.2 cm long, lobes equal in length, 1–2.1 cm \times 0.5–1 mm, linear– triangular, hispidulous with erect eglandular and sessile glandular trichomes usually only on the adaxial surface, trichomes with protuberances, margins rarely with flexuous glandular trichomes ca. 0.5 mm long; corolla yellow, 3.5-4.5 cm long, externally glabrous or hispidulous with erect eglandular trichomes on veins, internally pubescent with flexuous eglandular trichomes 0.2-0.3 mm long, tube 2.4-3.5 cm long, expanded into a throat distally, narrow proximal portion $8-10 \times 1.5-2$ mm, throat obconic, $1.8-2 \text{ cm} \times 5-6 \text{ mm}$, upper lip recoiled, $8-12 \times 2.5-3 \text{ mm}$, lip shortly bilobate, lower lip $7-12 \times 1.8-2.5$ mm, lobes equal, 6.5-11.5 mm long, recoiled; stamens 3.9-4 cm long, equal, inserted up to 8 mm distal to base of corolla tube, filaments hispidulous, thecae 2.1-3 mm long; pollen grains, heteroaperturate, 3-colporate, 6-pseudocolpate, 2 pseudocolpi per mesocolpium, exine reticulate, heterobrochate, membrane of colpori microverrucate; style ca. 3 cm long, glabrous or hispidulous. Capsules 1.2-1.5 cm long, stipe 6-7 mm long, glabrous; seeds ca. 3.2 mm wide, lenticular, reticulate with microgranules when immature, tuberculate, margin without tubercles.

Phenology: Flowering and fruiting throughout the year, usually from July to October.

Distribution area and habitat: Southeastern Brazil; Rio
de Janeiro state; in rain forests, from 150 to 700 m a. s. l. Additional specimens examined: Brazil. s.loc., s.d., F.
Sellow 179 (B destroyed, F [web!]); s.loc., D. Douglas s.n.
(K!); s.loc., 23 Sep 1902, s.col. (P barcode P04391245
[web!]); Rio de Janeiro, 1816–1821, A. de Saint-Hilaire B2-25^a (P [web!]); Rio de Janeiro, s.d., C. Gaudich. 457 (P
[web!]); Arraial do Cabo, 12 Jan 2000, C. Farney 3970
(RB!); Cabo Frio, s.d., M.A.P. Wied-Neuw. s.n. (BR
[photo!]); Maricá, 15 km da ponte sobre o rio Roncador, 4 km da estrada Amaral Peixoto e a 100 m da Lagoa de
Maricá, 11 Oct 1988, fl., fr., J. Fontella et al. 2607 (RB!); Niterói, Itaipuaçu, Parque Estadual da Serra da Tiririca, Morro das Andorinhas, 40 m a. s. l., 22°58′S, 43°02′W, 3 Jun
2009, fl., fr., A.L.A. Côrtes and A.C. Mota 160 (HUEFS!); ib., Pedra da Itacoatiara, 27 Aug 1995, bt., fl., M.G. Santos 391 (HUEFS!, RB!); Rio de Janeiro, Serra dos Órgãos, 1838, bt., fl., C. Gaudich. 839 (BM [photo!], CGE!, K!, NY!, OXF!, P [web!]); ib., Pedra da Gávea, caminho das Furnas, 300-500 m a. s. l., 19 Sep 1971, bt., fl., J.P.P. Carauta et al. 1402 (GUA!, HUEFS!, NY!, RB!, US!); Jacarepaguá, Parque Estadual da Pedra Branca, estrada Pau da Fome, 29 Aug 1977, fl., fr., I.A. Rodrigues et al. 113 (RB!); ib., Represa do Camorim, 30 Jun 1980, bt., fl., D. Araujo 3868 (GUA!); Cultivated—England. London, Laszlo Csiba 15,897 (K!); Cambridge, horto horticultural Society-HHS (now Royal Horticultural Society—RHS), 1845, G. Lindley s.n. (CGE!); Kew, 25 May 2003, G.V. Nash 9634 (NY!); Oxford, Cutia Lindle 1828 (OXF!); USA. 10 Mar 1985, N. Taylor 9634 (NY!); New York, Bronx, New York Botanical Garden, 14 Apr 2011, M. Nee 57842 (NY!).

Conservation status: Schaueria calytricha is known from 46 collections corresponding to ten subpopulations and EOO of 420 km². We observed subpopulations with ca. 200 mature individuals, but we did not find the species in Cabo Frio and Arraial do Cabo. In addition, the areas where the species is found in the city of Rio de Janeiro and vicinity are touristic and suffer high anthropic pressures, suggesting a decline of the species distribution range and quality of habitat. Therefore, the conservation status of this species is assessed as Endangered (EN), for reasons B1ab(i, iii) under IUCN (2014) guidelines. Fortunately, the species is protected in the Serra da Tiririca State Park (Niterói, Rio de Janeiro state) and is cultivated in many botanical gardens around the world.

Notes: Schaueria calytricha is characterized by pedunculate dichasia, linear-triangular bracts, bracteoles, and calyces, calyces 1.1–2.2 cm long, and yellow corollas, 3.5–4.5 cm long, with recoiled lobes.

Nees (1839 ["1838"]) described Schaueria based on Justicia calycotricha Link & Otto and cited three synonyms: J. calytricha Hook., J. flavicoma Lindl. and J. calycotricha Hook. Justicia calycotricha was described by Link and Otto (1826) based on a specimen collected in Rio de Janeiro, Brazil, by Beyrich and cultivated in Berlin, Germany. In the same year, Hooker (1826) published J. calytricha based on a specimen cultivated in the Liverpool Botanical Garden, received from Otto in 1825. In 1827, Lindley described J. flavicoma based on plants from Mr. Thomas Carey Palmer's collection, cultivated in Kent, UK, from seeds collected in Brazil. He noted the similarity between this species and J. calytricha, but considered the presence of glandular trichomes on inflorescences and lanceolate leaves with short petioles sufficient to recognise another species.

Not satisfied with the treatment of Lindley, Hooker (1828) described *Justicia calycotricha* based on the same specimen used by Lindley; he also treated *Justicia calycotricha* Link, *J. calytricha* Hook. and *J. flavicoma* Lindl.

as synonyms. According to him, the size and form of leaves, including petiole length, are regular variations and the "curious" indumentum only seen with microscopy can be easily missed. Trying to solve the disagreement between Hooker and Lindley regarding the concept of this species, Brown (1883) presented a brief background distinguishing the two species. In addition to those attributes used to separate them, he also maintained their distinction on the fact that Nees (1847a) erroneously included Gardner 239 (identical to Justicia flavicoma) in Schaueria virginea Nees (= S. litoralis), a different species. In this work, therefore, Brown recognised two species and transferred J. flavicoma to Schaueria. Rafinesque (1838), on the other hand, described a new genus, Flavicoma, to which J. flavicoma and J. calvcotricha were transferred, receiving new names: F. capitata and F. paniculata, respectively. Rickett and Stafleu (1960) synonymised Flavicoma with Schaueria.

Most specimens representing these taxa have ovate leaves and lack stalked glandular trichomes. Only *Douglas s.n.* (K), *Gardner 839* (BM, CGE, K, NY, OXF, P) and *Vianna 2067* (GUA) have characteristics (i.e., lanceolate leaves and glandular trichomes on the calyx) that would conform to Brown's concept of *S. flavicoma*. However, in the same locality, typical specimens of *S. calytricha* can also be found, suggesting that these differences represent intraspecific variations.

Justicia calytricha Hook. and J. calycotricha Link & Otto (non Hook.) were published in the same year. Justicia calytricha was published in May, but the date of publication of J. calycotricha is uncertain. In spite of that, knowing that the eighth issue of Icones Plantarum Selectarum... was published between January and July (Stafleu and Cowan 1981), the ninth issue of this work, where J. calycotricha appeared, was most likely published after May. Consequentely, J. calytricha has priority over J. calycotricha, and the former epithet is correct, thus the new combination S. calytricha is proposed here.

Since none of the specimens upon which these names were based have been located, the colorful illustrations published with original descriptions are designated as lectotypes.

2. *Schaueria lachnostachya* Nees in Martius, Fl. Bras. 9: 105. 1847.—TYPE: Brazil. Rio de Janeiro, s.l., 1815, *M.A.P. Wied-Neuw. s.n.* (lectotype: GZU barcode GZU000251417 [photo!]; isolectotypes: BR barcode BR0000008097736 [photo!], barcode BR0000008098580 ex herb. Mart. [photo!] designated by Moraes et al. 2013) (Figs. 3c, 4c, 5; 6b, c, 7c–e, 8, 9f–i; see also photos 32 and 33 in Côrtes 2013).

Subshrubs 0.3–1.5 m tall; young stems terete, pubescent with eglandular trichomes ca. 0.5 mm long, trichomes concentrated in two lines. Petiole 1–2.5 cm long; blade $3-7.5 \times 1.3-3.5$ cm, elliptic to ovate to oblong, acute to

cuneate, rarely truncate at base, acute to attenuate at apex. membranaceous, surfaces glabrous except for trichomes on major veins (eglandular trichomes ca. 0.4 mm long and sessile glandular trichomes abaxially), margin repand, ciliate with flexuous eglandular trichomes ca. 0.4 mm long, and rarely with appressed trichomes ca. 0.08 mm long. Racemes dichasiate, terminal and axillary, 2-3 cm long, rachis cylindrical, densely hirsute with erect eglandular trichomes, ca. 0.2 mm long and eglandular trichomes 0.3-0.5 mm long, or rarely with trichomes concentrated in 2 lines; dichasia congested, 1-3-flowered, sessile; bracts green, $5-7 \times ca$. 1 mm, triangular, hispidulous with eglandular trichomes 0.08-0.1 mm long with protuberances, sessile glandular trichomes also present, margin ciliate with flexuous eglandular trichomes 1-1.2 mm long (trichomes rarely absent); bracteoles green, $4-5 \times 0.4-0.6$ mm, triangular, hispidulous like that of bracts; pedicels ca. 0.5 mm long. Calyx green, 0.6-1.5 cm long, lobes unequal, $0.5-1.4 \text{ cm} \times \text{ca.} 0.6 \text{ mm}$, linear-triangular, hispidulous, margin ciliate like that of bracts; corolla white, 1.5-2 cm long, externally glabrous, internally puberulous, trichomes restricted to distal half of tube, tube 8-13 mm long, cylindrical, mouth 2.5-3 mm diam., upper lip recurved at apex, $4-8 \times 1.5-2$ mm, lobes shortly bilobate, lower lip $4-8 \times 1.5-2$ mm, lobes equal, recurved; stamens 6-8 mm long, equal, inserted up to ca. 5 mm distal to the base of corolla tube, filaments hispidulous, thecae 1.5-2.5 mm long; pollen grain, prolate, subcircular, heteroaperturate, 3-colporate, 6-pseudocolpate, 2 pseudocolpi per mesocolpium, exine reticulate, heterobrochate, membrane of colpori microverrucate; style ca. 1.2 mm long, hispidulous (rarely glabrous). Capsules 1.1-1.2 cm long, stipe ca. 5 mm long, glabrous; seeds ca. 4 mm wide, lenticular, reticulate, papillate in axils of muri when immature, tuberculate, tubercles absent on margin.

Phenology: Flowering and fruiting from April to October.

Distribution area and habitat: Southeastern Brazil; Rio de Janeiro state; in rain forests and *restingas*, from 40 to 200 m a. s. l.

Additional specimens examined: Brazil. s.loc., F. Sellow s.n. (B destroyed, F [photo!]); s.loc., F. Sellow 592 (BM!); Rio de Janeiro, Monte Corcovado, Schott 4743 (K!, W [web!]); Rio de Janeiro, 1886, Lehnvoelse s.n. (US!); ib., Armação de Búzios, centro da cidade próximo ao Bradesco, mata do estacionamento privativo, 46 m a. s. l., 22°45'S, 41°53'W, 1 Jun 2009, A.L.A. Côrtes and A.C. Mota 159 (HUEFS!); Arraial do Cabo, Pontal do Atalaia, próximo à casa 48 S, 92 m a. s. l., 22°58'S, 42°1'W, 1 Jun 2009, bt., fl., fr., A.L.A. Côrtes and A.C. Mota 154 (HUEFS!); Cabo Frio, Gabiel Cape, 6 Aug 1953, F. Segadas-Vianna et al. s.n. (US!); Niterói, Praia de Piratininga, 27 Oct 1963, bt., fl., L.F. Pabst s.n. (HB!, US!); Rio das Ostras, Balneário das Garças, estrada para a praia, 85 m a. s. l., 22°26′S 41°51′W, 31 May 2009, bt., fl., fr., *A.L.A. Côrtes* and *A.C. Mota* 147 (HUEFS!).

