



Hidden treasures in the cabinets: an overlooked new species of *Solanum* (Solanaceae) from northeastern Brazil described almost two centuries after its first collection

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ABSTRACT

As part of an ongoing treatment of species of the *Brevantherum* clade of *Solanum*, a new species from the Atlantic Forest of Brazil was discovered and is described here. *Solanum helix* Giacomini & Stehmann sp. nov. is a species well represented in herbaria that has been overlooked for almost two centuries. It has a unique expanded non-inflated fruiting calyx that resembles a propeller and that is not found in any unarmed species of *Solanum*. This discovery highlights the importance of continued herbarium and field work in hyperdiverse ecosystems, such as the Atlantic Forest in South America. Taxonomic affinities are discussed and images, as well as mapped distribution, are given. A key to closely related species for NE Brazil is also provided.

Keywords: seasonal forests, forest fragmentation, taxonomy, indument, herbaria.

Introduction

Among the ten most diverse genera of flowering plants, the economically important genus *Solanum* L. harbors crops such as the potato and the tomato (Humphreys & Linder 2009; Michelangeli *et al.* 2019). Despite its cosmopolitan distribution, at least 75% of its species are native to the Neotropics (Nee 1999; Solanaceae Source 2022). Within the Neotropics, most of the 11 to 14 recognized lineages of the genus (Särkinen *et al.* 2013; Gagnon *et al.* 2022) have a circum-Amazonian distribution, with centers of

diversity in the Andes or in eastern Brazil (e.g. Whalen 1983; Knapp 2002a).

The *Solanum* centers of diversity in eastern Brazil are all associated with the Atlantic rainforest (Knapp 2002a; BFG 2021), a phytogeographic domain known by its astonishing rates of plant diversity and endemism (Stehmann *et al.* 2009; <https://www.conservation.org/priorities/biodiversity-hotspots>), but also by a history of devastation and expansion of urban centers (Dean 1996; Ribeiro *et al.* 2009). Although only an estimated 12 to 16% of its native vegetation remains (Ribeiro *et al.* 2009; Rezende *et al.* 2018), most recent species

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discoveries within *Solanum* in Brazil are associated with the domain, and undoubtedly more species remain to be collected and described (e.g. Giacomin *et al.* 2013; Giacomin & Stehmann 2014; Knapp *et al.* 2015; Gouvêa & Stehmann 2016; Sampaio & Agra 2016; Stehmann & Moreira 2016; Gouvêa *et al.* 2018; 2020).

The Brevantherum clade is one of the main recognized lineages of *Solanum* (Weese & Bohs 2007; Gagnon *et al.* 2022), with a wide distribution from the southern United States to Argentina, with a few invasive species in the Old World tropics (Roe 1972; Giacomin 2015). The clade, which contains 95 described species and at least eight undescribed taxa, is somewhat heterogeneous morphologically. Within the Brevantherum clade, at least four main groups are phylogenetically supported (Gagnon *et al.* 2022): i) the *Solanum trachytrichium* Bitter species group, comprised of two small herbaceous species from Brazil and Argentina with unbranched trichomes, marked geminate sympodial units and leaf-opposed inflorescences (treated in Knapp *et al.* 2015), ii) section *Gonatotrichum* Bitter, with eight species, comprised of small widespread invasive weeds with explosive fruits (treated in Stern *et al.* 2013), iii) the *Solanum inornatum* Witasek species group, with four species, a group of montane herbs from southeastern Brazil with few seeded fruits (ca. 10) and very large seeds (treated in Giacomin & Stehmann 2014), and iv) a group of shrubs to trees characterized by an indument of stellate trichomes and lateral or terminal inflorescences [“stellate subclade” in Giacomin (2015)], where 80 of the 95 described species lie.

As part of an ongoing effort to list and monograph species belonging to the Brevantherum clade of *Solanum* (Giacomin, unpub. data), an overlooked undescribed species was identified occurring in seasonal forests of the Brazilian Atlantic Forest domain. The species is part of the “stellate subclade” of Giacomin (2015) and have considerable material available in herbaria as its first collection dates from almost two centuries ago. Its phylogenetic affinities, morphological characters, ecology, and conservation status are discussed below.

