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A synopsis of Byttnerieae (Malvaceae, Byttnerioideae) from the Atlantic Forest, with notes on geographical distribution, nomenclature, and conservation

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ABSTRACT

This synopsis presents diagnostic characters and comments on morphological variability, distribution, and conservation of species of Byttnerieae (Malvaceae, Byttnerioideae) from the Atlantic Forest. Byttnerieae is represented by species from two allied genera in this phytogeographic domain: *Ayenia* L. and *Byttneria* Loefl. An extensive literature survey along with herbarium collection analyses revealed the occurrence of 20 species in the Atlantic Forest, nine of which are endemic to Brazil. Seven species are restricted to the Southern portion of the Atlantic Forest, *i.e.*, occurring from southern São Paulo state to the state of Santa Catarina, with most records being in Brazil, but some species also occur in Argentina and Paraguay. Beyond the Southern portion of the Atlantic Forest, three species are restricted either to the state of Rio de Janeiro or to Bahia, in Brazil. An identification key focusing on vegetative characters, as well as illustrations and notes on species distribution and conservation, are presented. Nomenclatural comments or updates for some taxa were provided, including: the designation of lectotypes for six names; the amendment of authorship of one name (*B. gracilipes*); and reassessment of the distribution of *A. glabrescens*, an endemic species of dry deciduous forests of Bahia whose precise location was unknown.

Keywords: biogeography, Malvales, Neotropical flora, preliminary conservation assessment, Sterculiaceae

Introduction

Malvaceae is the species-richest family of Malvales, with over four thousand species in more than 200 genera (Bayer & Kubitzki 2005). Traditionally, the name "Malvaceae" was less inclusive, as several genera were ascribed to three other families: Bombacaceae, Sterculiaceae and Tiliaceae. A wider circumscription of Malvaceae was, then, adopted alongside the emergence of novel evidence from molecular data (Alverson *et al.* 1998; Baum *et al.* 1998; Bayer *et al.* 1999). Currently, nine subfamilies are recognized within "Malvaceae *sensu lato*" (*sensu* Alverson *et al.* 1998): Bombacoideae, Brownlowioideae, Byttnerioideae, Dombeyoideae, Grewioideae, Helicteroideae, Malvoideae, Sterculioideae and Tilioideae.

Malvaceae *s.l.* is distinctive by its typical actinodromous leaves, covered by stellate trichomes—a feature that is, in fact, shared with other families of the order—, and by its unique type of floral nectary, composed of glandular trichomes located on the inner side of the calyx (Bayer & Kubitzki 2005). Infrageneric and subfamily relationships,

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as well as evolutionary and biogeographical aspects, require more efforts and are at the core of new debates among malvologists (*e.g.,* Balthazar *et al.* 2004; 2006; Tate *et al.* 2005; Duarte *et al.* 2011; Carvalho-Sobrinho *et al.* 2016). For instance, there is increasing evidence that Bombacoideae may be paraphyletic (Balthazar *et al.* 2004; Bayer & Kubitzki 2005; Hernández-Gutiérrez & Magallón 2019), whilst morphological and molecular data indicate that groups previously inserted into Sterculiaceae are, each one, monophyletic, but, when assembled, they do not form a natural group (Whitlock *et al.* 2001; Richardson *et al.* 2015).

According to the most recent assessment for Brazil (see BFG 2018; also check the Flora do Brasil 2020 Project on http://floradobrasil.jbrj.gov.br/), there are 80 genera and 840 species of Malvaceae reported for the country, and Brazil is the largest and species-richest country of Tropical Americas (Ulloa-Ulloa *et al.* 2017). Most subfamilies of Malvaceae are common in South American open, seasonally dry formations, being expressive components of the Brazilian Caatinga, Pampas, Cerrado, and of Chaco's open/dry habitats. However, Malvaceae is also representative in the Atlantic Forest, with almost the same prevalence of species richness than, *e.g.,* the Cerrado (*ca.* 350 species in each, according to Flora do Brasil 2020 Project). In these locations, most groups of Malvaceae are native to forested environments, being intimately associated to transition and seasonal ecosystems.

Thus, current efforts in Malvaceae *s.l.* turned out to be fragmented after its recircumscription, and taxonomical contributions have been centered into particular subfamilies, namely Malvoideae and Bombacoideae. But as it was demonstrated that the former "Sterculiaceae" was polyphyletic, its genera were rearranged into three distinct subfamilies: Byttnerioideae, Helicteroideae and Sterculioideae. In addition to the seminal contributions of Cristóbal (1960; 1976) for many genera in these groups, we highlight further endeavors on the taxonomy of these subfamilies, such as: the "Flora da Serra do Cipó, Minas Gerais" (Esteves 1992; Colli-Silva *et al.* 2019; Yoshikawa *et al.* 2019); the "Flora do Grão-Mogol, Minas Gerais" (Cristóbal 2006; Esteves & Krapovickas 2009); and, in the Atlantic Forest, the "Flora Fanerogâmica do Estado de São Paulo" (Duarte *et al.* 2007; Cruz & Esteves 2009) and other targeted efforts (*e.g.,* Gonçalez & Esteves 2017).

In this work, we provide novel contributions for one of the nine subfamilies of Malvaceae—Byttnerioideae—, by presenting a synoptic taxonomical treatment with comments on the nomenclature, distribution and conservation of the tribe Byttnerieae *sensu* Whitlock *et al.* (2001) from the Atlantic Forest domain. Byttnerieae is the most species-rich tribe of Byttnerioideae (Bayer & Kubitzki 2005), and it is represented in the American Tropics by *Ayenia*, *Byttneria* and *Rayleya*, amounting to more than 200 species in these three genera. Species in this tribe are usually shrubs or lianas (Fig. 1) with unguiculate petals adnate to a staminal tube (Whitlock *et al.* 2001). Novel taxonomical treatments in hotspot areas such as the Atlantic Forest will strengthen taxonomical knowledge of Malvaceae subfamilies; we argue this is a necessary task, given the wider and novel diversity panorama of the family, which has arisen since its recircumscription in the early 2000s.

Materials and methods

Our study was based on a selection of species of Byttnerieae occurring in the Atlantic Forest domain from a manually revisited occurrence database of Colli-Silva & Pirani (2020). This database compiled *ca.* 15,000 occurrence records of Byttnerioideae, Helicteroideae and Sterculioideae that went through an extensive reviewing framework (check Colli-Silva & Pirani 2020, for more details). Moreover, we also consulted the following online repositories: 1) speciesLink, https://specieslink.net/, 2) GBIF—the Global Biodiversity Information Facility, https://gbif.org/, 3) JABOT—the Brazilian Flora database maintained by the Rio de Janeiro Botanical Garden, https://jabot.jbrj.gov.br/ and 4) JSTOR, https://jstor.org/. Additionally, for this work, we examined the following herbarium collections of *Ayenia* and *Byttneria*: K, R, RB, SP and SPF (acronyms according to Thiers (2020; continuously updated), assembling a fair portion of the known collections of the Atlantic Forest.

Only specimens' mature fragments were used for synoptic descriptions and illustrations. Measurements of leaves and inflorescences were taken from herbarium samples, while flowers and fruits were rehydrated before being measured and drawn. Photographs of leaf structures and petals were taken through a Leica M125 stereomicroscope.