Conservation status: Schaueria lachnostachya is found mainly in restingas and is known from 22 collections, which correspond to eight small subpopulations and an EOO of 5700 km². We observed subpopulations with ca. 20 mature individuals. It is being threatened by urban expansion and its total numbers are estimated to be in continuous decline. For these reasons, it is categorized as vulnerable (VU) for reasons B1ab(iii) under IUCN (2014) guidelines.

Notes: Nees (1847a) compared *Schaueria lachnostachya* to *S. lophura* and *S. virginea* (both = *S. litoralis*), and distinguished the former species by its leaves with acute (vs. obtuse to subcordate) bases, and long eglandular trichomes (vs. hispidulous) on bracts, bracteoles, and calyx (Fig. 4c). In addition, its dichasia are congested (vs. lax), and the corolla is nototribic (vs. sternotribic), with the upper lip shortly bilobed (vs. entire). The ciliate leaves and the long eglandular trichomes on the bracts, bracteoles, and calyx are important features for recognizing *S. lachnostachya*. Molecular data confirmed the close relationship between *S. lachnostachya* and *S. litoralis*, and place *S. calytricha* basal to them (Côrtes et al. 2015).

3. Schaueria litoralis (Vell.) A.L.A.Côrtes, comb. nov. \equiv Veronica litoralis Vell., Fl. Flumin.: 10. 1829; Fl. Flumin. Icon. 1: t. 24. 1831.—TYPE: Brazil. Rio de Janeiro, bairro Santa Cruz "sylvis maritimus regnii Praedii Sanctae Crucis prope litus, ad locus arenosa habitat", s.d., s.col. (lectotype designated here: illustration in Fl. Flumin. Icon. 1: t. 24. 1825, distributed in 1831; epitype designated here: Brazil. Rio de Janeiro, Bom Jesus de Itabapoana: Rodovia entre distrito de Carabuçu e vila mutum, Jorge de Assis farm, Mata do Macaco, 21°11′25″S, 41°33′87″W, 4 Oct 2009, bt., fl., fr., A.L.A. Côrtes, A.F.P. Machado, F. Moreira and G. Siqueira 193 (HUEFS)) (Figs. 3a–c, 4d, 5, 6d, 7f, g, 8, 10a–f; see also photos 34–36 in Côrtes 2013).

= Schaueria virginea Nees in Martius, Fl. Bras. 9: 105. 1847.—TYPE: Brazil. Rio de Janeiro, Cabo Frio, Sep 1815, *M.A.P. Wied-Neuw. s.n.* (lectotype: BR barcode BR0000008098948 [photo!]; isolectotype: GZU barcode GZU000251416 [photo!] (flower fragments), designated by Moraes et al. 2013). Cabo Frio, Sep 1815, *M.A.P. Wied-Neuw. s.n.* (syntypes: BR barcode BR0000008096975 [photo!], barcode BR000008096968 [photo!] (fr.), GZU barcode GZU000251416 [photo! (fruit fragments)]). Cabo Frio, Sep 1815, *M.A.P. Wied-Neuw. s.n.* (syntypes: GOET [photo (2 sheets!; Klaenze nr. 106)!]). *= Schaueria lophura* Nees & Mart. in Martius, Fl. Bras. 9: 104. 1847.—TYPE: Brazil. Rio de Janeiro, Cabo Frio, Aug 1815, *M.A.P. Wied-Neuw. s.n.* (lectotype: BR barcode BR0000008096937 [photo!]; isolectotypes: BR barcode BR0000008058744 [photo!], GZU barcode GZU000251420 [photo!], designated by Moraes et al. 2013). Bahia, Porto Seguro, Jul 1816, *M.A.P. Wied-Neuw. s.n.* (syntype: BR barcode BR0000006951733 [photo!]). *s.loc., s.d., M.A.P. Wied-Neuw. s.n.* (isosyntype, [photo Herbarium Wied nr. 122!]). **syn. nov**.

Shrubs 0.2–1.3 m tall; young stems terete, striate, glabrous, rare sparsely pubescent with flexuous eglandular trichomes ca. 0.3 mm long. Petiole 1.5-6 cm long; blade $4.5-15 \times 1.9-6$ cm, elliptic to oblong or rarely ovate, cuneate to irregular or rarely rounded at base, acute to acuminate at apex, membranaceous, surface glabrous or with sparse eglandular trichome, restricted to major veins and sessile glandular trichomes abaxially, margin repand with appressed eglandular trichomes ca. 0.1 mm long. Racemes dichasiate, terminal and axillary, 2.5-17 cm long, rachis quadrate, pubescent like stems, with trichomes concentrated in two lines; dichasia lax, 1-3-flowered, sessile; bracts green, $2-3.5 \times 0.7-1$ mm, triangular, glabrous or sometimes abaxially hispidulous with eglandular trichomes ca. 0.05 mm long, and adaxially with sparse sessile glandular trichomes, margin with erect trichomes 0.2-0.25 mm long or stalked glandular trichomes ca. 0.5 mm long; bracteoles green, $2-2.5 \times 0.5-0.7$ mm, triangular, indumentum like that of bracts; pedicels ca. 0.5 mm long. Calyx green, 4–11 mm long, lobes equal, $3.5-10 \times 0.5-0.6$ mm, triangular, indumentum like that of bracts; corolla white, sternotribic, 0.8-2 cm long, externally glabrous, internally pubescent on tube with eglandular trichomes 0.2–0.3 mm long, tube 4-8.5 mm long, cylindrical, mouth 1.5-2.5 mm diam., upper lip recurved at apex, $5-13 \times 2.5-3$ mm, lobes entire, lower lip $5-12 \times 2-3.5$ mm, lobes equal, recurved; stamens 0.7-1.5 mm long, equal, inserted up to 2-4 mm distal to base of corolla tube, filaments hispidulous up to middle, thecae (0.15-) 1.5-3 mm long; pollen grains subprolate, subcircular, heteroaperturate, 3-colporate, 6-pseudocolpate, 2 pseudocolpi per mesocolpium, exine reticulate, heterobrochate, membrane of colpori microverrucate; style 5.5-20 mm long, hispidulous. Capsules 7-17 mm long, stipe 2.5-10 mm long, glabrous; seeds 3-4 mm wide, lenticular, reticulate when immature, tuberculate, tubercles absent on margin.

Vernacular name: Erva-maria.

Phenology: Flowering from June to January; fruiting in February, August, October and November.

Distribution area and habitat: Eastern Brazil; from Bahia to São Paulo, in Bahia known only from the type



Fig. 10 Schaueria litoralis: **a** branch with inflorescence; **b** inflorescence; **c** calyx; **d** flower with bract and brateoles; **e** fruit with seeds; **f** seed (drawn from **a**–**d**:*C*ôrtes 193; E–F: Araujo 10476). S.

macrophylla: **g** branch with inflorescence; **h** dichasium with bracteoles and calyces; **i** bracteoles and calyx; **j** corolla and stamens (drawn from *Carauta 4389*). Drawing by Carla Lima

collection of *S. lophura*; most often in submontane semideciduous forests and *restingas*.

Additional specimens examined: Brazil. Rio de Janeiro, Aug 1815, M.A.P. Wied-Neuw. s.n. (BR [photo!]); Rio de Janeiro, F. Sellow s.n. (BM barcode BM000949836!); Rio de Janeiro, F. Sellow s.n. (CGE [photo!]); Rio de Janeiro, F. Sellow s.n. (K barcode K000529411 [photo!]); Rio de Janeiro, F. Sellow s.n. (K barcode K000529412 [photo!]); Rio de Janeiro, F. Sellow s.n. (K barcode K000529415 [photo!]); Rio de Janeiro, F. Sellow L70B304 (B [F photo No. 8778!]); Bahia, Porto Seguro, 1816, M.A.P. Wied-Neuw. s.n. (BR [photo ex herb. Mart.!]); Minas Gerais, s.loc., s.d., C. Gaudich. 5136 (isosyntype, BM!, CGE [photo!], K! ex herb. Hooker, INPA!); Espírito Santo, Alegre, Distrito de Reeve, 6 Dec 1924, fr., J. Vidal 39 (R!); Presidente Kennedy, Praia de Neves, a beira da estrada para Presidente Kennedy, 17 Oct 2008, fl., D. Araujo 11106 (GUA!); Rio de Janeiro, Armação dos Búzios, Rancho Dez, 2 Oct 1996, fl., D. Araujo et al. 10476 (GUA!); Arraial do Cabo, Pontal do Atalaia, 26 Sep 2002, C.A.L. Oliveira et al. 2060 (GUA!); Bom Jesus de Itabapoana, próximo ao Distrito de Carabuçu, fazenda Jorge de Assis, Mata do Macaco, 89 m a. s. l., 21°11′25″S, 41°33'87"W, 4 Oct 2009, bt., fl., fr., A.L.A. Côrtes et al.193 (HUEFS!); Cabo Frio, Morro o lado do canal de Cabo Frio, 1 Nov 1966, bt., fl., D. Sucre 1168 (HUEFS, RB); Campos dos Goytacazes, distrito de Ibitioca, fazenda Pedra Negra, 9 Oct 1993, fr., J.M.A. Braga s.n. (RB!); Nova Friburgo, caminho para o Morro da Cruz, 10 Jun 1978, bt., fl., F. Oliveira 424 (GUA!); Rio de Janeiro, Corcovado à Paineiras, 24 Jun 1863, A. Glaziou 222 (P [web!]); Estrada de Guaratiba-Grumari, 23 Jul 1968, bt., D. Sucre 3297 (HUEFS!); Rio de Janeiro, Vertente NW da Serra da Piaba, 40-80 m a. s. l., 17 Jul 1970, bt., fl., D. Sucre 7058 (HUEFS!, RB!); Campo Grande, Maciço de Gericino, Serra do Mendonça, Vale do Rio Guandu, 7 Nov 1994, fl., J.P.P. Carauta et al. 6951 (GUA!); Volta Redonda, Santa Cecília, Reserva Florestal da Companhia Siderúrgica Nacional, Reserva da Cicuta, 6 Nov 1984, fr., J.P.P. Carauta et al.4932 (GUA!, US!); São Paulo: São Paulo, Ilha de Alcatrazes, Oct 1920, fl., fr., H. Luederwaldt et al. s.n. (SP!).

Conservation status: Schaueria litoralis is known from 44 collections corresponding to 22 subpopulations. Approximately 100 mature individuals were observed in one of these subpopulations. However, excluding the isolated population from Bahia, the extent of occurrence of this species is 47,050 km² and includes mainly *restingas* of Rio de Janeiro and Espírito Santo, but also semideciduous forest, which are all progressively decreasing in extent by urban development and deforestation. Given this scenario, the species is categorized as near threatened (NT) under IUCN (2014) guidelines.

Notes: Although the material used by Vellozo in Flora Fluminensis was expected to be at herbaria in Paris or Lisbon (Carauta 1973; Stafleu and Cowan 1986), his Acanthaceae have not been located there. In spite of that, the diagnosis and illustration of Veronica litoralis show the 4-lobed corolla and the exserted stamens, two characteristics that most likely induced Vellozo to place this species in Veronica L. Nevertheless, the loculicidal capsule confirms this species in Acanthaceae. Nees (1847b, in addenda) synonymised Veronica litoralis under Schaueria virginea, which is confirmed by their morphological similarities. Because Veronica litoralis has priority over S. virginea, the former epithet must be used, thus Schaueria litoralis. Here, we designate the illustration in Vellozo (1831) as the lectotype and also an epitype to be used as interpretative type for this name (McNeill et al. 2012: Art. 9.3).