Material and methods

The description presented is based on field observations and examination of herbarium specimens, considering the following collections were visited (acronyms from *Index Herbariorum*, <http://sweetgum.nybg.org/ih/>): ALCB, ASE, BHCB, CEPEC, EAC, HST (non-indexed), HSTM, HUEFS, HURB, IPA, JPB, K, MBM, MO, NY, PEUFR, RB and UFP. Besides the examined material, images of types from related species were visualized on the Global Plants website (<https://plants.jstor.org>), especially from BR, M, G and P herbaria. Measurements presented were mostly taken from dried material in the case of vegetative characters and rehydrated or material preserved in 70% alcohol in

the case of reproductive characters. The terms used in the descriptions are based on Radford *et al.* (1974) and Roe (1971), the latter being applied mostly for the trichome terminology; for the definition and typology of sympodial units see Knapp (2002b) and the conservation status was assessed using IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee 2022). Extent of Occurrence (EOO) and Area of Occupancy (AOO) were calculated using the GeoCat tool (Bachman *et al.* 2011) available at <http://geocat.kew.org> using the standard 2 km² cell width for AOO calculation. The listed examined material is given as a supplementary file (Supplementary material), as a .xlsx spreadsheet. A key to all species of the Cordovense species group (sensu Giacomin 2015) occurring in NE Brazil is presented after the treatment [the Northeast political region of Brazil encompasses the following states: Alagoas (AL), Bahia (BA), Ceará (CE), Maranhão (MA), Paraíba (PB), Pernambuco (PE), Piauí (PI), Rio Grande do Norte (RN) and Sergipe (SE)]. For the morphological definition of the Cordovense species group, see Giacomin (2015). To identify main groups within *Solanum*, the multiaccess available at <http://www.xper3.com/xper3GeneratedFiles/publish/identification/3646482090706093198/mkey.html> should be consulted.

Results

Taxonomy

Solanum helix Giacomin & Stehmann, sp. nov. (Figs. 1, 2, 3)

urn:lsid:ipni.org:names:77322646-1

Type: BRASIL. Bahia: Mun. Santa Teresinha, Serra da Jibóia, estrada não pavimentada que leva ao topo da serra, nas torres de transmissão, passando pelo povoado de Pedra Branca, fragmento de floresta estacional marginal a estrada, 12°50'52"S, 39°28'50"W, 700 m, 6 November 2013 (fl, fr), L.L. Giacomin, L. Bohs, S. Knapp & L.C. Marinho 2000 (Holotype: BHCB [2 sheet holotype: sheet 1 (fl) BHCB019123, sheet 2 (fr) BHCB019124]! (Isotypes: BM!, HUEFS000109618!, NY02240756!, UT!).

Diagnosis: *Solanum helix* is similar to *S. didymum* Dunal and *S. anisocladum* Giacomin & Stehmann, but can be easily distinguished from both by its abaxial leaf surfaces with mostly stalked porrect-stellate trichomes with midpoints shorter than lateral rays and stalks uniform in length, giving it a unique appearance of a uniform “canopy”, while a variety of trichomes, both sessile and stalked, with midpoints longer than the rays are observed in the other two species. The calyx of *S. helix* is also unique: it does not become inflated and accrescent in fruit like that of *S. didymum* and *S. anisocladum*, but instead the deltate lobes become spreading and very elongated (oblong), giving it a characteristic aspect at maturity, resembling a propeller (Fig. 2E).



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Figure 1. Holotype specimen (sheet one) of *Solanum helix* Giacomín & Stehmann (L.L. Giacomín *et al.* 2000, BHC B19123). Reproduced with permission of BHC B Herbarium, Universidade Federal de Minas de Gerais.