Species descriptions emphasized vegetative features, especially in *Byttneria,* as they are expressive and practical to distinguish when identifying collected specimens. We followed Cristóbal (1976) and Dorr (1996) terminologies of inflorescence and flower morphology, as well as their concepts of leaf nectaries. Terminologies of leaf size, shape and venation were based on Ellis *et al.* (2009). For laminar sizes, we also considered measurements taken from the leaves in the examined vouchers, along with those reported in the literature (Cristóbal 1960; 1976). Those measurements were used to estimate leaf area according to Ellis *et al.* (2009) blade classes: leptophyllous (leaf area < 25 mm^2), nanophyllous (25–225 mm^2), microphyllous (225–2,025 mm^2), notophyllous (2,025–4,500 mm^2), mesophyllous (4,500–18,225 mm^2), macrophyllous (18,225–164,025 mm^2) or megaphyllous (> 164,025 mm^2). By attributing blade area classes in addition to informing

leaf minimum/maximum length/width values (as it is usually done in taxonomical treatments), we can obtain a fair approach to leaf dimensions without examining all vouchers for all species—which is the case of this synoptic study.

The section "Additional specimens examined" covers selected vouchers of specimens from the Atlantic Forest domain. We considered the Atlantic Forest in its broader delimitations *sensu* Galindo-Leal & Câmara (2003), including Brazil and nearing countries (Argentina, Paraguay, Uruguay).

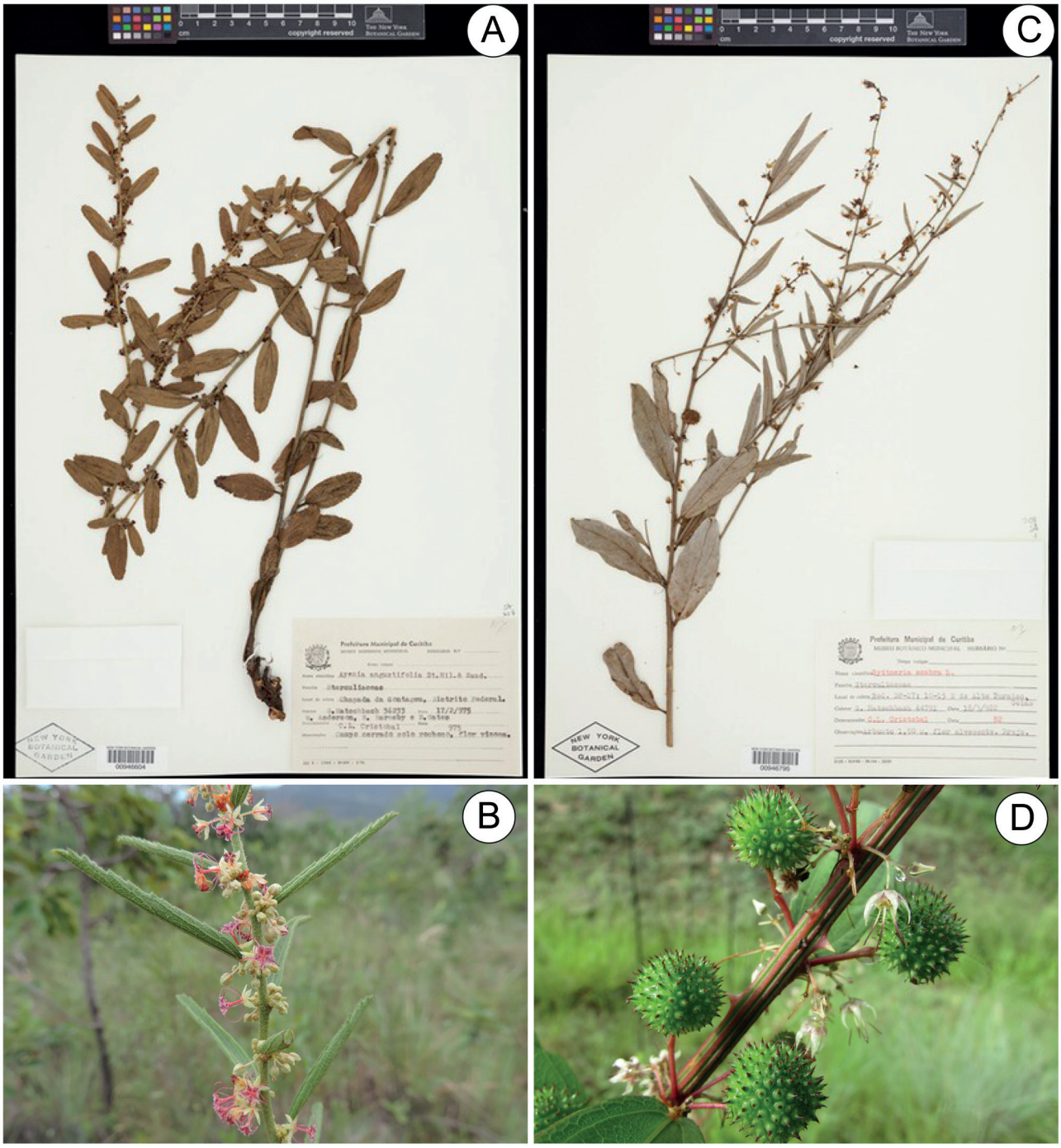

Figure 1. General aspect of *Ayenia* L. (**A**-**B**) and *Byttneria* Loefl. (**C**-**D**). *Ayenia* are small, mainly shrubs to herbs, up to 1 m high, with some species forming rhizomes. On the other hand, *Byttneria* has a more variable set of lifeforms: from shrubs to subshrubs, herbs and lianas. Both species have small reproductive structures, with flowers varying from purplish to whitish, and aculeate fruits (**B** and **D**). Photos: (**B**) *Ayenia angustifolia*, by Gabriela Camargo; (**D**) *Byttneria scabra*, by Luciano Pedrosa. Voucher photos taken from (**A**) *G. Hatschbach 36255* (*A. angustifolia*) and (**C**) *G. Hatschbach 44791* (*B. scabra*), from the MBM digitized collection of the speciesLink repository (https://specieslink.net/).

However, as most of the Atlantic Forest is centered in Brazil, this synopsis will ultimately focus on features of occurrence and distribution primarily in this country, and later in other South American countries.

Maps were generated using QGIS software (https://qgis.org/en/site/) based on point occurrence data. Habitat and updated geographical distribution data were assessed considering the literature and the examined vouchers. We selected materials of Brazilian first-level administrative divisions ("Brazilian states") of the Atlantic Forest, making an effort to mention at least one voucher per state. We also presented a section of "iconography", summarizing relevant available illustrations from previous studies. Selected specimen materials or images are cited right after the description, and the full list of examined material can be found as a "List of Exsiccatae" (see List S1 in supplementary material).

Finally, for the preliminary conservation assessment, species were categorized under IUCN (the International Union for Conservation of Nature) criterion B categories, *i.e.,* either as NT (Near Threatened), LC (Least Concern), VU (Vulnerable), EN (Endangered) or CR (Critically Endangered) according to the "ConR" package v. 1.2.4. in R Environment (Dauby *et al.* 2017). The scores of AOO (Area of Occupancy) and EOO (Extent of Occurrence) were calculated using occurrence point information. Although the preliminary conservation assessment is not a full assessment, as it only considers one of the five criteria used by IUCN to build red lists, it is still a fast and efficient proxy to properly evaluate, although partially, conservation data when only occurrence point information is available (Dauby *et al.* 2017). Still, when we deemed it convenient, we critically evaluated and discussed preliminary assessments provided by the "ConR" package, considering the expert-knowledge on species exactitudes and suggesting an alternative preliminary category if necessary.

Results and discussion

We found records for twenty species of Byttnerieae in the Atlantic Forest: six species of *Ayenia* and fourteen of *Byttneria*.