Schaueria lophura and *S. virginea* were described in the same work (Nees 1847a). Nees considered the former species most likely a variety of the latter one. He distinguished them only by the size of leaves, calyx and corolla, which are smaller in *S. lophura*. Study of types and additional specimens revealed that this variation reflects only differences between populations. Therefore, we treat *Schaueria lophura* and *S. virginea* as synonyms of *S. litoralis*.

4. *Schaueria macrophylla* Pohl ex Nees in Martius, Fl. Bras. 9: 105. 1847.—TYPE: Brazil. "Serra do Macaco, prov. Goyazanae" *J.B.E. Pohl 4736* (lectotype designated here, W barcode W33652 [web]!; isolectotype: W barcode W33653 [web]!, barcode W33654 [web!], GZU barcode GZU000251414 [photo!]). (Figs. 3b, 5, 6e, 8, 10g–j).

Subshrubs ca. 1 m tall; young stems quadrate, glabrous. Petiole 1.5–3.5 mm long; blade $17-26.5 \times 5-7$ cm, elliptic, acute at base, acute to attenuate at apex, chartaceous or membranaceous, surfaces glabrous or hispidulous with erect eglandular trichomes ca. 0.1 mm long, margin crenate, glabrous or with appressed eglandular trichomes ca. 0.1 mm long. Racemes dichasiate, terminal, 13-21 cm long, rachis quadrate, puberulous with eglandular trichomes ca. 0.3 mm long; dichasia 3-7-flowered, sessile; bracts green, $8-19 \times \text{ca. 1}$ mm, linear-triangular, surfaces hispidulous with eglandular trichomes ca. 0.08 mm long and sessile glandular trichomes adaxially, margin with erect trichomes; bracteoles green, $6-11 \times 0.4-0.6$ mm, linear-triangular, hispidulous like that of bracts; pedicels 1-2 mm long. Calyx green, 1-2.5 cm long, lobes equal, $9-24 \times ca. 0.5$ mm, linear, hispidulous with eglandular trichomes 0.08-0.1 mm long with protuberances, sessile glandular trichomes also present adaxially, margin hispidulous and with sparse stalked glandular trichomes in the apex to 0.5 mm long; corolla white, 1-2.4 cm long, externally sparsely pubescent, internally pubescent where stamens inserted with eglandular trichomes ca. 0.2 mm

tube 0.6–1.5 mm long, cylindrical. mouth long. 1.5-3.0 mm upper lip slightly diam., incurved, $4-11 \times 1.5-4$ mm, lobes shortly bilobate, lower lip $4-9 \times ca.$ 1.5 mm, lobes ca. 7 mm long, apex involute; stamens 8-14 mm long, equal, inserted up to 7-8 mm distal to base of corolla tube, filaments hispidulous, thecae 2-3 mm long; pollen grains prolate, heteroaperturate, 3-colporate, 6-pseudocolpate, 2 pseudocolpi per mesocolpium, exine reticulate, heterobrochate, membrane of colpori microverrucate; style 9-18 mm long, glabrous. Capsules 1.7–2 mm long; stipe 1–1.1 mm long, glabrous; seeds 4-4.5 mm wide, lenticular, surfaces tuberculate when immature, tubercles absent on margin.

Phenology: Probably flowering and fruiting in May–September.

Distribution area and habitat: Southeastern Brazil; Rio de Janeiro and Espírito Santo states, also known in Goias from the type collection; in semideciduous forests.

Additional specimens examined: Brazil. Espírito Santo, Cachoeiro do Itapemirim, fazenda Santo Antonio da Pedra Branca, 25 May 1949, fr., A.C. Brade 19899 (HUEFS!, RB!); Goiás, "Serra do Macaco", J.B.E. Pohl 4736 (GZU!, W!); Rio de Janeiro, Bom Jesus de Itabapoana: Distrito Carabuçu, Vila Mutum, fazenda Boa Esperança, 11 Sep 1982, bt., fr., A.A. Santos et al. 94 (GUA!); ib., 12 Sep 1982, bt., fl., J.P.P. Carauta et al. 4389 (GUA!).

Conservation status: Schaueria macrophylla is known only from three collections corresponding to three subpopulations. However, excluding the isolated subpopulation from Goiás, the EOO is approximately 193 km². It is threatened by deforestation and agriculture suggesting a decline of the species distribution range and quality of habitat so it should be assessed as Endangered (EN), for reasons B1ab(iii) under IUCN (2014) guidelines.

Notes: In herbaria, *Schaueria macrophylla* can be confused with *S. litoralis* because they share the same habitat and can occur in close proximity. However, *S. macrophylla* has larger leaves (>16 cm long) with crenate margins and dense (vs. loose) inflorescences, most often with larger bracts and calyx (>8 and >9 mm long, respectively), the corolla upper lip is bilobed, apparently incurved (vs. upper lip entire and recurved), and the stamens are protected by upper lip (vs. exposed).

The label on the type of *S. macrophylla* indicates its occurrence in Goiás city, Serra do Macaco, an area predominantly covered by savanna. However, recent collections of this species come only from semideciduous forests in Espírito Santo and Rio de Janeiro.

Amongst Pohl's collections, we designated as the lectotype of *Schaueria macrophylla* the specimen at his herbarium (W) identified by Nees' own hand and with complete morphological structures and label information. 5. *Schaueria capitata* Nees in De Candolle, Prodr.11: 316. 1847.—TYPE: Brazil. "In montosis prov. Rio Grande", *s.d., J. Tweedie s.n.* (holotype: K barcode K529417!; isotype: GZU barcode GZU000251421 [photo! (Fragment)]). (Figs. 3a–d, 4e, f, 5, 6f, 7h, i, 8, 11a–d; see also photos 25–27 in Côrtes 2013).

Subshrubs 0.30-1 m tall; young stems terete, hirsute, eglandular trichomes 0.3-0.5 mm long, trichomes concentrated in 2 lines. Petiole 0.9-3.2 cm long; blade $3.7-18 \times 2.7-7.7$ cm, ovate to elliptic, cuneate to obtuse, rarely truncate at base, obtuse to attenuate at apex, membranaceous, surfaces glabrous except for trichomes on major veins (eglandular trichomes 0.2-0.3 mm long and sessile glandular trichomes adaxially), margin repand to crenate, with appressed eglandular trichomes 0.07-0.08 mm long. Racemes dichasiate, terminal and axillary, 2.5-7.5 cm long, rachis quadrate, hispidulous with erect eglandular and glandular trichomes 0.06-0.3 mm long and trichomes concentrated in 2 lines; dichasia congested, 1-3-flowered, sessile; bracts green, $3-5.5 \times 1-1.5$ mm, triangular, surfaces glabrous or hispidulous with glandular trichomes 0.08-0.1 mm long, margin equal with 0.1-0.2 mm long or with stalked glandular trichomes 0.3-1 mm long; bracteoles green, $2-5 \times 0.6$ –0.7 mm, triangular, indumentum like that of bracts; pedicels 0.5-0.7 mm long. Calyx green, 6.5–13 mm long, lobes unequal, $6-12 \times 0.5-0.7$ mm, linear triangular, surfaces hispidulous with eglandular trichomes 0.08-0.1 mm long and sessile glandular trichomes or with stalked glandular trichomes 0.4-1.5 mm long only abaxially, margin ciliate with glandular trichomes, 0.4-1.5 mm long (rarely with eglandular trichomes); corolla white or yellow, 1.2-2 cm long, externally glabrous and eglandular trichomes restricted to veins, internally with eglandular trichomes restricted to proximal half of tube, 0.1-0.2 mm long, tube 0.8–1.5 cm long, cylindrical, mouth 2–3 mm diam., upper lip straight, $4.5-5 \times ca. 2 \text{ mm}$, lobes shortly bilobate, lower lip $3.8-5 \times 1.5-2$ mm, lobes 3-4 mm long, straight; stamens 5-5.5 mm long, equal, rarely unequal, inserted up to 5.5-6 mm distal to base of corolla tube, filaments hispidulous, thecae 1.5-2 mm long; pollen grains prolate, heteroaperturate, 3-colporate, 6-pseudocolpate, 2 pseudocolpi per mesocolpium, exine reticulate, heterobrochate, membrane of colpori microverrucate; style 0.8-1.5 mm long, glabrous or hispidulous. Capsules ca. 1.3 cm long, stipe ca. 5 mm long, glabrous, rarely puberulous with flexuous eglandular trichomes ca. 1 mm long; seeds ca. 2.5 mm wide, lenticular, papillate in axils of muri, tuberculate, tubercles present on margin.

Phenology: Flowering in June and from September to February; fruiting in April and from October to January.

Distribution area and habitat: Eastern Brazil; Bahia to Rio de Janeiro, also known from Rio Grande do Sul, but



Fig. 11 *Schaueria capitata:* **a** branch with inflorescence; **b** inflorescence; **c** bract, bracteoles and calyx; **d** flower, showing stamens (drawn from *Côrtes 200). S. paranaensis:* **e** branch with inflorescence;

f inflorescence; **g** bract, bracteoles, and calyx; **h** corolla, showing stamens (drawn from **e** *Falkenberg 4472*; **f–h** *Côrtes 266*). Drawing by Carla Lima

only from the type collection; mainly in submontane semideciduous forests, from 50 to 200 m a. s. l., usually occurring along trails and borders of cacao plantations, but also in shrubby *restingas* of Rio de Janeiro.

Additional specimens examined: Brazil. s.loc., s.d., P.W. Lund s.n. (BM!); Bahia, Prado, Km 21 da rodovia Itamaraju-Prado, 17°09'41"S, 39°23'57"W, 19 Jun 1996, bt., fl., R. Mello-Silva et al. 1170 (SPF!); Espírito Santo, Cachoeiro do Itapemirim, Morro Grande, floresta remanescente no lado sul da estrada para Jerônimo Monteiro (BR-242), 2 km NW da junção com estrada para Muqui (BR-393), 22 Feb 1994, fl., fr., J. Kallunki et al. 602 (NY!, SPF!); ib., Pedra do Itabira, 20°50'S, 41°04'W, 6 Oct 2009, bt., fl., fr., A.L.A. Côrtes et al. 200 (HUEFS!); Muqui, Retiro, fazenda Sabiá, Sr. Constantino, 20°56'S, 41°21'W, 6 Oct 2010, bt., fl., fr., A.L.A. Côrtes et al. 198 (HUEFS!); Santa Teresa, Pedra da Onça, propriedade do Sr. Antônio Rocon, 6 Jan 2000, bt., V. Demuner and E. Bausen 472 (MBML!, RB!); ib., São José de Petrópolis, E.A.S.T. mata da escola agrícola, 19°48'15"S, 40°40'22"W, 2 Oct 2009, bt., fl., fr., A.L.A. Côrtes et al. 187 (HUEFS!); Minas Gerais, Governador Valadares, estrada para Bugre, 12 Sep 1943, bt., M. Magalhães 2527 (RB!, US!); Rio de Janeiro, Campos, Oct 1939, bt., A. Sampaio 8629 (R!); Maricá, APA, 29 Nov 1984, bt., fr., D. Araujo and M.C.A. Pereira 6463 (GUA!).

Conservation status: Schaueria capitata is known from 18 collections corresponding to 12 subpopulations. Approximately 30 mature individuals were observed in three of these subpopulations. However, excluding the isolated population from Rio Grande do Sul, where no specimen has been collected since the type, the species EOO is 72,666 km². Its habitat is continuously threatened because of cacao plantations and other anthropogenic activities in a large part of its range. Therefore, the species is categorized as Near Threatened (NT) under IUCN (2014) guidelines.

Notes: Nees (1847b) considered *Schaueria capitata* close to *S. calytricha*, distinguishing it essentially by smaller calyx lobes. However, other characters also help to differentiate them, such as the dichasiate racemes in *S. capitata* (vs. dichasiate thyrses in *S. calytricha*), smaller $(6-12 \times 0.5-0.7 \text{ vs. } 10-21 \times 0.5-1 \text{ mm})$ and unequal (vs. equal) calyx lobes, white or yellow (vs. only yellow) and smaller (1.2-2 vs. 3.5-4.5 cm long) corollas. In herbaria, it is more often confused with *S. lachnostachya*, from which it can be distinguished mainly by the glandular trichomes 0.4-1.5 mm long on the margin of calyx (vs. eglandular trichomes 1-1.2 mm long in *S. lachnostachya*), apex of upper lip and lobes of lower lobes straight (vs. recurved) and stamens 5-5.5 mm long (vs. 6-8 mm long).