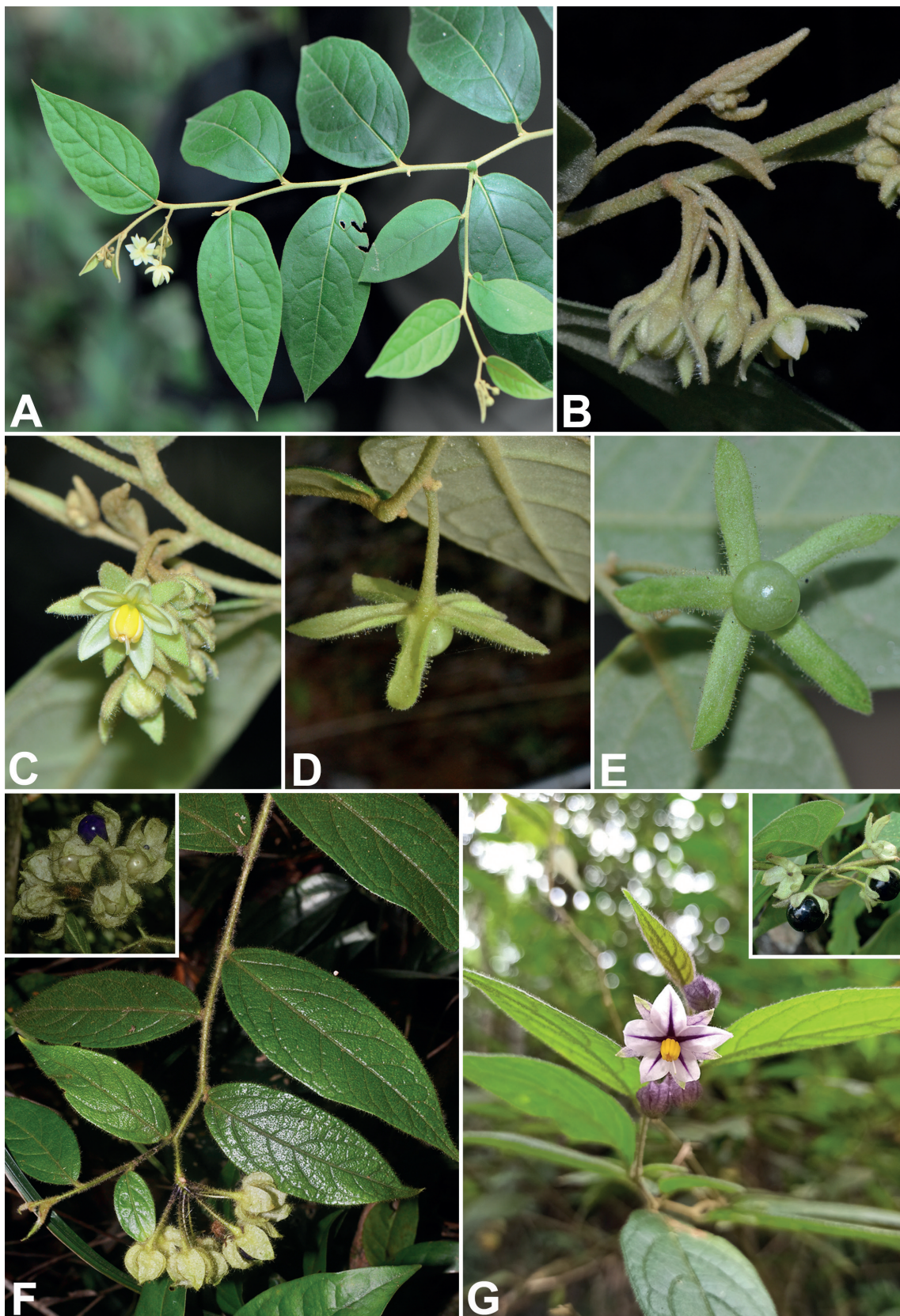


Figure 2. *Solanum helix* Giacomini & Stehmann and related species. **A.** Sympodial units. **B.** Inflorescence architecture. **C.** Flower and buds. **D.** Abaxial fruiting calyx with trichome details. **E.** Fruit with unique spreading calyx. **F.** *S. anisocladum* Giacomini & Stehmann, with fruit detail in the upper left corner. **G.** *S. didymum* Dunal, with fruit detail in the upper right corner. Photos: A, B, C, D, E, F = L. L. Giacomini; G = J. D. Tovar.



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Figure 3. Known distribution of *Solanum helix* Giacomini & Stehmann (circles). States abbreviations shown: AL (Alagoas), BA (Bahia), CE (Ceará), DF (Distrito Federal), ES (Espírito Santo), GO (Goiás), MA (Maranhão), MG (Minas Gerais), PB (Paraíba), PE (Pernambuco), PI (Piauí), SE (Sergipe), SP (São Paulo), TO (Tocantins), RJ (Rio de Janeiro) and RN (Rio Grande do Norte).