Species' distributions are summarized in Figure 2. Nine species are endemic to Brazil (*B. abutiloides*, *B. beyrichiana*, *B. cristobaliana*, *B. gayana*, *B. hatschbachii*, *B. implacabilis*, *B. triadenia*, *A. erecta* and *A. glabrescens*) and six of them are endemic to the Atlantic Forest domain (*B. abutiloides*, *B. beyrichiana*, *B. cristobaliana*, *B. implacabilis*, *B. triadenia* and *A. glabrescens*). Interestingly, some species are restricted and centered in two main regions of the Atlantic Forest: 1) in the Southern portion, with *B. australis*, *B. gracilipes*, *B. hatschbachii*, *B. pedersenii*, *B. urticifolia* being widespread, while *B. implacabilis* and *B. triadenia* are restricted to the coastal region of the Brazilian states of Santa Catarina and Paraná and *A. aprica* is known only from Rio Grande do Sul state and northeastern Argentina; 2) in the region between Rio de Janeiro and Espírito Santo states, in Brazil (with *B. abutiloides*, *B. beyrichiana* and *B. gayana*).

Species extending beyond the Atlantic Forest domain exhibit conspicuously disjunct distributions, mainly *B. catalpifolia, B. filipes, B. scabra* and *A. tomentosa*. In general, both genera are scanty or almost absent in the central region of the Amazon Basin, and the above-mentioned disjunct species apparently show a peri-Amazonian distribution (Fig. 2; but see also Colli-Silva & Pirani 2020).

As we have spotted some names with nomenclatural issues, we provided the second-step lectotypification for four synonyms, two lectotypifications for correct names (*A. erecta* and *A. glabrescens*), and an authorship amendment of one name (*B. gracilipes*). Also, we first formally described the distribution of *A. glabrescens*, which was known only by the type from an unprecise location.

Despite such amendments, we highlight Cristóbal's exceptional pioneering in her monographs of *Ayenia* and *Byttneria* (Cristóbal 1960; 1976). Our results follow what she mentioned in her monographs, as variations within vegetative characters, especially in the leaves, are important taxonomic features for infraspecific variation in the tribe. As a matter of fact, in some cases, these can be even more diagnostic than floral characters. For instance: in *Byttneria*, leaf shape and dimensions are quite noticeable (Fig. 3) and have been used as diagnostic features for species circumscriptions (Cristóbal 1976; Arbo 1977).

Therefore, although flowers and fruits are quite variable in *Ayenia* and *Byttneria,* these genera can be easily distinct without the need of reproductive structures. The main diagnostic feature is the presence, in *Byttneria*, of at least one extrafloral nectary on the midvein of the abaxial side of the leaves (occasionally on the main veins) (Fig. 3). It should be noted that these nectaries are actually linear cavities, rather than gland-like structures (Fig. 4), as usually found in, *e.g.,* Passifloraceae, Euphorbiaceae, and *Inga* (Leguminosae).

Nevertheless, flowers of *Ayenia* and *Byttneria* differ significantly as well (Fig. 5). In fact, morphological definitions of different portions of an unguiculate petal in *Ayenia* and *Byttneria* can bear terminological inconsistencies, as pointed out by Dorr (1996) and Whitlock *et al.* (2001). Herein, we chose not to integrate these definitions, and maintained each specific terminology for each genus, following Cristóbal (1960; 1976) monographs separately. Thus, on one hand, the term "hood" is adopted only when regarding *Byttneria*; on the other hand, the so-called "appendix on the abaxial portion of a petal" (Cristóbal 1960) is a terminology adopted only for *Ayenia*, despite the potential homology between this structure and flowers of *Byttneria* (Whitlock *et al.* 2001).

Identification key for the species of Byttnerieae from the Atlantic Forest

1. Shrubs, decumbent subshrubs to herbs. Leaf veins lacking extrafloral nectaries abaxially. Petals with a cylindrical claw, more prominent than the lamina, up to five times longer than it. Anthers with three thecae ..... ***Ayenia***

2. Leaves sub-orbicular. Stem and leaves pubescent. Base of the petal lamina concave, subtriangular ..... ***A. aprica***

2'. Leaves ovate, oblong, elliptic, or lanceolate, rarely sub-orbicular (*A. nummularia*). Base of the petal lamina convex, sub-rhomboid or rhomboid **3**

3. Leaves glabrous, with few sparse trichomes, heterophyllous, with leaf dimensions varying along the branches ..... ***A. glabrescens***

3'. Leaves pubescent or tomentose, more or less of the same size **4**

4. Leaves and branches conspicuously tomentose ..... ***A. tomentosa***

4'. Leaves and branches densely pubescent **5**

5. Leaf blade sub-orbicular; adaxial face with branched trichomes ..... ***A. nummularia***

5'. Leaf blade ovate, ovate-lanceolate, lanceolate or oblong; trichomes simple, not branched **6**

6. Leaf blade lanceolate to elliptic, subcoriaceous, with prominent veins ..... ***A. praecipua***

6'. Leaf blade ovate, membranous, with flat veins ..... ***A. erecta***

1'. Decumbent or erect shrubs or subshrubs to lianas. Leaves with one or more extrafloral nectaries on the abaxial side of the blade, each provided with one or more openings (*i.e.,* uni or multiaperturate), usually visible at naked eye. Petals with a fleshy or membranous claw, smaller and less prominent than the upper portion (= petal lamina). Anthers with two thecae ..... ***Byttneria***

7. Leaf nectary with a single conspicuous aperture; venation prominent on both sides ..... ***B.* sect. *Byttneria***

8. Petiole and branches ribbed and aculeate. Leaf blade lanceolate, margin untoothed or serrate or dentate only at the apex ..... ***B. scabra***

8'. Petiole and branches unarmed. Leaf blade linear, ovate or elliptic, margin untoothed **9**

9. Leaves petiolate. Branches cylindrical ..... ***B. hatschbachii***

9'. Leaves sessile to subsessile. Branches angulose ..... ***B. pedersenii***

7'. Leaf nectary with multiple inconspicuous apertures, each one visible only under magnification; venation prominent only on the abaxial side **10**

10. Lianas. Unarmed branches ..... ***B.* sect. *Vahihara***

11. Leaf blade widely ovate, mesophyllous to macrophyllous (4,500–164,025 mm² of blade area). Petal lamina flat. Fruit subglobose, flattened, 2–4 cm diam ..... ***B. catalpifolia***

12. Leaves slightly pubescent. Lobed fruits, flattened, more sparsely prickled, prickles much smaller in proportion than the fruit dimensions ..... ***B. catalpifolia* subsp. *sidifolia***

12'. Leaves densely pubescent. Fruits globose, not flattened, densely prickled, prickles much longer in proportion than fruit dimensions ..... ***B. catalpifolia* subsp. *catalpifolia***

11'. Leaf blade ovate to lanceolate, notophyllous (2,025–4,500 mm² of blade area). Petal lamina narrow, cylindrical. Fruits globose, spherical, *ca.* 1 cm diam ..... ***B. gayana***

10'. Shrubs or subshrubs erect to decumbent. Branches aculeate **13**

13. Thecae divergent. Fruits dehiscent ..... ***B.* sect. *Urticifolia***

14. Leaf blade with 3-5 extrafloral nectaries **15**

15. Petal claw and lamina pubescent ..... ***B. abutiloides***

15. Petal claw glabrous and lamina pubescent **16**

16. Branches angulose and fistulose. Petal lamina fragile, with sparse trichomes. Anthers subsessile ..... ***B. implacabilis***