The presence of eglandular trichomes and smaller flowers (1.2 vs. 2 cm long) in some specimens is not sufficient for recognizing separate species. 6. Schaueria paranaensis (Rizz.) A.L.A.Côrtes, comb. nov. \equiv Duvernoia paranaensis Rizz., Dusenia 3: 192. 1952. \equiv Justicia paranaensis (Rizz.) Wassh. & L.B.Sm., Fl. Ilustr. Catarin. 1, Fasc. Acan.: 122. 1969.—TYPE: Brazil. Paraná, Morretes: Estação Marumbi, 1 Sep 1946, *G.* Hatschbach 359 (holotype: RB!; isotype: MBM!). (Figs. 3d, 5, 6g, 7j, k, 8, 11e–h; see also photos 39–41 in Côrtes 2013).

Shrubs 1.5–1.7 m tall; young stems quadrate, glabrous. Petiole 1–1.5 cm long; blade 9.5–15.5 \times 3.2–5 cm, elliptic, acute to obtuse at base, acuminate to falcate at apex, membranaceous, glabrous, margin repand, glabrous. Spikes dichasiate, terminal and axillary, 3.5-7 cm long, rachis quadrate, strigose with eglandular trichomes 0.08-0.1 mm long: dichasia 1-flowered, sessile; bracts green. $2-3.5 \times 0.5-1$ mm, triangular, surfaces hispidulous with eglandular trichomes ca. 0.05 mm long with protuberance, sessile glandular trichomes also present adaxially, margin with erect trichomes; bracteoles green, $2-5 \times 0.8-1$ mm, triangular, indumentum like bracts. Flowers sessile, calyx green, ca. 7 mm long, lobes unequal, $5-6 \times ca. 1$ mm, triangular, indumentum like bracts; corolla yellowish, ca. 1.1 cm long, externally puberulous, internally hispidulous where stamens inserted and near the mouth and on lobes with erect eglandular trichomes ca. 0.3 mm long, tube 4-5 mm long, cylindrical, mouth ca. 2.1 mm diam., upper lip incurved, ca. 7 \times 1.5 mm, lower lip 5–6 \times ca. 2 mm, lobes equal, ca. 5 mm long, recurved; stamens ca. 8 mm long, equal, inserted up to 3 mm distal to base of corolla tube, filaments hispidulous up to the middle, thecae 2-2.5 mm long; pollen grains prolate, heteroaperturate, 3-colporate, 6-pseudocolpate, 2 pseudocolpi per mesocolpium, exine reticulate, heterobrochate, membrane of colpori microverrucate; style ca. 8 mm long, glabrous. Capsules 1.2-1.4 cm long, stipe 5-6 mm long, glabrous; seeds ca. 3.5 mm wide, obovoid, reticulate with sinuous muri and reduced lumina when immature, granulate, tubercles absent on margin.

Phenology: Flowering and fruiting in February and from September to October.

Distribution area and habitat: Southern Brazil; Paraná and Santa Catarina states; in montane and submontane dense rain forests.

Additional specimens examined: Brazil. Paraná, Morretes, Cadeado, 14 Sep 1966, bt., fl., *G. Hatschbach* and *O. Guimarães 14717* (K!, MBM!, US!); ib., rio Bromado, 17 Sep 1979, bt., fl., *G. Hatschbach* and *A.E. Kasper 42495* (MBM!); ib., taquaral, 23 Nov 1984, bt., fl., *R. Kummrow* and *G. Hatschbach 2539* (MBM!); ib., Parque Estadual Estação Marumbi, trilha Cemitério dos Grampos, rio Taquaral, 469 m a. s. l., 25°26'14"S, 48°55'8"W, 4 Oct 2010, bt., fl., *A.L.A. Côrtes* and *R.L.B. Borges 266* (HUEFS!); Santa Catarina, Monte Crista: Garuva, São

Francisco do Sul, 2 Sep 1960, bt., fl., *R. Reitz* and *R.M. Klein 9813* (US!); Parque Botânico Morro do Baú, 18 Sep 1965, fl., fr., *R. Reitz 6768* (MBM!, US!); Joinvile, Reserva CELESC, usina Piraí, 17 Oct 1987, bt., fl., fr., *D.B. Falkenberg 4472* (MBM!).

Conservation status: Schaueria paranaensis is known from 12 collections corresponding to seven subpopulations and EOO of 525 km². Approximately 20 mature individuals were observed in one of these subpopulations. Most collections are from the Pico do Marumbi State Park, where the species is protected. Three others subpopulations are threatened by deforestation and urban development suggesting a decline of the species distribution range and quality of habitat. Therefore, its conservation status is assessed as endangered (EN), for reasons B1ab(iii, iv) under IUCN (2014) guidelines.

Notes: DNA sequences (Côrtes et al. 2015) and pollen grains characters show that *Schaueria paranaensis* is more similar to *Schaueria* than to *Justicia*. In contrast to the other species of the genus, it has corolla lobes that are extremely incurved and the seeds are obovoid, lack tubercles, and have a reticulum with reduced lumina and sinuous muri. It is similar to *S. spicata*, from which it differs by the absence of glandular pedicellate trichomes on inflorescences, smaller (2–3.5 × 0.5–1 mm vs. ca. 5×2 mm), triangular (vs. lanceolate) bracts, and corollas that are internally hispidulous (vs. glabrous) where the stamens are inserted, at the mouth, and on the lobes.

7. Schaueria spicata (Vell.) A.L.A.Côrtes, comb. nov. \equiv Dianthera spicata Vell., Fl. Flumin.: 12. 1829; Fl. Flumin. Icon. 1: t. 28. 1831.—TYPE: Brazil. "habitats sylvis maritimis prope Taguayenses Alpes", *s.d.*, *s.col.* (lectotype **designated here**: illustration Fl. Flumin. Icon. 1: t. 28. 1825, distributed in 1831). (Figs. 3c, 5; 6h).

= *Schaueria schottii* Pohl ex Nees in Martius, Fl. Bras. 9: 107. 1847.—TYPE: Brazil. "in sylvis inter Paraiba et Canta Gallo, circa Aldeam da Pedra et in Serra d'Estrella, prov. Sebastianopolitanae", *H.W. Schott 4723* (Diarium n. Pohl 1893) (lectotype **designated here**: W barcode W0004561 [web!]; isolectotypes: GZU barcode GZU000250353 [photo!], fragment from GZU in US barcode US1105501!, K barcode K529407!).

Subshrubs; young stems terete, sparsely pubescent with eglandular trichomes 0.2-0.3 mm long. Petiole 1-1.5 cm long; blade $9-11 \times 2.5-3.5$ cm, elliptic, acute to attenuate at base, attenuate to falcate at apex, membranaceous, surfaces glabrous except for trichomes on major veins (flexuous eglandular trichomes 0.3-0.4 mm long), margin repand, strigose to pubescent, with appressed and flexuous eglandular trichomes 0.08-0.3 mm long. Spike dichasiate, terminal, ca. 11 cm long, rachis quadrate, pubescent with

flexuous eglandular trichomes 0.2–0.3 mm long and stalked glandular trichomes ca. 0.5 mm long; dichasia 1-flowered, sessile; bracts ca. 5×2 mm, lanceolate, pilose with stalked glandular trichomes ca. 0.5 mm long, margin ciliate with stalked glandular trichomes 0.5–0.6 mm long; bracteoles ca. 4×1 mm, lanceolate, indumentum like bracts. Flowers sessile; calyx 7.5-8 mm long, lobes unequal, $6.5-7 \times ca. 0.7$ mm, narrowly triangular, glabrous, margin ciliate with stalked glandular trichomes 0.5–0.6 mm long; corolla ca. 1.2 cm long, externally pilose with eglandular trichomes 0.4-0.5 mm long, internally glabrous, tube ca. 6 mm long, cylindrical, mouth ca. 4.5 mm long, upper lip slightly incurved (in protologue), lobes shortly bilobate, ca. 6×3 mm, lower lip ca. 6×2 mm, lobes equal, ca. 5 mm long; stamens ca. 5 mm long, filaments glabrous, thecae ca. 2.5 mm long; pollen grains heteroaperturate, 3-colporate, 6-pseudocolpate, 2 pseudocolpi per mesocolpium, exine reticulate, heterobrochate, membranes of colpori microverrucate; style ca. 8 mm long, glabrous. Capsules not seen.

Distribution area and habitat: Southeastern Brazil; Rio de Janeiro state; in submontane semideciduous forests.

Additional specimens examined: Brazil. Rio de Janeiro, forest, descent from Serra dos Orgãos to Frechal, s.d., W.J. Burchell 2538 (K!).

Conservation status: Schaueria spicata is known only by three old collections from Rio de Janeiro with uncertain localities. This species has not been collected in 200 years. The only data available to evaluate this species is declining habitat quality because of deforestation and urban development. The lack of additional information precludes an assessment of the species conservation status, which is therefore assessed as Data Deficient (DD) under IUCN (2014) guidelines.

Notes: Schaueria spicata can be recognised by the long inflorescences covered by stalked glandular trichomes, lanceolate bracts ca. 5×2 mm, corollas ca. 1.2 cm long and with short tube and upper lip incurved, and glabrous filaments.

Nees (1847b, in addenda) included *Dianthera spicata* in the synonymy of *Schaueria schottii*. However, *D. spicata* was published first, having priority over *S. schottii*, hence the combination *Schaueria spicata* proposed here. Because the material of Vellozo has been lost, we designate the illustration as lectotype of *Dianthera spicata*. And the specimen *Schott 4723* deposited at W is chosen as lectotype of *S. schottii*.

8. *Schaueria sulfurea* Pohl ex Nees in Martius, Fl. Bras. 9: 104. 1847.—TYPE: Brazil. "in Serra Grande", *H.W. Schott* 4741 (lectotype **designated here**: W barcode W0033649 [photo!]; isolectotype: GZU barcode GZU0002501419 [photo! Fragment]) (Figs. 3c, 4g, h, 5, 6i–k, 12a, b).

Subshrubs ca. 1 m tall; young stems terete, hirsute with erect eglandular trichomes 0.4-0.5 mm long, trichomes concentrated in 2 lines. Petiole 1-3.5 cm long; blade $6.5-16 \times 2.5-4.7$ cm, lanceolate to elliptic, obtuse at base, attenuate at apex, membranaceous, surfaces sparsely hirsute with eglandular trichomes 0.4-0.7 mm long and sessile glandular trichomes only abaxially, margin repand with erect eglandular trichomes 0.3-0.5 mm long. Thyrses terminal and axillary, 9-14 cm long, rachis cylindrical, hispidulous with erect eglandular trichomes ca. 0.08 mm long; dichasia 1-3-flowered, peduncles ca. 2 mm long; bracts $1.5-2 \times ca. 0.5$ mm, triangular, abaxially strigose with appressed eglandular trichomes ca. 0.2 mm long, adaxially strigose with appressed eglandular trichomes ca. 0.08 mm long, these trichomes with protuberances, margin equal; secondary peduncles 1.5-2 mm long; bracteoles ca. 1.5×0.4 mm, triangular, indumentum like that of bracts; pedicels 1-2.5 mm long. Calyx 3-4 mm long, lobes equal, $2-3.5 \times ca.$ 0.6 mm, triangular, strigose like bracts; corolla yellow, 4-4.5 cm long, externally and internally hirsute-hirsutellous with erect eglandular trichomes 0.1-0.4 mm long generally on veins, tube 2.2-3 cm long, gradually expanded into a throat, narrow at proximal portion ca. $5 \times 1-1.5$ mm diam., throat obconic, ca. $2.5 \text{ cm} \times 6-7 \text{ mm},$ upper lip incurved, 1.3–1.7 cm \times 3–4 mm, entire, lower lip 1.1–1.2 \times ca. 2 mm, lobes equal, 1–1.1 cm long; stamens ca. 4 cm long, inserted near the throat, 1-3 mm up, filaments hispidulous up to middle, thecae 2-3 mm long; pollen grains subprolate, circular, 3-colporate, exine perforate, granulate and microechinate, membrane of colpori microechinate; style ca. 4 cm long, hispidulous. Capsules not seen.