Description: Shrubs, up to 4 m, apical branches pendant, young stems with a markedly uniform golden-ochraceous indumentum, densely covered by 8-rayed short-stalked porrect-stellate trichomes, up to 1 mm diameter, with a ca. 0.5 mm multiseriate stalk and a one-celled midpoint much shorter than the rays (old growth glabrescent, with a few remnant trichomes). Bark of older stems yellowish-brown, delicately fissured, with remaining trichome bases. Sympodial units 1–2-foliolate, not geminate. *Leaves* entire, petioles sulcate, 2–4 mm long, blades 5.2–14.3 × 1.7–5.5 cm, narrowly elliptic to lanceolate, sometimes obovate, chartaceous, strongly discoloured when dried, pale green to brown above, pale yellow to green beneath, the adaxial surface slightly bullate, along the blade densely to sparsely covered with three types of trichomes: unbranched 1–2-celled eglandular trichomes ca. 0.5 mm long, small unbranched glandular capitate trichomes with less than 0.5 mm, a single-celled base and single-celled glandular head, and less frequent 4–8 rayed sessile to short-stalked porrect-stellate trichomes with a midpoint usually as long as the rays; the blade surface always visible abaxially (not entirely covered by the trichomes), usually with porrect-stellate trichomes only in the midrib, these more densely packed, the abaxial surface densely covered with 8-rayed short- to long-stalked porrect-stellate trichomes, stalks from 0.5 to 1 mm, midpoint always shorter than the rays, forming a very uniform indumentum on the blade and midrib, with only a few unbranched glandular-capitate trichomes observed underneath the stellate “canopy”, with the blade surface barely visible (almost completely covered by the trichomes), midrib and secondary veins slightly impressed above, raised beneath, the secondaries in 4–6 pairs, ascending, base cordate to rounded, sometimes asymmetric, apex acute to acuminate (acumen, when present, ca. 1.5 cm long), margins entire, slightly revolute. *Inflorescence* 1.5–3.5 cm long, lateral or more often subopposite the leaves, unbranched cyme, 4–15 flowered, but usually bearing 1–4 flowers at a time, densely covered with trichomes like those of the stem, subsessile or with peduncles up to 4 mm, pedicels 1–1.7 cm long, widening towards the apex (from 0.5 at base to 1 mm at the apex), articulated at base, unevenly spaced from 1 to 4 mm apart. *Buds* obovoid, with the corolla completely covered by the calyx lobes at anthesis. *Flowers* all perfect, 5-merous. *Calyx* tube 1–2 mm long, conical, the lobes 4–5 mm long, 2–2.5 mm wide at base, lanceolate, the abaxial surface densely covered by porrect-stellate trichomes like those of the stem, adaxially with a more sparse indumentum of mixed sessile 1-celled unbranched eglandular trichomes, sessile to short-stalked porrect stellate trichomes with 4–8 rays and a midpoint as long as the rays, and uniseriate multicellular unbranched glandular trichomes usually at the margins and apex. *Corolla* white, without colored stripes, stellate, 10–12 mm in diameter, membranous, lobed up to ¾ the way to the base, tube 1–1.5 mm long, lobes 3–5 mm long, ca. 3 mm wide at base, abaxial surface covered by sessile and short-stalked

porrect-stellate trichomes, with 4–8 rays and midpoint shorter than the rays, glabrous adaxially, with the apex minutely papillose. Stamens 3–3.5 mm long, filament tube ca. 0.4 mm, the free portion ca 0.8–1 mm long, equal in length, anthers 2–2.5 × 0.8–1 mm, ellipsoid, slightly connivent, yellow, poricidal at the tips, the pores directed introrsely, elongating to longitudinal slits with age. Ovary glabrous, style 4.5–5 mm long, glabrous, stigma clavate, green when fresh. *Fruit* a globose berry, 5–8 mm in diameter, whitish at maturity, shiny, drying dull brown, glabrous (fruiting pedicels reaching 1.7–2.1 cm long, expanded distally (i.e. obconical), ca. 0.8 mm in diameter at base, ca. 1.5 mm at apex, calyx lobes in fruit very elongated and spreading, appearing propeller-shaped, the lobes reaching 9–12 × 3–3.5 mm. Seeds 6–10 per fruit, 3–3.5 × 2–2.5 mm, flattened, reniform, golden-yellow, surface irregularly pitted, with undulate anticlinal cell walls, margins not flattened.

Etymology: The epithet *helix* is applied as a noun in apposition and represents a Latin and English word for spiral or coil. Its usage in English also applies to a propeller of a boat or plane, to which the fruiting calyx is similar, with its spreading lobes (see Fig. 2E).

Distribution, habitat, and phenology: *Solanum helix* is known from the states of Alagoas, Bahia, Pernambuco and Sergipe in northeastern Brazil (Fig. 3), in seasonal forests, ranging from sea level (ca. 90 m) to mid-elevations (900 m). It is found in secondary to preserved forests. The known fertile specimens were collected throughout the year.

Preliminary conservation status: *Solanum helix* has an estimated EOO of 93,179 Km² [Least Concern (LC)] and AOO of 96 Km² [Endangered (EN)]. Even though the AOO could allow its assignment in the Endangered category, the species is widely distributed, occurring in a broad elevational range in seasonal forests. Monitoring is recommended, nevertheless, as it is a locally rare species in a very fragmented landscape, and seasonally dry forests associated with the Atlantic Forest domain are usually neglected and have fewer dedicated protected areas when compared to more wet formations (Teixeira *et al.* 2021). The species is known from only one protected area in Pernambuco state (Reserva Ecológica de Dois Irmãos).