16'. Branches cylindrical and not fistulose. Petal lamina fleshy, densely pubescent. Anthers not sessile ..... ***B. triadenia***

14'. Leaf blade with only one nectary **17**

17. Leaf veins unarmed. Fruit sparsely aculeate with prickles *ca.* 1 mm long ..... ***B. gracilipes***

17'. Leaf veins aculeate. Fruit densely aculeate with prickles *ca.* 3 mm long ..... ***B. urticifolia***

13'. Thecae non-divergent. Fruits indehiscent ..... ***B.* sect. *Crassipetala***

18. Petal lamina cylindrical, straight **19**

19. Leaf margin serrate. Fruit dehiscent, regularly pubescent ..... ***B. beyrichiana***

19'. Leaf margin untoothed or, if serrate, toothed only in the apex. Fruit indehiscent, irregularly pubescent ..... ***B. filipes***

18'. Petal lamina flat, markedly curved **20**

20. Concolor leaves, not maculate. Secondary veins curved, not perpendicular to the midvein ..... ***B. australis***

20'. Maculate leaves with a cinereous blotch around the midvein. Secondary veins regularly spaced, perpendicular to the midvein ..... ***B. cristobaliana***

1. *Ayenia* L., Kongl. Svenska Vetensk. Acad. Handl. 17: 24. 1756. Type: *Ayenia pusilla* L., Syst. Nat., 10(2): 1247. 1759.

Shrubs, **subshrubs**, or **herbs**; branches cylindrical, unarmed, glabrous or pubescent, trichomes simple and stellate, hirsute or adpressed. **Leaves** simple, petiolate, blade entire, serrate or dentate, with stellate trichomes. Inflorescence a cincinnus, axillary or terminal, with one or more flowers. **Flowers** bisexual, sometimes unisexual by abortion, actinomorphic, dichlamydeous and heterochlamydeous; calyx symsepalous, pubescent, valvar aestivation; corolla choripetalous, petals purple to yellowish-green, unguiculate, lower basal portion (= claw) long and cylindrical, with an expanded portion (= hood) and usually with an appendix dorsally; upper portion (= petal lamina) less prominent and smaller than the claw, linear, glabrous (sometimes understood as appendix of the petal lamina; check Dorr 1996); staminal tube campanulate to cylindrical; stamens 5, opposite to petals; anthers trithecae, divergent, free or partially connate on the base; staminodes 5, cucullate, alternate to petals; gynoecium syncarpous, 5-carpelar, 5-locular; styles 5, connate, stigma inconspicuous or capitate, with 5 globose lobes; ovules 2 per locule. **Fruit** schizocarpic, spherical, aculeate, dehiscence septicidal or loculicidal; seeds ovoid, grayish to black, smooth, or tuberculate, not winged.

Ayenia is a Neotropical genus of shrubs to herbaceous plants with *ca.* 70 species (Fig. 2A, B), but only 68 species

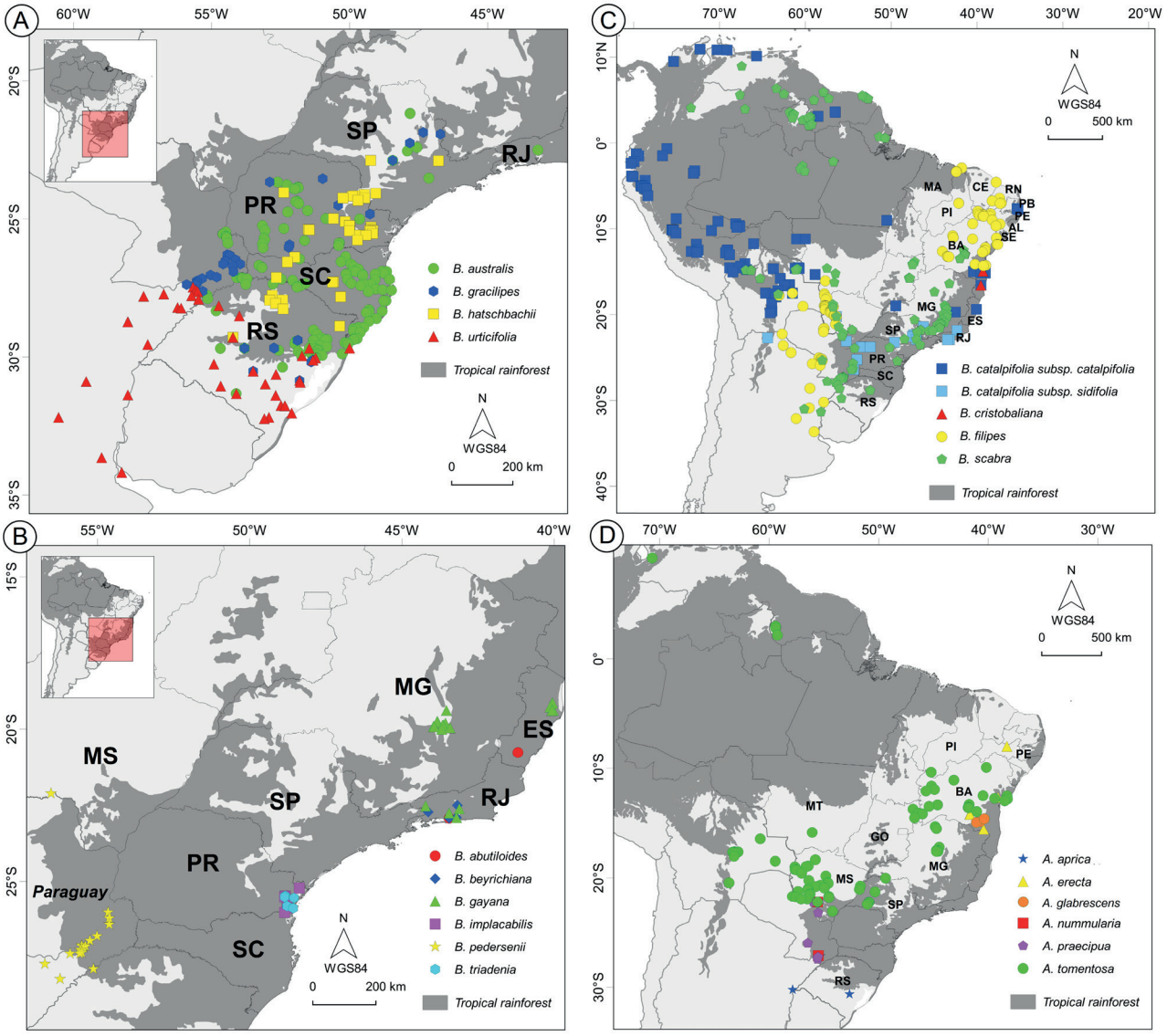

Figure 2. Species distribution of Byttnerieae from the Atlantic Forest: (**A**) *Byttneria* species from the Southern Atlantic Forest portion; (**B**) endemic species of *Byttneria* from Southern and central portions of the Atlantic Forest; (**C**) widespread species of *Byttneria*; and (**D**) species of *Ayenia*. We highlight species occurrence in the Atlantic Forest domain, and for Brazil in the following states: Alagoas (AL), Bahia (BA), Ceará (CE), Espírito Santo (ES), Maranhão (MA), Minas Gerais (MG), Paraíba (PB), Paraná (PR), Pernambuco (PE), Piauí (PI), Rio de Janeiro (RJ), Rio Grande do Norte (RN), Rio Grande do Sul (RS), Santa Catarina (SC), São Paulo (SP) and Sergipe (SE).