Phenology: Flowering from January to April.

Distribution area and habitat: Southeastern Brazil; Rio de Janeiro state; in submontane semideciduous forests, at 380 m a. s. l.

Additional specimens examined: Brazil. s.loc., 1816–1821, A. de Saint-Hilaire D-14 (P barcode P02901560 [web!] barcode P02901561[photo!]); s.loc., 1816-1821, A. de Saint-Hilaire B2-2474 (P barcode P02901562 [web!]); Rio Janeiro, "In sylvis fluvium Pirahi", Mar 1818, J.E.B. Pohl 5011 (W barcode W0033650 [web!]); Rio de Janeiro-São Paulo, Feb 1861, J. Weir 17 (CGE [photo!], K!, US!); Volta Redonda, Reserva Florestal da Cicuta, 23 Mar 1988, M.F. Frigoletto and C.D. Catete 20 (GUA!, US!).

Conservation status: Schaueria sulfurea is known from eight collections corresponding to three subpopulations. The most recent collections are known from the Cicuta Forest Reserve, between the cities of Barra Mansa and Volta Redonda. Five years ago, access to the reserve was restricted by the Companhia Siderúrgica Nacional and new collections have been forbidden. The species EOO is 330 km². It is

being threatened by urban development and deforestation and its total numbers are estimated to be in continuous decline. Therefore, this species is assessed as Endangered (EN), for reasons B1ab(iv) under IUCN (2014) guidelines.

Notes: Schaueria sulfurea is similar to S. calytricha by the dichasiate thyrses and yellow corollas 4–4.5 cm long; but, in S. sulfurea, the upper lip of the corolla is incurved whereas in S. calytricha, it is recoiled. In addition, the bracts and calyx are smaller in S. sulfurea (bracts $1.5-2 \times$ ca. 0.5 vs. 7–10 × ca. 1 mm and calyx 3–4 mm long vs. 1.1-2.2 cm long). Schaueria sulfurea differs from the other species of the genus by the 3-colporate pollen grains, with perforate, granulate and microechinate exine (Fig. 6i–k), and smooth, appressed trichomes on the calyx (Fig. 4g, h). Furthermore, this is the sole species of Schaueria with plants that have been reported as malodorous (Carauta et al. 6021, in sched.).

Nees (1847a) cited two collections from Rio de Janeiro in the original description of *S. sulfurea*, *Schott 4741* and *Pohl 5011*, both illustrated by Pohl (illustrations at W). The choice of "sulfurea" for the epithet of this name suggests Nees's preference for the collection of Schott, which is designated here as the lectotype of this name (McNeill et al. 2012: Art. 9.3). The original orthography "*sulfurea*", instead of "*sulphurea*" (adopted later by Nees; Nees 1847b), is maintained.

9. *Schaueria thyrsiflora* A.L.A.Côrtes, **sp. nov**.—TYPE: Brazil. Rio de Janeiro, Paracambi: Parque Natural Municipal do Curió, 25 Oct 2010, *D.M. Braz* and *A.H.N. Souza 333* (holotype: HUEFS!; isotype: RBR!). (Figs. 3c, 5, 6l, 7l, m, 8, 12c–g; see also photo 42 in Côrtes 2013).

Herbs; young stems quadrate, hirsute with erect eglandular trichomes ca. 0.3 mm long., trichomes concentrated 2 lines. Petiole 2.7-3.7 cm long; in blade $9.5-12.5 \times 3.5-4.5$ cm, ovate to elliptic or oblong, acuminate at apex, blunt at base, glabrous, margin repand, strigose with appressed eglandular trichomes ca. 0.1 mm long. Thyrses terminal, ca. 4.5 mm long, rachis quadrate, sulcate, hispidulous with erect eglandular trichomes 0.05–0.06 mm long, trichomes concentrated in two lines; dichasia 1-3-flowered, peduncles 2-4 mm long; bracts $1-1.5 \times \text{ca. } 0.5 \text{ mm}$, triangular, adaxially hispidulous with eglandular trichomes ca. 0.1 mm long, trichomes with protuberances, abaxially glabrous; secondary peduncles 2–4 mm long, hispidulous like rachis; bracteoles $1-1.2 \times ca. 0.3$ mm, triangular, indumentum like that of bracts; pedicels ca. 1 mm long. Calyx 6-7 mm long, lobes equal, $5-6 \times ca$. 0.4 mm, linear-triangular, adaxially hispidulous with eglandular trichomes ca. 0.1 mm long with protuberances, sessile glandular trichomes also present abaxially; corolla white, ca. 1 cm long, externally glabrous, tube ca. 6 mm long, cylindrical, mouth ca. 2 mm



Fig. 12 Schaueria sulfurea: **a** branch with inflorescence; **b** bract, bracteoles, and calyx (drawn from *Frigoletto 20*). S. thyrsiflora: **c** branch with inflorescence; **d** inflorescence; **e** bract, bracteole and

calyx; **f** detail of calyx abaxial surface; **g** corolla with stamens and style (drawn from holotype *Braz 333*). Drawing by Carla Lima

diam., upper lip incurved, ca. 4.5×1 mm, entire, lower lip ca. 4.5×1 mm, lobes equal, ca. 3.5 mm long, recurved; stamens ca. 7 mm long, glabrous, thecae ca. 1.5 mm long; pollen grains prolate, heteroaperturate, 3-colporate, 6-pseudocolpate, 2 pseudocolpi per mesocolpium, rarely syncolporate and synpseudocolpate, exine reticulate, heterobrochate, membrane of colpori and colpi microverrucate; style ca. 8 mm long, glabrous. Capsules 1–1.2 cm long, stipe ca. 0.5 mm long, glabrous; seeds ca. 2.5 mm wide, lenticular, reticulate when immature, tuberculate, tubercles on margin.

Diagnosis: Schaueria thyrsiflora is morphologically similar to *S. calytricha*, differing from that species by the hispidulous rachis with erect eglandular trichomes 0.05–0.06 mm long, trichomes concentrated in 2 lines (vs. puberulous to pilose rachis with flexuous eglandular trichomes 0.2–0.3 mm long, trichomes not concentrated in two lines), dichasia 1–3-flowered (vs. 3–5-flowered), smaller (1–1.5 mm vs. 7–11 mm long) and triangular (vs. linear–triangular) bracts, and smaller (ca. 1 vs. 3.5–4.5 cm long) and white (vs. yellow) corollas, with cylindrical tube (vs. tube distally expanded into a throat) and upper lip slightly incurved (vs. recoiled).

Etymology: The epithet refers to the thyrses that characterize the species.

Phenology: Flowering and fruiting in October.

Distribution area and habitat: Southeastern Brazil; Rio de Janeiro state, Paracambi, Curió Municipal Natural Park, between the cities of Engenheiro Paulo de Frontin and Mendes; in semideciduous forest.

Conservation status: Schaueria thyrsiflora is known only from the type collection in Curió Municipal Natural Park, and is assessed as Data Deficient (DD) under IUCN (2014) guidelines.

Notes: Schaueria thyrsiflora, S. calytricha, and S. sulfurea are the only species with flowers borne in thyrses. Schaueria thyrsiflora differs from the other two by the herbaceous habit and loose, green inflorescences. The corolla color (white) and size (ca. 1 cm long) are more similar to S. marginata, S. gonatistachya, and S. hirta.

10. Schaueria gonatistachya (Nees & Mart.) Nees & Mart. in Martius, Fl. Bras. 9: 106. 1847. \equiv Justicia gonatistachya Nees & Mart. in Roemer & Schultes, Mant. 1: 248a. 1822. \equiv Justicia gonystachya (Nees & Mart.) Nees & Mart. in Wied-Neuw., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 11: 52. 1823.—TYPE: Brazil. Bahia, "Ad. Viam Felisbertiam," Jan. 1817, *M.A.P. Wied-Neuw. s.n.* (lectotype: GZU barcode GZU000250357 [photo!], designated by Moraes et al. 2013; isolectotypes: BR barcode BR0000005849376 [photo!, BR0000005849703 [photo!]; lectoparatype GZU barcode GZU000251410 [photo! (fragment)]). (Figs. 3a, 5, 6m, n, 7n, o, 8, 13a–d; see also photos 28 and 29 in Côrtes 2013).

Subshrubs 0.3–2 m tall; young stems terete, glabrous. Petiole 1–1.5 mm long; blade $11.5-21.5(-25) \times 4-7.5(-8)$ cm, elliptic to lanceolate, acute to decurrent at base, rarelly long decurrent, attenuate at apex, membranaceous, glabrous, margin repand, glabrous. Spike dichasiate, terminal and axillary, 3.5-15 cm long, rachis cylindrical, glabrous or sparsely hispidulous with eglandular trichomes ca. 0.06 mm long; dichasia 1-flowered, sessile; bracts green, $1.5-2 \times ca$. 0.7 mm, triangular, glabrous to sparsely hispidulous with eglandular trichomes 0.06-0.08 mm long, these trichomes with protuberances, margin equal; bracteoles green, $1-1.5 \times$ ca. 0.3 mm, triangular, indumentum like that of bracts. Flowers sessile; calyx green, 1.5-2 mm long, lobes unequal, $0.9-1.5 \times ca. 0.3$ mm, triangular, glabrous to sparsely hispidulous with eglandular trichomes 0.06-0.08 mm long, these trichomes with protuberances, adaxially sessile glandular trichomes are present, margin like bracts; corolla white, 1-1.2 cm long, externally glabrous, internally puberulous with eglandular trichomes restricted to the tube ca. 0.2 mm long, tube 6-7.5 mm long, cylindrical, mouth 1.5–2 mm diam., upper lip straight, $3-4 \times 1-1.3$ mm, lobes shortly bilobate, lower lip $2.8-4 \times 1-1.3$ mm, lobes equal, 2.7-3.5 mm long, straight; stamens ca. 4 mm long, equal, inserted up to ca. 4 mm distal to base of corolla tube, filaments hispidulous, thecae ca. 1.5 mm long, slightly oblique; pollen grains subprolate, heteroaperturate, 3-colporate, 6-pseudocolpate, 2 pseudocolpi per mesocolpium, rarely syncolpate and parasyncolporate, exine reticulate, heterobrochate, membrane of colpori microverrucate and rugulate, membrane of pseudocolpi rugulate; style ca. 9 mm long, glabrous. Capsules ca. 1 cm long, stipe ca. 2.5 mm long, glabrous; seeds ca. 3 mm wide, lenticular, reticulate when immature, tuberculate, tubercles on margin.

Phenology: Flowering and fruiting throughout the year. *Distribution area and habitat:* Northeasteastern Brazil; Bahia state, São Felipe in the reconcave region (geographic region located around Baía de Todos os Santos, extending from the coast to the interior of the state, including the cities surrounding the bay) to southern Bahia; in relicts of rain forests, usually along trails and borders of cacao plantations.

Brazil. Additional specimens examined: Bahia, "Nazareth". 1817, F. Sellow s.n. (K barcode K000529416!); Bahia, Ilhéus, Km 22 da rodovia Ilhéus/ Itabuna (BR-145), CEPLAC, quadra D, 106 m a. s. l., 14°46'191"S, 39°13'171"W, 31 Mar 2010, bt., fl., fr., A.L.A. Cortes 237 (HUEFS!); ib., rodovia BA-263, entre Itabuna e Ibicaraí, fazenda São José 2, próxima ao arraial 41, 195 m a. s. l., 14°51′S, 39°31′W, 2 Apr 1987, bt., fl., fr., A.L.A. Côrtes and R.L.B. Borges 239 (HUEFS!); Mascote, Rod. BR-101, próximo ao trevo de Mascote, 11 Oct 1998,



Fig. 13 Schaueria gonatistachya: **a** branch with inflorescence; **b** inflorescence; **c** bracteole and calyx; **d** corolla with stamens and style (drawn from *Côrtes 237*). *S. hirta*: **e** branch with inflorescences; **f** detail of leaf abaxial surface; **g** detail of leaf adaxial surface;

h calyx; **i** detail of calyx abaxial surface; **j** corolla and stamens; **k** fruit; **l** seed (drawn from holotype, *Amorim 6814*). Drawing by Carla Lima

fl., fr., *G. Hatschbach* et al. 68413 (INPA!, MBM, US); São Felipe, Serra da Copioba, 17 May 1993, bt., fl., fr., *C. Kameyama* et al. 67 (HUEFS!, SPF!, US!); Ubaitaba, 8 km de Ubaitaba para Maraú, 15 Apr 1965, bt., fl., fr., *M. Magalhães 19540* (US!).