Additional material examined (paratypes): BRAZIL.
Alagoas: Mun. Murici, Bananeiras, 9°13'47''S 35°52'78''W, 572 m, 16 March 2002 (fr), A.M. de Carvalho *et al.* 7118 (CEPEC, MO, RB); Mun. Murici, Poço D'anta, ca. 16–19 km NNW of Murici by road, 9°13.530'S, 35°52.776'W, 500–600 m, 14 May 2001 (fr), W.W. Thomas *et al.* 12437 (CEPEC, JPB, NY, RB). **Bahia:** sin. loc., (fl, fr), sin. coll. (K000983206); sin. Loc., 1835 (fr), sin. coll. (K000963208); Mun. Amargosa, Serra do Timbó, Mata do Centro Sapucaia, 13°10'0''S, 39°9'0''W, 28 April 2007 (fr), J.L. Paixão *et al.* 1167 (CEPEC, HUEFS); Mun. Amargosa, Serra do Timbó, Área de estudos do Projeto Timbó/Centro Sapucaia, 12°52'S, 39°28'W, 750–900 m, 24 January 2007 (fr), D. Cardoso *et al.* 1544 (CEPEC, HUEFS); Mun. Apuarema, Concessão do Rio Tinto, 13°53'46''S,



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39°41'10"W, 5 March 2013 (fr), *L.Y.S. Aona et al.* 2248 (RB); Mun. Castro Alves, Serra da Jibóia, 12°51'11"S, 39°28'19"W, 22 December 1992 (fl, fr), *L.P. de Queiroz & T.S.N. Sena* 2993 (CEPEC, HUEFS); Mun. Castro Alves, Serra da Jibóia, ca. 10 km do povoado de Pedra Branca, 12°51'11"S, 39°28'19"W, 7 May 1993 (fr), *L.P. de Queiroz et al.* 3164 (HUEFS); Mun. Castro Alves, Serra da Jibóia, January 1997 (fl), *M. Sobral et al.* 8413 (HUEFS); Mun. Castro Alves, Serra da Jibóia, 12°51'6"S, 39°28'32"W, 820 m, 10 January 1997 (fl, fr), *R.M. Harley et al.* 28487 (HUEFS); Mun. Conde, Fazenda do Bu, Mata da Maré, 12°2'7"S, 34°43'43"W, 24 April 1996 (fl, fr), *T. Jost & H.P. Bautista* 270 (HUEFS, IPA, RB); Mun. Conde, Fazenda do Bu, trilha 1 da Mata da Maré, 12°2'11"S, 37°44'9"W, 31 May 1995 (fr), *M.C. Ferreira & L.N. Silva* 717 (ALCB, IPA, MBM, RB); Mun. Conde, Fazenda do Bu, Mata da Maré, 12°2'7"S, 37°43'43"W, 25 October 1994 (fr), *R. Marquete et al.* 2072 (RB); Mun. Elísio Medrado, Serra da Jibóia, Fazenda Jequitibá, na estrada para Monte Cruzeiro, 12°52'5"S, 39°28'47"W, 435 m, 3 March 2001 (fr), *L.P. Queiroz et al.* 6481 (HUEFS); Mun. Elísio Medrado, Serra da Jibóia, 12°51'S, 39°28'W, 8 February 2011 (fr), *M.L. Guedes et al.* 17970 (ALCB); Mun. Entre Rios, estrada do Conde para Esplanada, 11°46'17"S, 37°44'5"W, 42 m, 23 January 2004 (fl), *M.N.S. Stapf & B.R.N. Araújo* 224 (HUEFS); Mun. Entre Rios, Estrada de Conde para Esplanada, 13,5 Km do entroncamento em direção a Esplanada, 6 February 1998 (fl, fr), *M.R. Fonseca et al.* 300 (INPA); Mun. Entre Rios, Imbé, 12°3'S, 38°0'W, 21 April 2010 (fl), *A.V. Popovkin & J.C. Mendes* 655 (HUEFS); Mun. Entre Rios, Imbé, 12°3'S, 38°0'W, 7 Oct. 2010 (fl, fr), *A.V. Popovkin & J.C. Mendes* 678 (HUEFS); Mun. Entre Rios, 11°56'S, 38°5'W, 4 December 2000 (fl, fr), *M.L. Guedes et al.* 7370 (ALCB, CEPEC); Mun. Ilhéus, on road to Vila Brasil, 10 km west of junction with BA-001, 15°06'S, 39°04'W, 10 May 1993 (fl), *W.W. Thomas et al.* 9845 (CEPEC, MO, NY, RB); Mun. Ilhéus, 20 km north, along road from Una to Ilhéus, 15°11'S, 39°02'W, 100 m, 23 January 1977 (fl), *R.M. Harley et al.* 18196 (CEPEC, E, K, MO, RB); Mun. Itanagra, Fazenda Córrego Verde, 12 January 1975 (fl, fr), *E. Gusmão s.n.*, (ALCB03787); Mun. Itanagra, road from Itanagra to Subaúma, 8 Km W of Itanagra, 50 m, 27 May 1981 (fr), *S.A. Mori & B.M. Boom* 14132 (CEPEC, NY); Mun. Joazeiro, 17 November 1963 (fl), *A.L. Costa s.n.* (ALCB03770); Mun. Mata de São João, Praia do Forte, 14 February 1987 (fr), *A.J. Ribeiro et al.* 190 (ALCB); Mun. Pojuca, Mariquito, 9 December 2007 (fr), *C.S. Silva-Lima et al.* 126 (ALCB, HUEFS); Mun. Santa Teresinha, Serra da Jibóia, 12°50'42"S, 39°29'22"W, 640 m, 3 April 1999 (fl, fr), *L.R. Senna & F. Franca* 21 (HUEFS); Mun. Santa Teresinha, Serra da Jibóia, 12°51'17"S, 41°48'53"W [coordinates suspicious, not included in map], 15 April 2000 (fr), *B.M. da Silva* 56 (HUEFS); Mun. Santa Teresinha, Serra da Jibóia, à margem da estrada da Serra da Pioneira, 12°50'S, 39°28'W, 14 February 2001 (fl, fr), *A.A. Ribeiro-Filho* 185 (HUEFS); Mun. Santa Teresinha, Serra da Jibóia, à margem da estrada da serra da Pioneira, 12°51'10"S, 39°28'32"W, 31 March 2001 (fl), *M.M. da Silva et al.* 512 (HUEFS); Mun.