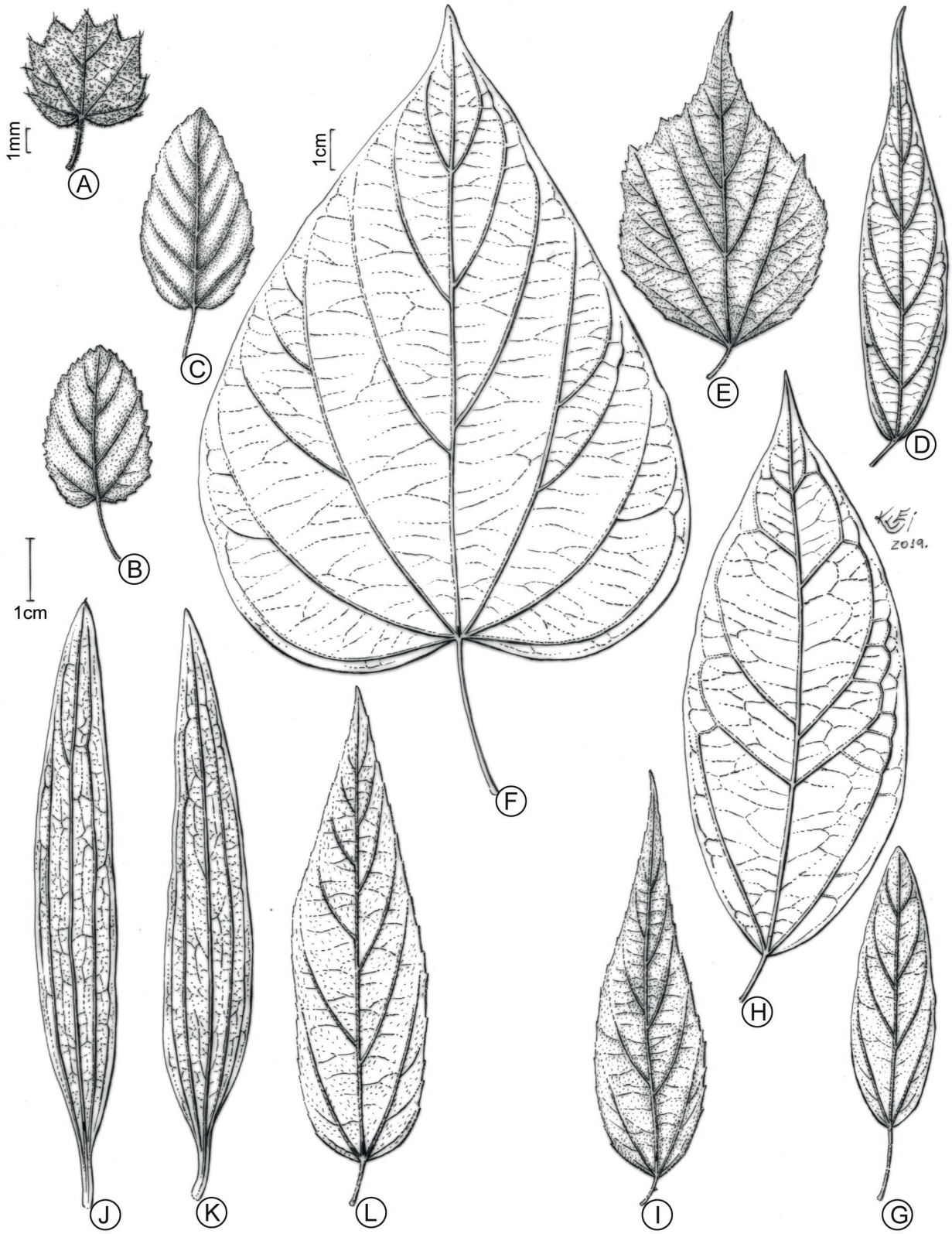

Figure 3. Leaves of selected Byttnerieae species of the Atlantic Forest, depicting variations in form and venation. (**A**) *A. aprica* (*Krapovickas 24220* [RB198067]); (**B**) *A. erecta* (*Silva 618* [RB762811]); (**C**) *A. tomentosa* (*Pirani 2886* [SPF81745]); (**D**) *B. australis* (*Joly* s.n. [SPF80238]); (**E**) *B. beyrichiana* (*Carauta 1692* [RB166547]); (**F**) *B. catalpifolia* subsp. *catalpifolia* (*Fiaschi 1948* [SPF165690]); (**G**) *B. filipes* (*Zardini 49866* [RB370921]); (**H**) *B. gayana* (*Kuhlmann 1050* [SPF196846]); (**I**) *B. gracilipes* (*Martins 31477* [SPF98515]); (**J**) *B. hatschbachii* (*Silva 224* [SPF70631]); (**K**) *B. triadenia* (*Silva 3577* [SPF156413]); (**L**) *B. urticifolia* (*Arbo 5861* [SPF48433]). All leaves are on the same scale (indicated near (**B**), except for (**A**) and (**F**), where the proper scale is indicated near each).