Conservation status: Schaueria gonatistachya is known from 18 collections corresponding to five small subpopulations. We observed approximately 30 mature individuals per population. However, most collections came from only one locality (Ilhéus, CEPEC—Comissão Executiva do Plano da Lavoura Cacaueira). The species EOO is 17,654 km². It is being threatened by agriculture and deforestation and its total numbers are estimated to be in continuous decline due to the maintenance of cacao plantations. The species is categorized as Vulnerable (VU), for reasons B1ab(iii) under IUCN (2014) guidelines.

Notes: Schaueria gonatistachya is easily recognised by the long inflorescences with flowers diagonally arranged, calyx lobes 0.9–1.5 mm long, and the nectariferous disc, which is evident after the corolla falls.

Originally, Nees and Martius (in Roemer and Schultes 1822) used "gonatistachya", soon changing it to "gonystachya" (Nees and Martius 1823). When Nees (1847a) transferred the species to Schaueria, he changed the epithet to "gonyostachya", a variant also used in the Prodromus (Nees, 1847b). Both variants highlight the inflorescences with flowers diagonally arranged, but the original orthography should be retained (McNeill et al. 2012, Art. 60.1).

11. *Schaueria maximilianii* Nees in Martius, Fl. Bras. 9: 106. 1847.—TYPE: Brazil. Bahia, "Ad viam Felisbertiam", Dec. 1816, *M.A.P. Wied-Neuw. s.n.* (lectotype: GZU barcode GZU000251413 [photo!], designated by Moraes et al. 2013; isolectotypes: BR barcode BR0000006951450 [photo!], BR0000006951405 [photo!], GZU barcode GZU000251415 [photo! (fragment)], W barcode W0004604—F Neg. 32725 [photo!]) (Fig. 3a).

= Justicia nitida auct. non Jacq., Nees & Mart. in Wied-Neuwied, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 11: 56. 1823. \equiv Justicia nitida Nees & Mart. in Martius, Fl. Bras. 9: 106. 1847, hom. post. and pro syn.

Subshrubs; young stems terete, hispidulous with eglandular trichomes ca. 0.1 mm long. Petioles ca. 1 cm long; blade ca. 10×2.4 cm, lanceolate, acute at base, acuminate to slightly falcate at apex, glabrous or sparsely strigose (restricted to major veins) with appressed eglandular trichomes ca. 0.2 mm long, sessile glandular trichomes also present, margin repand, sparsely ciliate. Racemes dichasiate, terminal, rachis quadrate, hispidulous with eglandular trichomes ca. 0.1 mm long (in fruiting); dichasia lax, 1–3-flowered, sessile; bracts $2.5-3 \times$ ca. 0.6 mm, linear–triangular, glabrous, margin ciliate with flexuous eglandular trichomes ca. 0.3 mm long; bracteoles ca. 2.5×0.5 mm, linear– triangular, trichomes like those of bracts; pedicels ca. 2 mm long. Calyx ca. 7 mm long, lobes equal, ca. 6×0.6 mm, linear-triangular, adaxially strigose with appressed eglandular trichomes 0.2–0.3 mm long, abaxially glabrous, margin ciliate with flexuous eglandular trichomes ca. 0.3 mm long; corolla not seen. Capsules ca. 1.3 cm long, stipe ca. 5 mm long, glabrous; seeds ca. 4 mm wide, lenticular, tuberculate when immature, with tubercles on margin.

Phenology: Fruiting in December.

Distribution area and habitat: Northeastern Brazil; Bahia state; in the protologue, *Schaueria maximilianii* was attributed to the Atlantic coast ("*Dryas*"; Martius's classification), probably in rain forests.

Conservation status: Schaueria maximilianii is known only from the type, collected more than 150 years ago in Via Felisbertia—a road where Wied made collections. This road, linking São Pedro de Alcântara to Barra da Vareda, goes through an area strongly disturbed by human activities, such as cacao plantations, agriculture and livestock. The lack of additional information precludes an assessment of the species conservation status. The species is assessed as data deficient (DD) under IUCN (2014) guidelines.

Notes: The description above is based on a fragment in fruit at US, but the original description of the species also includes information about the corolla: white, ca. 11.25 mm long, with emarginate upper lip. Although the species was not included in phylogenetic analyses (Côrtes et al. 2015), it is most likely closely related to species distributed mainly in Bahia. *Schaueria maximilianii* differs from *S. gonatistachya, S. hirta*, and *S. pyramidalis* by the racemose inflorescences with dichasia loose and 1–3-flowered (vs. spicate inflorescences with dichasia dense and 1-flowered), and from *S. marginata* by the lax (vs. congested) racemes and smaller calyx (ca. 7 mm vs. 1–1.3 cm long).

Schaueria maximilianii was collected in via Felisbertia, a road linking São Pedro de Alcântara to Barra da Vareda (Moraes 2009). Nees and Martius (1823) identified it as Justicia nitida Jacq., a species originally described from Martinique. Realising the error, Nees (1847a) described Schaueria maximilianii. However, by trying to exclude Jacquin's species from the synonymy of *S. maximilianii* ("excl. syn."), he inadvertently cited the taxon described in Nees and Martius (1823) as "Justicia nitida N. et M." rather than Justicia nitida Jacq. Thus, the name Justicia nitida was misapplied in Nees and Martius (1823), and Nees (1847a) inadvertently published a posterior homonym by considering Nees and Martius authors of the species described in Nees and Martius (1823).

12. *Schaueria hirta* A.L.A.Côrtes, **sp. nov**.—TYPE: Brazil. Bahia, Itamaraju, Serra do Pescoço, 128 m a. s. l., 16°59'14″S, 39°34'40″W, 4 Apr 2010, bt., fr., *A.L.A.* *Côrtes* and *R.L.B. Borges* 253 (holotype: HUEFS) (Figs. 3a, 4i, 5, 6o, 7p–r, 8, 13e–l; see also photos 30 and 31 in Côrtes 2013).

Perennial herbs ca. 40 cm tall; young stems subcylindrical, hirsute with erect eglandular trichomes, 1-1.7 mm long, trichomes concentrated in 2 lines. Petioles 0.3-1 cm long; blade $10-14 \times 3.5-6$ cm, lanceolate to elliptic, cuneate to acute at base, acuminate at apex, hirsute with erect eglandular trichomes 1-1.7 mm long, margin repand, ciliate with similar trichomes. Spikes dichasiate, terminal and axillary, 7.5-9.5 mm long, rachis subcylindrical, glabrous or sparsely hispidulous with erect eglandular trichomes ca. 0.2 mm long; dichasia 1-flowered, sessile; bract ca. 1.5×1 mm, triangular, sparsely hispidulous with eglandular trichomes bearing protuberances ca. 0.06 mm long on abaxial surface and ca. 0.3 mm long on adaxial surface, sessile glandular trichomes also present; bracteoles ca. 1.5×0.5 mm, lanceolate, indumentum like that of bracts. Flowers sessile; calyx ca. 3.5 mm long, lobes ca. 3×0.5 mm, triangular, indumentum like that of bracts; corolla white, ca. 1.2 cm long, externally glabrous, tube ca. 8.5 mm long, cylindrical, mouth ca. 2.5 mm diam., upper lip straight, ca. 3.5 mm long, bilobate, lower lip ca. 3.5×1.5 mm, lobes equal, straight; stamens ca. 1 cm long, filaments glabrous, thecae ca. 1.5 mm long; pollen grains subprolate, heteroaperturate, 3-colporate, 6-pseudocolpate, 2 pseudocolpi per mesocolpium, exine reticulate, heterobrochate, membrane of colpori microverrucate; style ca. 1 cm long, glabrous. Capsules ca. 1.1 cm long, glabrous, stipe ca. 6 mm long; seeds 3-4 mm wide, lenticular, reticulate when immature, granulate in muri and lumina, tuberculate, tubercles present on margin.

Diagnosis: *Schaueria hirta* is similar to *S. gonatis-tachya*, but with stems and leaves hirsute with eglandular trichomes 1–1.7 mm long (vs. glabrous) and longer calyces (ca. 3.5 vs. <3 mm long).

Etymology: The specific epithet refers to the hirsute indumentum that covers most parts of the plant.

Phenology: Flowering and fruiting in February and April. *Distribution area and habitat:* Eastern Brazil; Bahia and Espírito Santo states; in semideciduous forests, to 300 m a. s. l. In Bahia it is common in cacao plantations.

Additional specimens examined: Brazil. Bahia, Itamaraju, Morro do Pescoço, 15 km da entrada da cidade, 16°59'20"S, 39°35'27"W, 11 Feb 2007, bt., fl., A.M. Amorim et al. 6814 (CEPEC!); Espírito Santo, Nova Venécia, APA Pedra do Elefante, Serra de Baixo, 313 m a. s. l., 18°46'37"S, 40°26'38"W, 19 Feb 2008, bt., fl., fr., R.C. Forzza et al. 5104 (CEPEC!, MBML!, RB!).

Conservation status: Schaueria hirta is known from only three collections corresponding two small subpopulations. Approximately 30 mature individuals were observed in one of these subpopulations. The species' EOO is 1,700 km², it is being threatened by human activity, and the quality of its habitat is in continuous decline because of cacao plantations and deforestation. Based on this, the species is categorized as Endangered, for reasons B1ab(iii) under IUCN (2014) guidelines.

Notes: Although morphologically similar to *Schaueria gonatistachya*, *S. hirta* can be easily recognised by the hirsute indumentum on foliar blades, branches, and inflorescence rachis, longer calyces (ca. 3.5 vs. <3 mm long in *S. gonatistachya*), and seeds with granules in the lumina and muri (vs. granules absent).

13. Schaueria pyramidalis A.L.A.Côrtes, sp. nov.— TYPE: Brazil. Bahia, Jussari, RPPN Serra do Teimoso, entrada 7,5 km da rodovia Jussari-Palmira, 15°10'S, 39°35'W, 1 Sep 2001, bt., fl., *R.P.Oliveira, F.R. Nonato, J.G.C. Sobrinho, E. Bebert* and *L. Bebert* 747 (holotype: HUEFS!). (Figs. 3a, 4j, 5, 6r, 7s, t, 8, 14a–c).

Subshrubs 1.5–1.8 m tall; young stems terete, glabrous to glabrate, sometimes with sessile glands. Petiole 1-3.5 cm long; blade $8-17 \times 2.6-6$ cm, oblong to elliptic, acute to oblique at base, acuminate at apex (rarely slightly falcate), glabrous (rarely with eglandular trichomes restricted on the veins), sessile glandular trichomes present adaxially, margin repand, glabrate. Spikes dichasiate, terminal and axillary, 8-17 cm long, rachis cylindrical, puberulous with flexuous eglandular trichomes 0.1-0.2 mm long; dichasia 1-flowered, sessile; bracts $1.7-2.7 \times 1-1.5$ mm, largely triangular, glabrous, margin with erect eglandular trichomes, ca. 0.08 mm long; bracteoles $1.5-2.5 \times 0.7-1$ mm, narrowly triangular, glabrous, indumentum like that of bracts. Flowers sessile; calyx 6–7 mm long, lobes unequal, $3.5-5.5 \times$ ca. 1 mm, narrowly triangular, adaxial surface slightly hispidulous with eglandular trichomes ca. 0.08 mm long (bearing protuberances on surfaces), sessile to short stalked glandular thricomes also present, margin with erect trichomes; corolla yellow, 3.8–5 cm long, externally glabrous, internally muricate with erect eglandular trichomes ca. 0.05 mm long restricted to the tube, tube 2.5-3 cm long, expanded into a throat distally, narrow proximal portion, ca. $1 \text{ cm} \times 2 \text{ mm}$, throat obconic, ca. $2 \text{ cm} \times 5 \text{ mm}$, upper lip straight, $1.1-1.7 \text{ cm} \times \text{ca.} 2 \text{ mm}$, lobes shortly bilobate, lower lip 0.9–1.7 cm long, lobes unequal, $1-1.6 \text{ cm} \times 0.15-0.2 \text{ mm}$; stamens 3-4 cm long, inserted up to 6-8 mm base of the throat, filaments muricate, thecae ca. 3 mm long; pollen grains prolate, circular amb, heteroaperturate, 3-colporate, 6-pseudocolpate, 2 pseudocolpi per mesocolpium, exine reticulate, heterobrochate, membrane of colpori verrucate and microverrucate; style 3.5–4 mm long, glabrous. Capsules ca. 2 cm long, stipe 1.1-1.2 cm long, glabrous; seeds 5-5.5 mm wide, lenticular, papillate in the axils of muri, reticulate with microgranules when immature, tuberculate, tubercles absent on margin.