Santa Teresinha, Serra da Jibóia, 12°51'10"S, 39°28'32"W, 31 March 2001 (fl, fr), *M.M. da Silva et al.* 520 (HUEFS); Mun. Santa Teresinha, Serra da Jibóia, 12°51'11"S, 39°28'21"W, 14 November 1986 (fl), *L.P. Queiroz et al.* 1079 (HUEFS); Mun. Santa Teresinha, Vila da Pedra Branca, Serra da Jibóia, estrada para torre de TV, 800–850 m, 11 June 2000 (fr), *M. Alves et al.* 2000 (CEPEC, RB); Mun. Santa Teresinha, 14,5 km na rod. Elísio Medrado/Sta. Teresinha, Torre da Embratel, ca. de 7 km do Distrito de Pedra Branca, Serra da Jibóia, 12°51'13"S, 39°28'33"W, 750 m, 24 February 2000 (fr), *J.G. Jardim et al.* 2828 (ALCB, CEPEC, HUEFS); Mun. Santa Teresinha, Serra da Pioneira, 3 km de P. Branca, 12°45'S, 39°32'W, 800 m, 16 May 1984 (fr), *L. Noblick et al.* 3210 (HUEFS); Mun. Santa Teresinha, Serra da Pioneira, 3 Km de P. Branca, 12°45'S, 39°32'W, 800 m, 6 June 1984 (fr), *L. Noblick et al.* 3331 (HUEFS, MO); Mun. Santo Amaro, Mata entre Santo Amaro e Cachoeira, 5 April 1962 (fl, fr), *A.L. Costa s.n.* (ALCB03771); Mun. São Sebastião do Passé, 12°32'28"S, 38°22'51"W, 25 March 2001 (fl), *M.L. Guedes et al.* 9740 (ALCB, CEPEC); Mun. Uruçuca, estrada de Itacaré para Serra Grande, pouco após km 43, ramal à direita após acesso para a cachoeira do Tijúipe, 14°23'12"S, 39°4'45"W, 5 April 2004 (fr), *P. Fiaschi et al.* 2262 (CEPEC). **Pernambuco:** Mun. Igarassu, 8 November 1887 (fl), *H.N. Ridley et al. s.n.* (BM000935744); Mun. Igarassu, Mata do Pezinho, 18 April 2009 (fl), *E. Pessoa* 83 (CEPEC, IPA); Mun. Igarassu, Mata da Piedade, 7°49'45.5"S, 34°69'35.7"W, 90 m, 21 April 2010 (fr), *J.D. García G.* 1487 (CEPEC, UFP); Mun. Igarassu, Usina São José, fragmento de mata com acesso posterior ao Km 10, 7°50'20"S, 34°59'43"W, 12 October 2013 (fr), *L.C. Marinho et al.* 490 (ALCB, CEPEC, HUEFS); Mun. Recife, Reserva Ecológica de Dois Irmãos, 11 May 1993 (fr), *A.M. Miranda et al.* 736 (ALCB, HST, UEC); Mun. Recife, Mata de Dois Irmãos, 1990 (fr), *M.L. Guedes* 2202 (ALCB). **Sergipe:** Mun. Indiaroba, P.A. Sepé Tiajuru II, 11°30'44"S, 37°34'47"W, 28 February 2007 (fl), *C. Gomes s.n.* (ASE33264); Mun. Indiaroba, P.A. Sepé Tiajuru II, 11°30'44"S, 37°34'47"W, 25 January 2008 (fl), *C. Gomes s.n.* (ASE33283); Mun. Indiaroba, P.A. Sepé Tiajuru II, 11°30'44"S, 37°34'47"W, 9 September 2014 (fl, fr), *R.S. Andrade* 2 (ASE); Mun. Indiaroba, P.A. Sepé Tiajuru II, 11°30'44"S, 37°34'47"W, 25 November 2014 (fl), *R.S. Andrade* 53 (ASE); Mun. Itabaiana, Serra de Itabaiana, Margem do 1° riacho, 16 March 1983 (fr), *E. Gomes* 220 (ASE); Mun. Itaporanga D'Ajuda, Mata Rio Fundo, 11°04'29"S, 37°19'44"W, 7 March 2015 (fl), *J.P. Santana* 398 (ASE).