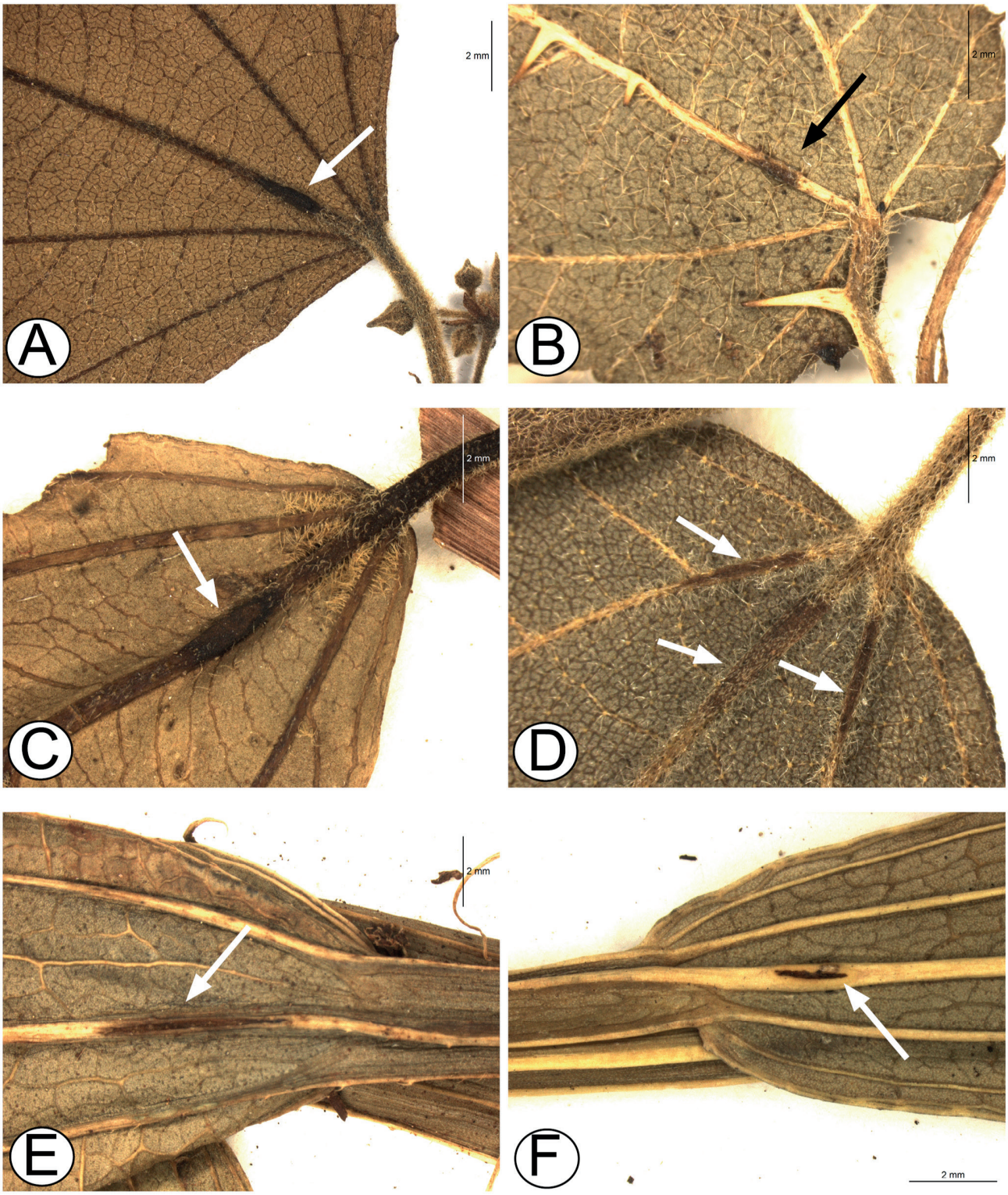

Figure 4. Selection of nectaries of some species of *Byttneria*, highlighting the diversity of form, number of apertures and position of the leaf nectary. (**A**) Multiaperturate nectary of *B. beyrichiana* (*Carauta 1692* [RB166547]); (**B**) *B. urticifolia* (also note the prickles on the midveins, something uncommon in the genus) (*Arbo 5861* [SPF48433]); (**C**) *B. filipes* (also note the concentration of trichomes in the base of the midveins) (*Zardini 49866* [RB370921]); (**D**) *B. triadenia*, with three multiaperturate nectaries (*Silva 3577* [SPF156413]); (**E**) *B. pedersenii*, with a uniaperturate nectary with a large aperture (*Vanni 659* [SPF48513]); (**F**) *B. triadenia*, with a uniaperturate nectary (*Silva 3577* [SPF156413]). For a more in-depth description and schematic, and an anatomic view of nectary types, check Cristóbal (1976) and Arbo (1977).

were recognized by Cristóbal (1960). In Brazil, there are 15 recognized species, mainly native to open seasonally dry formations throughout the Cerrado or Caatinga phytogeographic domains, with a less recurrent presence of species in Argentina, Paraguay and Uruguay. Few species can be found in the Atlantic Forest, these latter growing in ecotone areas to other domains, such as the Brazilian Pampas, the Chaco or with the Brazilian Caatinga.

Unlike its allied genus *Byttneria* (Fig. 5A), *Ayenia* has three thecae, a prominent androgynophore and a petal claw that