Fig. 14 Schaueria pyramidalis: a branch with inflorescence; b bract, bracteole, and calyx; c corolla, showing stamens (drawn from holotype, *Oliveira* 747). S. marginata: d branch with inflorescence;

e inflorescence; **f** bract, bracteoles and calyx; **g** bracteoles, calyx, and corolla, showing stamens and style (drawn from *Côrtes 231*). Drawing by Carla Lima

Diagnosis: Schaueria pyramidalis is closely related to *S. gonatistachya*, but has calyces $6-7 \times ca$. 1 (vs. $2-3 \times ca$. 0.3) mm; corollas yellow (vs. white), 3.8-5 (vs. 1-1.2) cm long, and internally muricate (vs. puberulous); and capsules ca. 2 (vs. ca. 1) cm long.

Etymology: the epithet refers to the pyramidal form of inflorescences.

Phenology: Flowering and fruiting from July to February.

Distribution area and habitat: Northeastern Brazil; southern Bahia; in submontane semideciduous forests on granitic soils (Amorim et al. 2005) from 300 to 450 m a. s. l.

Additional specimens examined: Brazil. Bahia, Jussari, RPPN Serra do Teimoso, entrada 7,5 km da rodovia Jussari-Palmira, 300–450 m a. s. l., 15°09'29"S, 39°31'43"W, 4 Feb 1998, fl., J.G. Jardim et al. 1511 (CEPEC!); ib., 17 Feb 1998, bt., fl., O. Harvey et al. 30 (CEPEC!, NY!); ib., 20 Jul 1998, bt., fl., J.L. Paixão et al. 67 (CEPEC!, NY!); US!); ib., 8 Nov 1998, bt., A.M. Amorim et al. 2589 (CEPEC!, NY!); ib., 8 Aug 2001, bt., fr., J.G. Jardim et al. 3728 (CEPEC!, NY!); ib., 20 Sep 2002, fl., fr., P. Fiaschi and S.C. Sant'Ana 1094 (CEPEC!); ib., 17 Sep 2004, bt., fr., A.M. Amorim et al. 4263 (CEPEC!, NY!); ib., 15 Dec 2004, bt., fl., R.N. Querino and M. Pinheiro 84 (CEPEC!).

Conservation status: Schaueria pyramidalis is known only from the Serra do Teimoso Permanent Protected Reserve, in Jussari, Bahia. The area of occupancy (AOO) is $<10 \text{ km}^2$. It is being threatened by human activity and its total numbers are estimated to be in continuous decline due to the maintenance of cacao plantations. Therefore, the species is categorized as Critically Endangered (CR), for reasons B2ab(iii) under IUCN (2014) guidelines.

Notes: The placement of *Schaueria pyramidalis* in the genus is supported by phylogenetic analyses (Côrtes et al. 2015). It is closely related to *S. gonatistachya*, *S. marginata*, and *S. hirta*, which are also predominantly endemic to Bahia, but with the latter species also occurring in northern Espírito Santo. However, it can be distinguished from these three species by the yellow, larger (>3.5 cm long) and internally muricate corollas, whereas the other species possesses white, smaller (<2 cm long), and internally puberulous corollas.

14. *Schaueria marginata* Nees in Martius, Fl. Bras. 9: 102. 1847.—TYPE: Brazil. "In sylvis Soteropolin", *s.d.*, *C.F.P. Martius s.n.* (holotype: M photo F No. 20503!; isotype: GZU barcode GZU000251424 [photo! fragment]). (Figs. 3a, 4k, l, 5, 6p, q, 7u, v, 8, 14d–g; see also photos 37 and 38 in Côrtes 2013).

Subshrubs 30–80 cm tall; young stems quadrate, hirsute with eglandular trichomes ca. 0.4 mm long, trichomes concentrated in two lines. Petiole 1–2.5 mm long; blade

 $10-21.5 \times 2-4.5$ cm. lanceolate, attenuate at base, acute to acuminate at apex, chartaceous, glabrous or hispidulous with erect eglandular trichomes ca. 0.1 mm long and ca. 0.08 mm long mostly on the major veins and margin, margin repand. Racemes dichasiate, terminal, 2.5-5.5 cm long, rachis quadrate, hispidulous with erect eglandular trichomes ca. 0.3 mm long and glandular ca. 0.5 mm long; dichasia congested, 1- or 2-flowered, sessile; bracts green, $5-7 \times 2-2.5$ mm, oblong, hispidulous with erect eglandular trichome ca. 0.3 mm long and stalked glandular trichomes, sessile glandular trichomes also present adaxially; bracteoles green, $4-6 \times ca$. 1 mm, triangular, hispidulous like that of bracts; pedicels ca. 1 mm long. Calyx green, 1–1.3 cm long, lobes unequal, $8-12 \times ca.$ 1 mm, triangular, surfaces hispidulous with erect eglandular trichomes ca. 0.3 mm long, stalked glandular trichomes ca. 0.7 mm long and sessile glandular trichomes, margin ciliate with stalked glandular trichomes ca. 0.7 mm long; corolla white, ca. 1.7 cm long, externally puberulous with glandular trichomes (from the mouth to the apex of lobes), internally puberulous with eglandular and glandular trichomes on tube, tube ca. 1.1 cm long, cylindrical, mouth ca. 2.5 mm wide, upper lip straight, ca. 5.5×2.5 mm, lip shortly bilobate, lower lip ca. 5.5×2.5 mm, lobes equal, straight; stamens ca. 7 mm long, inserted up to 8 mm from the base of corolla tube, filaments hispidulous, thecae ca. 1.5 mm long; pollen grains prolate, subtriangular amb. heteroaperturate, 3-colporate, 6-pseudocolpate, 2 pseudocolpi per mesocolpium, exine reticulate, heterobrochate, membrane of colpori microverrucate; style ca. 1.2 cm long, glabrous. Capsules ca. 1 mm long, stipe ca. 4 mm long, glabrous; seeds ca. 3.5 mm wide, lenticular, slightly reticulate when immature, papillate in axils of reticulum, tubercles present on margin.

Phenology: Flowering and fruiting in March to November.

Distribution area and habitat: Northeastern Brazil; Bahia state, Cruz das Almas and São Felipe, two cities enclosed in the reconcave region (geographic region located around Baía de Todos os Santos, extending from the coast to the interior of the state, including cities surrounding the bay); in relicts of rain forest, from 100 to 200 m a. s. l.

Additional specimens examined: Brazil. Bahia, Cruz das Almas, Mata do EBDA, 12 Nov 1983, bt., J.C.A. Lima et al. 219 (MBM!, HRB!, HUEFS!); ib., 17 May 1993, bt., C. Kameyama and G.L. Esteves 65 (HUEFS!, SPF!); ib., 259 m a. s. l., 12°39'S, 39°6'W, 27 Mar 2010, fl., fr., A.L.A. Côrtes et al. 231 (HUEFS!); São Felipe, Serra da Copioba, Oct 1950, fr., G. Pinto 588 (IAC!).

Conservation status: Schaueria marginata is known from five collections corresponding to three small subpopulations. Approximately 50 mature individuals were observed in one

of these subpopulations. Its EOO is 1300 km^2 , it is being threatened by urban development and deforestation. Based on this, the species is assessed as Endangered (EN) for reasons B1ab(iii) under IUCN (2014) guidelines.

Notes: Schaueria marginata is phylogenetically related to the other species from Bahia, and emerges as sister to the clade consisting of *S. gonatistachya*, *S. pyramidalis*, and *S. hirta* (Côrtes et al. 2015). It can be easily distinguished from these three species by the chartaceous (vs. membranaceous) leaves with a deccurent (vs. acute) base, larger $(5-7 \times 2-2.5 \text{ vs. } 1.5-3 \times 0.7-1.5 \text{ mm})$ and oblong (vs. triangular to widely triangular) bracts, and larger (>7 vs. <6 mm long) calyx lobes with stalked glandular trichomes (vs. without). The corollas are similar to those of *S. gonatistachya* and *S. hirta*, but larger (ca. 1.7 cm long vs. 1-1.2 cm long), whereas in *S. pyramidalis*, the corolla is larger (3.8–5 mm long) and yellow.

Excluded and Dubious species

Phylogenetic analyses based on DNA sequences (Fig. 1; Côrtes et al. 2015; McDade and Darbyshire personal comm.) revealed that six species traditionally treated in *Schaueria*—*S. azaleiflora*, *S. hirsuta*, *S. humuliflora*, *S. malifolia*, *S. parviflora*, and *S. populiflora*—are more closely related to other lineages of Justicieae, other genera in the *Tetramerium* lineage, or other groups of Acanthaceae. One species of *Fittonia* (*F. albivenis* (Lindl. ex Veitch) Brummitt) is sister to *Schaueria* and could be included in it. Because *Fittonia*, with its variegated leaves, is widely known in horticulture (Brummitt 1978), possible taxonomic changes are deferred until the generic status of its species can be firmly established based on both morphological and molecular data.

Excluded here

1. Schaueria azaleiflora Rusby, Mem. New York Bot. Gard. 7: 365. 1927.—TYPE: Bolivia. 1800 m a. s. l., 23 Aug 1921, O.E. White 990 (holotype: NY!; isotypes: BKL, K!, MICH!).

Notes: Schaueria azaleiflora is strongly supported as diverging at the root of *Pachystachys* s.l. and is being transferred to that genus (Côrtes et al. 2015).

2. Justicia ilhensis (Moric. ex Nees) A.L.A.Côrtes, comb. nov. \equiv *Rhytiglossa ilhensis* Moric. ex Nees in Martius, Fl. Bras. 9: 122. 1847. \equiv *Ecbolium ilhense* (Moric. ex Nees) Kuntze, Revis. Gen. Pl. 2: 980. 1891.—TYPE: Brazil. Bahia, "prope oppidum Ilheos", *s.d., J.S. Blanchet s.n.* (holotype: G barcode G236398 [web!]).

= Schaueria hirsuta Nees in Martius, Fl. Bras. 9: 103. 1847. — TYPE: Brazil. Bahia, "prope Soteropolin", 1840, *J.S. Blanchet 3131* (holotype: G barcode G308098 [web!]; isotype: GZU barcode GZU000250356 [photo!]), **syn. nov.** (Figure 6s, t).

Notes: Examining specimens of *Schaueria hirsuta* and *Rhytiglossa ilhensis*, we realised that characteristics such as chartaceous and oblong leaves and chartaceous bracts and calyx in *S. hirsuta* (vs. elliptic, membranaceous leaves and membranaceous bracts and calyx in *Rhytiglossa ilhensis*) are insufficient to separate them. Furthermore, molecular data and macro- and micromorphological studies—presence of rugulae, displaced thecae and 2-colporate pollen grains with reticulate exine, membrane of colpori rugulate and 7–9 pairs of areolae per colpori—confirm its placement in *Justicia*. The two names were published simultaneously, but because the specific epithet "hirsuta is already occupied in *Justicia, J. ilhensis* should be the correct name for the species in this genus.