Discussion

As stated previously, the *Brevantherum* clade of *Solanum* is one of the main lineages recognized in many previous works that dealt with the systematics of the genus [e.g. Gagnon *et al.* (2022)] that congregates non-aculeate species with or without stellate trichomes. *Solanum helix* belongs to a group of species with porrect-stellate trichomes (and derivatives) within the



Brevantherum clade of *Solanum*, informally named as “stellate subclade” (Giacomini 2015), which is quite species-rich (ca. 80 species). Within the “stellate subclade” in Giacomini (2015), *S. helix* was recovered in the in the Cordovense clade [treated as *S. sp. nov.* (2)].

The Cordovense clade is a broadly distributed lineage with species found from Mexico to Argentina, containing part of the sect. *Extensum* D’Arcy (D’Arcy 1972; Nee 1999) and many other species (ca. 18 species in total; Giacomini 2015). Species assigned to the Cordovense clade in Giacomini (2015) have a quite diverse morphology of terminal to lateral inflorescences that can be unbranched, sessile, and quite small and discrete, like those observed in *S. helix*, to huge and many times branched, as in *Solanum lantana* Sendtn.. Also, some species can have accrescent fruiting calyces, but this is undoubtedly a homoplastic feature within the lineage. Despite the diverse morphology, species of the Cordovense clade share a shrubby scandent habit, are usually associated with the edge of moist forests and most are locally rare (except for *S. didymum*), with individuals usually found very apart from each other (Giacomini 2015).

Within the Cordovense clade, *S. helix* most resembles *S. didymum* and *S. anisocladum*, which are also found in northeastern Brazil (Giacomini *et al.* 2013). Vegetatively, *Solanum helix* can be easily identified by the following combination of characters: sympodial units without geminate leaves and an indument on the abaxial leaf surfaces mostly composed of stalked porrect-stellate eglandular trichomes, with short midpoints and stalks roughly of the same length, giving it a very uniform and unique appearance (like a “canopy”) that is soft to the touch. In *S. didymum* it is quite common to find geminate leaves and the indument on the adaxial surface is quite variable, with sessile to long-stalked stellate trichomes, with at least some of the trichomes with midpoints longer than the lateral rays, and glandular or eglandular rays, often with a sticky touch. *Solanum anisocladum*, although also lacking geminate leaves (i.e., leaves are most solitary), has a very dense indument on the abaxial leaf surface, with short- to long-stalked porrect-stellate trichomes and midpoints longer than lateral rays that are hard and rough to the touch. Although it is possible to distinguish *S. helix* vegetatively, it is most easily recognized while fruiting: its fruiting calyx becomes quite elongated (with expanded lobes) and spreading and, in association with the small fruit, gives it a propeller-like aspect not found in any other species of the Cordovense clade, nor of the more inclusive Brevantherum clade (see Fig. 2E). Another species of the Cordovense clade that also occurs in northeastern Brazil is *Solanum maranguapense* Bitter, but it can be easily distinguished from *Solanum helix* by its sessile porrect-stellate trichomes on both leaf surfaces, and leaves with a much more delicate texture, somewhat membranaceous. *Solanum helix* is also a species from markedly seasonal forests, while *S. maranguapense* is mostly found in wet forests.

It is intriguing that *S. helix* has not been described before, given the oldest known collections are from almost 200 years ago. The two oldest collections of the species were located at Kew herbarium (K000983206 and K000983208), but they both have imprecise dates (1857 and 1835 respectively), as they are assigned to “Hooker”, but both botanists Joseph Dalton Hooker (1817-1911) and his father William Jackson Hooker (1785-1865), former directors of Kew, have never been to Brazil. These dates are likely the ones in which the specimens were incorporated into the herbarium and the collection date is expected to be earlier, therefore. Consequently, the oldest collection of the species is expected to be at least 188 years old. The oldest collection to which a precise date can be attributed is that of Ridley (BM000935744), from 1887.