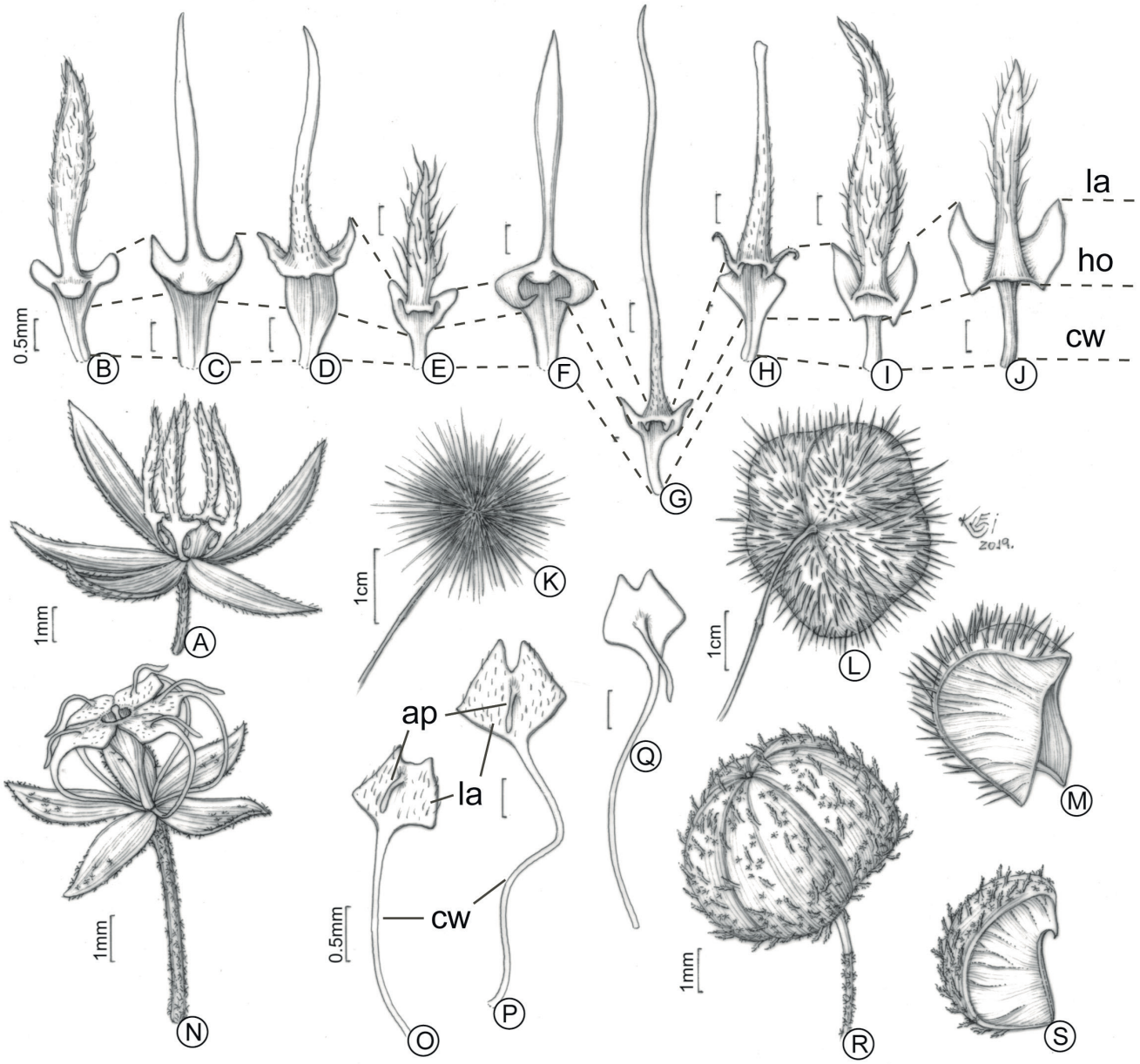

Figure 5. Some of the reproductive diversity of the Byttnerieae of the Atlantic Forest. (**A**) General aspect of the flower of *B. australis* (*Joly* s.n. [SPF80238]); (**B**-**J**) petals from selected *Byttneria* species in a same scale perspective. Petals from, respectively, (**B**) *B. australis* (*Joly* s.n. [SPF80238]), (**C**) *B. beyrichiana* (*Carauta 1692* [RB166547]), (**D**) *B. filipes* (*Zardini 49866* [RB370921]), (**E**) *B. gracilipes* (*Martins 31477* [SPF98515]), (**F**) *B. gayana* (*Kuhlmann 1050* [SPF196846]), (**G**) *B. hatschbachii* (*Silva 224* [SPF70631]), (**H**) *B. pedersenii* (*Vanni 659* [SPF48513]), (**I**) *B. triadenia* (*Silva 3577* [SPF156413]), (**J**) *B. urticifolia* (*Arbo 5861* [SPF48433]); (**K**) fruit of *B. catalpifolia* subsp. *catalpifolia* (*Fiaschi 1948* [SPF165690]); (**L**-**M**) fruit of *B. catalpifolia* subsp. *sidifolia* (general aspect in (**L**) and a mericarp in (**M**) (*Hatschbach 62463* [SPF112502]); (**N**) General aspect of the flower of *Ayenia erecta* (*Silva 618* [RB762811]); (**O**-**Q**) petals from (**O**) *A. aprica* (*Krapovickas 24220* [RB198067]), (**P**) *A. erecta* (*Silva 618* [RB762811]), (**Q**) *A. tomentosa* (*Pirani 2886* [SPF81745]); (**R**-**S**) Fruit and a mericarp of *A. tomentosa* (*Pirani 2886* [SPF81745]). Structure legends: cw = lower portion of the claw (or claw *sensu stricto*), ho = hood (or upper portion of the claw *sensu lato*), la = lamina, ap = appendix of the lamina in *Ayenia*. Note that, in *Ayenia*, lamina, claw and appendix can vary, as Cristóbal (1960) considers the lamina as part of a "hood" of the claw and the appendix as the lamina *sensu stricto*, different from what is schemed in here. Dashed lines in Figures **B**-**J** indicate homology of structures among *Byttneria* species.

is always more prominent than the petal lamina (Fig. 5N). The fruit is small, aculeate with little infraspecific variation (Fig. 5R, S). Besides, in *Ayenia*, vegetative variation is less expressive than in *Byttneria*, and species circumscriptions rely mostly on floral features, such as size, form, margin, and petal indumentum.

1.1. *Ayenia aprica* Cristóbal, Opera Lilloana 4: 126-128. 1957. Type: ARGENTINA, Misiones, Candelaria, 1957, *J.E. Montes 10037* (Holotype: LIL, LIL [photo]!; isotypes: CTES, CTES [photo]!, S, S [photo]!, SI, SI [photo]!, UC, UC [photo]!). (Figs. 2D, 3A, 5O).

Decumbent subshrubs. Leaves leptophyllous (< 25 mm² of area), 7 × 4 mm, blade sub-orbicular, symmetrical, convex to rounded at the apex, cordate at the base, margin serrate, stem and leaves densely pubescent; primary venation actinodromous, major secondary veins craspedrodomous. Flowers pinkish to purple; claw hood entire, base subtriangular, concave, glabrous adaxially, pubescent abaxially, with a filiform appendix of almost half the size of the lamina; petal lamina cylindrical. Fruit cylindrical, pubescent.

Iconography – Cristóbal (1960), Fig. 42.

Distribution and Habitat – Brazil (Rio Grande do Sul); Argentina (Misiones). A species occurring mostly in the Southern portion of the Atlantic Forest, growing in transition areas between decidual forest formations and the Pampas (Fig. 2D).

Preliminary conservation assessment – According to the IUCN criterium B, *A. aprica* is categorized as VU (Vulnerable) due to the relatively wide extension of occupancy (93,312 km²). However, as collections of *A. aprica* are scarce, with only eight unique occurrences, such assessment is likely overestimated. In fact, as the last collection in Brazil is from 1948, with no further novel collections (Cristóbal 1960), *A. aprica* may be locally extinct if no new collections are made, especially to confirm other records in Brazil.

Comments – *Ayenia aprica* resembles *A. mansfeldiana* Cristóbal, and both species almost overlap in distribution. However, *A. mansfeldiana* is restricted to the Pampas, not evidently occurring in the Atlantic Forest domain. *Ayenia aprica* and *A. mansfeldiana* differ due to the following characters: (i) the base of the petal claw (obtuse in *A. mansfeldiana vs*. subtriangular in *A. aprica*), (ii) the lifeform (small subshrubs in *A. mansfeldiana vs*. decumbent and larger subshrubs in *A. aprica*), (iii) leaf indumentum (densely pubescent adaxially with trichomes equally distributed in *A. aprica vs*. glabrous to slightly pubescent and concentrated on the midveins and secondary veins in *A. mansfeldiana*).

Additional specimens examined – BRAZIL. Rio Grande do Sul: "Camino a Encruzilhada, 45 km", 12 February 1948, fl., *M.A. Palacios & A.R.C. Palacios 1296* (LIL, MO [photo]!).

1.2. *Ayenia erecta* Mart. ex K.Schum. in Mart., Fl. bras. 12(3): 103. 1886. Type: BRAZIL, Bahia, Juazeiro ["*Joazeiro*"], s.a., *C.F.P. Martius 2315* (Syntypes: M 8x, M 8x [photos]! (M0211151! (lectotype here designated), M0211152!, M0211153!, M0211154!, M0211155!, M0211156!, M0211157!, M0211158!)). (Figs. 3B, 5P).

Erect subshrubs. Leaves nanophyllous (25–225 mm² of area), 2.0 × 1.5 cm, blade ovate, symmetrical, convex at the apex, cordate at the base, margin serrate, almost forming two lobes at the base, stem and leaves pubescent; primary venation pinnate, major secondary veins craspedrodomous. Flowers yellowish-green; claw hood entire, base rhomboid, convex, glabrous adaxially, slightly pubescent abaxially, with an appendix smaller than half size of the lamina; petal lamina filiform. Fruit small, almost glabrous, with pubescent prickles.

Iconography – Schumann in Martius (1886), v. XII, part. III, fasc. 96, pl. 23 (I); Cristóbal (1960), Fig. 52.

Distribution and Habitat – Brazil (Bahia, Ceará, Paraíba, Pernambuco, Piauí, Rio Grande do Norte). *Ayenia erecta* is mostly found in the arboreous Caatinga (the Carrasco Vegetation) and less recurrently in decidual or riverine forests. In the Atlantic Forest, few specimens are found in seasonally dry deciduous formations and ecotone areas (Fig. 2D).

Preliminary conservation assessment – According to the IUCN criterium B, this species should be potentially assigned as EN (Endangered; AOO = 20 km²; EOO = 97,672 km²). New collections of Caatinga and Atlantic Forest are required for a better definition of the species distribution and habitat.

Comments – *Ayenia erecta* differs from other *Ayenia* due to its shrub or herb lifeform and the pubescent indumentum of branches and leaves (Cristóbal 1960). Here, we designated one lectotype from syntype sheets from Munich Herbarium's collection.

Additional specimens examined–BRAZIL. Bahia: Macarani, 2 August 2001, fl. & fr., *L.A. Mattos-Silva et al. 194* (CEPEC [photo]!, IPA).

1.3. *Ayenia glabrescens* K.Schum., Fl. bras. 12(3): 102. 1886. Type: BRAZIL, "*In silvis Brasiliae*", *s.a.*, *W. Neuwied s.n.* (Holotype not found; isotype F [photo]! (F007348F) (lectotype here designated))

Decumbent subshrubs. Leaves heterophyllous, usually nanophyllous (25–225 mm² of area) varying from 5–8 × 2–3 cm, blade lanceolate to ovate, symmetrical, acute at the apex, obtuse to subcordate at the base, margin irregularly serrate, slightly pubescent abaxially and adaxially; primary venation actinodromous, major secondary veins craspedrodomous. Flowers purplish, claw hood entire, base subrhomboid, convex, glabrous adaxially and pubescent abaxially, with

an appendix with almost half the size of the lamina; petal lamina filiform. Fruit not found.