Specimens examined—Brazil. Bahia, Amargosa, Serra do Timbó, barragem do Timbó. Área de estudos do projeto Timbó/Centro Sapucaia, 697 m a. s. l., 13°4'57"S, 39°39'15"W, 29 Jan 2007, D.B.O.S. Cardoso, J.S. Souza and Manuel "Cheira-Cheira" 1716 (HUEFS!); Ilhéus, estrada Una-São José da Vitória Km 18, 15°12'56"S, 39°10'32"W, 23 Oct 2004, M.N.S. Stapf et al. 349 (HUEFS!).

3. Schaueria humuliflora (Nees & Mart.) Nees & Mart. in Martius, Fl. Bras. 9: 102. 1847. \equiv Justicia humuliflora Nees & Mart., Nov. Act. Ac. Nat. Cur. 11(1): 53. 1823.—TYPE: Brazil. Bahia, "ad viam Felisbertiam", *M.A.P. Wied-Neuw. s.n.* (holotype: BR barcode BR0000006952068 [photo!]).

Notes: Schaueria humuliflora is more closely related to *Thyrsacanthus* (Fig. 1; Côrtes et al. 2015). It is morphologically distinct from the other species of that clade by the larger, broad bracts and small white corolla (vs. narrow bracts and large red corolla). Additional attention should be given to this species in further studies on *Thyrsacanthus*.

4. Chamaeranthemum malifolius (Nees) A.L.A.Côrtes, comb. nov. \equiv Schaueria malifolia Nees in Martius, Fl. Bras. 9: 103. 1847.—TYPE: Brazil. Rio de Janeiro, "Ad Rio de Janeiro, Septembri", *L. Riedel or B. Luschnath s.n.* (holotype: LE; isotype: GZU barcode GZU000250355 [photo!]).

Notes: This species consists of herbs with leaves ovate, basally truncate and with the major veins white, inflorescences consisting of 1-flowered dichasia arranged in spikes with the rachis hirsute, bracts lanceolate and flowers with 4 fertile stamens (two bithecous and two unithecous). Originally described in *Schaueria*, these plants are more similar to *Chamaeranthemum* Nees, in the *Pseuderanthemum* lineage (McDade et al. 2000). *Chamaeranthemum* comprises seven species, distributed in Central America and Brazil, and can be distinguished from *Pseuderanthemum* by the androecium (two bithecous and two unithecous stamens vs. two fertile stamens and two staminodes in *Pseuderanthemum*) (Nees 1847a).

Specimen examined—Brazil. Rio de Janeiro, Rio de Janeiro, Barra da Tijuca, Morro do Focinho do Cavalo, vertente sul, 100–175 m a. s. l., 1 Oct 2001, *C.A.L. Oliveira* 1917 (GUA!).

5. Schaueria parviflora (Leonard) T.F.Daniel, Proc. California Acad. Sci. 46(12): 286. 1990. \equiv Streblacanthus parviflorus Leonard, J. Wash. Acad. Sci. 31: 103. 1941.— TYPE: Guatemala. Izabal, Escoba, a cross bay (West) from Puerto Barrios, 3 May 1939, *P. Standley 72949* (holotype: F [photo!]; isotype: US!).

= Schaueria calycobractea Hilsenb. & D.L.Marshall, Brittonia 35: 362. 1983.—TYPE: Mexico. Veracruz, Estación de Biología Tropical Los Tuxtlas, 22 Jul 1978, D.L. Marshall 1 (holotype: US!; isotypes: MEXU, TEX!, US!).

Notes: Although the position of *Schaueria parviflora* is not resolved, its placement in *Schaueria* is contradicted by molecular phylogenetic data. The species appears to be closely related to the *Mirandea* clade or to the core *Tetramerium* lineage, both of which, like *S. parviflora*, are predominantly distributed in North and Central America (Côrtes et al. 2015 and McDade's unpublished data).

 Schaueria populifolia C.B.Clarke in Oliver, Fl. Trop. Afr. 5(2): 242. 1900.—SYNTYPES: Camarões. Fernando Po, 1862. G. Mann 1426 (K barcode K5419169 [photo!], 419170 [photo!]); Bipinde, 1896, G. Zenker 1205 (BM!).

Notes: Unpublished molecular data by McDade (Ian Darbyshire 2012, personal comm.) show that *S. populifolia* is more closely related to the Isoglossinae lineage.

Excluded previously

7. *Carlowrightia linearifolia* (Torr.) A.Gray, Proc. Amer. Acad. Arts 13: 364. 1878, non *C. linearifolia* Lindau (1897). \equiv *Schaueria linearifolia* Torr., Rep. U.S. Mex. Bound., Bot. [Emory]: 123. 1859.—TYPE: "Collected in expedition from Western Texas to El Paso, New Mexico" 5 Oct 1849, *C. Wright 436* (lectotype: US!, designated by Daniel 1981; isolectotypes: GH!, 2 sheets, K!, PH!, TEX!).

8. *Carlowrightia torreyana* Wassh., Phytologia 12: 427. 1965, non *C. parvifolia* T.S.Brandegee. \equiv *Schaueria parvifolia* Torr., Rep. US Mex. Bound., Bot. [Emory] 122. 1859. —TYPE: "Coll. N. Mex." 1851-52, *C. Wright 1460*

(lectotype: NY!, designated by Daniel 1981; isolectotypes: GH!-2 sheets, MO!, NY!)

9. *Pseuderanthemum paniculatum* (Nees) V.M.Baum, Brittonia 34(4): 433. 1982. \equiv *Schaueria paniculata* Nees in Martius, Fl. Bras. 9: 106. 1847. \equiv *Odontonema paniculatum* (Nees) Lindau in Engler & Prantl, Nat. Pflanzenfam. IV(3b): 335. 1895.—TYPE: Brazil. "in Brasilia, loco incerto", *F. Sellow* s.n (holotype: B destroyed, F [web 8771!], NY!)

10. *Thyrsacanthus boliviensis* (Nees) A.L.A.Côrtes & Rapini, Taxon 59(3): 967. 2010.

= Schaueria caduciflora Griseb., Symb. Fl. Argent.: 261. 1879. \equiv Anisacanthus caduciflorus (Griseb.) Ariza, Bol. Soc. Argent. Bot. 22: 255. 1983.—TYPE: Argentina. Gran Chaco, Laguna del Palmar, *P.G. Lorentz* and *G.H.E.W. Hieronymus* 554 (holotype, GOET [photo!]).

Dubious species

11. *Schaueria decipiens* Nees in De Candolle, Prodr. 11: 316. 1847.—TYPE: In protologue "Supra Rio Grande Regno Mexico" *s.d.*, *C.G. Ehrenberg s.n.* (holotype: B destroyed; isotype: GZU [photo! (fragment)]).

Notes: Nees (1847b) compared *Schaueria decipens* with *Justicia pectolaris* Jacq., which is widely distributed in the Neotropics and, according to him, presents flowers and fruits similar to those in *Schaueria*. The corolla of *S. decipiens* is extremely short with respect to the other species of the genus. Study of the type fragments at GZU reveals that it most likely pertains to *Carlowrightia*, as suggested by Hilsenbeck and Marshall (1983), a genus that also bears small flowers. Unfortunately, the fragments at GZU are insufficient to identify them to species.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

Appendix

Specimens examined (the numbers of the species in the text are in brackets)

A. Dziewa 122 (6); A. Frazão s.n. (1), s.n. (2); A. Glaziou 222 (3); A. Saint-Hilaire 14 (8), B2-25^a (1), B2-2474, 2774 (8); A. Sampaio 8529 (3), 8629 (5); A.A. Santos 94 (4); A.C. Brade 14974 (2), 19899 (4); A.L.A. Cortes 147, 152-154, 159 (2), 160 (1), 187 (5), 193 (3), 198, 200 (5), 231 (14), 237, 239 (10), 243 (12), 266 (6); A.M. Amorim 2589, 4263 (13), 6814 (12); A.M. Carvalho 273 (10); A.P. Duarte 5041 (5); A.P. Fontana 203 (5); A.S. Leão 128 (1); B. Lutz 646 (3); C. Farney 3870, 4126, 4477 (1); C. Kameyama 65 (14), 67 (10); C. Lindle 1828 (1); C.A.L. Oliveira 1508, 2060 (3); C.F.P. Martius s.n. (F20503) (14); C.M. Rizzini 166, 24877 (3); C.M.S. Lira 169, 246 (1); C.V. Freire 379 (5); D. Araujo 3168, 3239, 3738, 3868 (1), 4840, 6463 (5), 9408 (1), 9430 (2), 10476, 11106 (3); D. Braz 333 (9); D. Douglas s.n. (1); D. Flores 97 (3); D. Sucre 1168 (2), 1168, 3297, 7058 (3); D.B. Falkenberg 4472 (6); E. Bausen 472 (3); E. Costa 195 (3); E. Pereira 4041, 7192 (3); F. Segadas-Vianna s.n. (US 677), (US 1392) (2); F. Sellow 179 (1), 592 (2), s.n. (K 000529416!) (10), s.n. (BM 000949836!), s.n. (K 000529411), s.n. (K 000529412), s.n. (K 000529415) (3), L0B304 (3); F.E. Miranda 7 (1); F.Oliveira 424 (3); G. Gaudich, 457, 839 (1), 5136 (3); G. Hatschbach 359, 14697, 14717, 42495 (6), 68412 (10); G. Lindley s.n. (1); G. Pinto 588 (14); G.V. Nash 9634 (1); H. Luederwaldt s.n. (SP14699) (3); H.W. Schott 4723 (7), 4741 (8), 4743 (2); H.Z. Berardi 15 (1); I.A. Rodrigues 113 (1); I.H. Alcântara 123 (3); J. Fontella 2607 (1); J. Kallunki 602 (5); J. Miers 3739 (1); J. Tweedie s.n. (K 529417) (5); J. Vidal 39 (3); J. Weir 17 (8); J.B.E. Pohl 4736 (4), 5011 (8); J.C.A. Lima 219 (14); J.G. Jardim 1511, 3728 (13); J.L. Hage 508, 600, 962, 2133, 2212 (10); J.L. Paixão 67 (13); J.M.A. Braga 1823 (2), s.n. (3); J.P.P. Carauta 1402 (1), 4389 (4), 4932, 5053, 6951 (3), 6021 (8), 6948 (3); K. Csiba 15897 (1); L. Emygdio 1479, 45098 (5); L. Lollmann 10783 (5); L. Sergio 282 (3); L.B. Smith 6545 (2); L.F. Pabst s.n. (US, HB28125) (2); Lehnvoelse s.n. (US14915) (2); M. Magalhães 2527 (5), 19540 (10), s.n. (5); M. Rosa 73 (3), 52205 (5), s.n. (GUA 23304) (3); M.

Sobral 5468 (10); M.A.P. Wied-Neuw. s.n. (BR 2562175) (1); s.n. (BR 000008058744), s.n. (BR 000008096937), s.n. (BR 000008096975), s.n. (herbarium Wied nr. 122) (3); s.n. (GZU 000250357) (10); s.n. (GZU 000251413) (11); M.B. Casari 116, 355 (1); M.C. Vianna 1526 (1), 1666 (3), 2094 (1), 2632 (2); M.C.F. Santos 81 (3), 230 (1); M.F. Frigoletto 20 (8); M.G. Santos 391 (1); N. Taylor 9634 (1); N.T. Lund s.n. (5); O. Harvey 30 (13); P. Fiasch 1094 (13); P.H.E. Labiak 1904 (6); P.J.M. Maas 6977 (10), 8414 (1); R. Andreata 479 (1); R. Kummrow 2539 (6); R. Mello-Silva 1170 (5); R. Reitz 6768, 9813 (6); R. Ribeiro 231, 293 (3), 680, 2135 (1); R.B. Pineschi 31 (3); R.C. Forzza 5104 (12); R.N. Querino 84 (13); R.P. Belém 897 (10); R.P. Oliveira 747 (13); R.S. Bianchini 259 (2); S.R. Profice 11 (1); T.B. Croat 53725 (1); T.S. Santos 3409 (10); V. Demuner 472 (5); V.F. Ferreira 3949 (1); V.G. Trice 49 (1); W.J. Burchell 2538 (7).

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