In addition to the time lapse from the first records, the species is widespread in herbaria (see Suppl. Material) and has a strikingly different morphology from other species. Some specimens found in visited herbaria were labeled as *Solanum gemellum* Mart., a name treated currently as a synonym of *S. didymum* (Giacomini 2015; BFG 2021). Species limits within what was previously treated as *Solanum* sect. *Extensum* have been misunderstood, as most species are broadly distributed but locally rare, and specimens available usually present an enormous variation within a small set of collections [for example, see comments of Nee (1999) under *Solanum extensum* Bitter]. With an increasing number of collections and images available online in initiatives that aggregate herbarium databases (such as speciesLink, <https://specieslink.net/>, and Reflora, <http://reflora.jbrj.gov.br/>), it is likely that a greater diversity will be unveiled in the Cordovense clade in the future.

The discovery here of an undescribed species after many decades since its first collection highlights the importance of continued work in the field and herbaria in megadiverse ecosystems and reinforces how herbaria can be a frontier for discoveries (Bebber *et al.* 2010). The fact that *S. helix* is widespread in herbaria, but mostly represented in regional small collections, also reinforces the outsize contribution of these to reduce the incomplete knowledge on organism distribution (described as “Wallacean shortfall” in literature; Hortal *et al.* 2015), and therefore their major role in the advance of evolutionary and biogeographical studies and conservation initiatives (Ribeiro *et al.* 2009).

The Atlantic Forest, although mostly degraded in northeastern Brazil (Ribeiro *et al.* 2009), is a source of discoveries within its small remnants, a scenario predicted by Pimm *et al.* (2010) and realized in the case of *Solanum* (e.g. Sampaio & Agra 2016, and this paper). Nevertheless, continued work in herbaria is a task intimately associated with continued training of human resources (Bebber *et al.* 2014), considering a learning curve is expected in taxonomy (Ahrends *et al.* 2011), as getting acquainted with patterns of variation within groups might take time. Unfortunately, Brazil, the country that retains the greatest known plant diversity on earth (Forzza *et al.* 2012), has faced alarmingly



Hidden treasures in the cabinets: an overlooked new species of *Solanum* (Solanaceae) from northeastern Brazil described almost two centuries after its first collection

decreased science funding in recent years (Fernandes *et al.* 2017). We advocate for a reversal of this trend and anticipate the discovery of many species as biodiversity studies are

continuously supported, which should be done together with human resources training programs, fundamental to form a well-trained task force for the years to come.

Key to the *Solanum cordovense* species group (Cordovense clade of Giacomini 2015) in NE Brazil (see Materials and Methods for a geographical definition)

1. Stems, inflorescences and leaves with porrect-stellate trichomes with central rays (midpoints) notably shorter than the lateral rays 2
- 1'. Stems, inflorescences and leaves with at least part of the porrect-stellate trichomes with central rays (midpoints) notably longer than the lateral rays 3
2. Leaves usually drying dark, abaxially with mixed sessile and short stalked porrect-stellate trichomes (mostly sessile); fruiting calyx lobes deltate, only partially accrescent, adhered to the fruit, usually not longer than the fruit length, never spreading (AL, BA, CE, PE) *Solanum maranguapense* Bitter
- 2'. Leaves usually drying brownish yellow, abaxially with mostly short stalked porrect-stellate trichomes, with stalks roughly at the same size, forming a “canopy”; fruiting calyx lobes getting oblong, usually way longer than the mature fruit, the sepals spreading in a propeller-like aspect (AL, BA, PE, SE) *Solanum helix* Giacomini & Stehmann
3. Stems hirsute to hispid, rough to the touch in old growth, with very long stalked porrect-stellate trichomes reaching > 2 mm, all eglandular; inflorescence emergence usually associated with a change in stem growth direction (AL, BA, PE) *Solanum anisocladum* Giacomini & Stehmann
- 3'. Stems pubescent, not rough to the touch, with sessile or stalked porrect-stellate trichomes in various sizes, usually < 2 mm, with a glandular or eglandular midpoint; inflorescence emergence never causing a change in stem growth direction 4
4. Fruiting calyx becoming inflated, somewhat plicate, usually covering the fruit at maturity (accrescent); sepals cordate (BA) *Solanum didymum* Dunal
- 4'. Fruiting calyx not becoming inflated, not plicate, usually not completely covering the fruit at maturity (not markedly accrescent); sepals deltate to elliptic (MA) *Solanum cordovense* Sessé & Moc.

Supplementary material

Searchable XLS file of all specimens examined of *Solanum helix* Giacomini & Stehmann.

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