Iconography – Schumann in Martius (1886), v. XII, part. III, fasc. 96, pl. 23 (II); Cristóbal (1960), Fig. 55.

Distribution and Habitat – Brazil (Bahia). Endemic to the Atlantic Forest domain, growing in the dry deciduous forests of Southern Bahia. The type had no precise location, and the distribution of *A. glabrescens* remained unknown since the 18th century. We found and determined new vouchers of this species at K and SPF Herbaria, from Southern Bahia, Brazil. The precedence of the type is likely from the Bahian Atlantic Forest, considering the documented journey of Prince Maximilian of Wied, who made the first collections of this species (Moraes 2009).

Preliminary conservation assessment – There are four preserved specimens for this taxon in the surroundings of Vitória da Conquista, in Bahia state. According to the IUCN preliminary assessment, this species is categorized as EN (Endangered), with an EOO of 550 km², and an area of occupancy of 12 km². There might be other specimens in surrounding areas as well.

Comments – *Ayenia glabrescens* is remarkable by its heterophyllous membranous leaves, with irregularly serrate margin. There was no previous record of *A. glabrescens* other than the type until Cristóbal (1960) provided the genus monograph. Like Cristóbal (1960), we could not locate the holotype during our survey, so we decided to designate the so-called "isotype" as a lectotype of *A. glabrescens*.

Additional specimens examined–BRAZIL. Bahia: "Km 19 da rodovia Conquista/Barra da Choça", 22 November 1972, fl., *T.S. Santos 2510* (CEPEC, SPF!); Vitória da Conquista, "*ca*. 14 km na rodovia Vitória da Conquista/Brumado, 26 December 1989, fl., *A.M. Carvalho 2606* (CEPEC, RB!, SPF!); Barra do Choca, "Estrada que liga a Rod. BR-116 a São Sebastião, 4 km a W da cidade", 21 November 1978, fl., *S.A. Mori 11263* (CEPEC [photo]!, K!, NY [photo]!, RB!).

1.4. *Ayenia nummularia* Cristóbal, Opera Lilloana 4: 176. 1960. Type: ARGENTINA, Misiones, San Ignacio, 1948, *G.J. Schwarz 6429* (Holotype: LIL [photo]!).

Decumbent subshrubs. Leaves nanophyllous (25–225 mm² of area), 1–2 cm diam, blade orbicular to suborbicular and symmetrical, obtuse at the apex, cordate at the base, margin irregularly dentate, densely pubescent in both sides; primary venation actinodromous, major secondary veins craspedrodomous. Flowers yellowish-green; claw hood entire, base rhomboid and attenuate towards the apex, glabrous adaxially, pubescent abaxially, with an appendix smaller than half size of the lamina length; petal lamina filiform. Fruit not seen.

Iconography – Cristóbal (1960), Fig. 62; Cruz & Esteves (2009), pl. 1, p. 265.

Distribution and Habitat – Brazil (Mato Grosso do Sul); Argentina (Misiones). A species harboring transitional areas between moist forests and open formations. In Brazil, there is one record in the Pantanal too (*Krapovickas 34513*), and in ecotone areas between Pantanal and the Atlantic Forest domains. Further collection efforts are required in areas between the two known records (Fig. 2D).

Preliminary conservation assessment – Species should be considered as DD (Data Deficient) due to scarce collections.

Comments – *Ayenia nummularia* is remarkable by its ovate (orbiculate) leaves with 1–2 cm diam., distinct from *A. aprica,* which bears much smaller orbiculate leaves.

1.5. *Ayenia praecipua* Cristóbal, Opera Lilloana 4: 176. 1960. Type: ARGENTINA, Misiones, Loreto, 1956, *J.E. Montes 10031* (Holotype: LIL; isotype: SI [photo]!). (Fig. 2D).

Decumbent subshrubs. Leaves nanophyllous (25–225 mm² of area), 1–2 × 0.5–0.7 cm, blade elliptic to lanceolate, symmetrical, obtuse at the apex, cordate at the base, margin serrate with small teeth, glabrous adaxially and pubescent abaxially; veins prominent in both sides, primary venation pinnate, major secondary veins craspedrodomous. Flowers purplish; claw entire, base rhomboid, glabrous adaxially, pubescent abaxially, with an appendix smaller than half size of the lamina; petal lamina filiform. Fruit globose, with caducous prickles.

Iconography – Cristóbal (1960), Fig. 66; Cruz & Esteves (2009), pl. 1, p. 265.

Distribution and Habitat – Brazil (Mato Grosso do Sul, São Paulo); Argentina (Misiones); Paraguay (Caaguazú). As *A. nummularia*, *A. praecipua* is also common to transition areas between forested and open environments, with records in the Atlantic Forest, in transition areas with the Chaco and Pantanal, mostly found on rocky soils.

Preliminary conservation assessment – According exclusively to the IUCN criterium B (AOO = 16 km²; EOO = 33,628 km²), this species should be categorized as EN (Endangered).

Comments – *Ayenia praecipua* is distinct by its prominent veins, especially in both sides of the leaf, alike its relative *A. mansfeldiana*, which has smaller leaves and occurs partially in sympatry, predominantly in the Argentinean Chaco. The number of available collections is higher than for *A. nummularia*, but still scarce.

1.6. *Ayenia tomentosa* L., Syst. Nat., 10(2): 1247. 1759; Sp. Pl., 2(2): 1354. Type: GUYANA, Rapununi, Dadanawa, 1995, *M.J. Jansen-Jacobs 3986* (Neotype [designated by Dorr & Wiersema 2010]: US [photo]!; isoneotypes: NY [photo]!, K!, P [photo]!). (Figs. 2D, 3C, 5Q).

Small erect shrubs. Leaves microphyllous (215–2,025 mm² of area), 4–6 × 2–3 cm, blade ovate to lanceolate,

symmetrical, acute at the apex, cordate at the base, margin crenate, densely tomentose in both sides; primary venation pinnate, major secondary veins craspedrodromous. Flowers lilac to purplish; claw filiform, margin entire, base usually triangular, glabrous adaxially, pubescent abaxially, with an appendix of the same length of the claw; petal lamina cylindric. Fruit spherical, with caducous and pilose prickles.

Iconography – Cristóbal (1960), Fig. 75; Cruz & Esteves (2009), pl. 1, p. 265.

Distribution and Habitat – Brazil (Bahia, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Piauí, São Paulo); Bolívia (Santa Cruz, Chuquisaca); Guyana (Upper Takutu-Upper Essequibo), Paraguay (Amambay), Venezuela (Mérida). This is the most widespread species of *Ayenia*, found in dry areas of Venezuela, in the Guyana Shield, in open or seasonally dry areas of Central Brazil, in the Chaco and in riverine, decidual forests or anthropic areas, in transition between the Cerrado or Caatinga and the Atlantic Forest. In the Atlantic Forest, there are some representatives in Bahia, São Paulo and Mato Grosso do Sul states.

Preliminary conservation assessment – *Ayenia tomentosa* is a widespread species through the South American continent that is LC (Least Concern) according to the IUCN criterium B.

Comments – *Ayenia tomentosa* is quite distinctive due to its shrubby lifeform and densely tomentose, larger leaves, and by bearing an androgynophore with almost the same length of the staminal tube.

Additional specimens examined – BRAZIL. Bahia: Camaçari, "Monte Gordo", 14 July 1983, fl. & fr., *H.P. Bautista & G.C.P. Pinto 829* (FCAB, NY [photo]!). **São Paulo**: Rancharia, 14 February 1970, fl. & fr., *G. Hatschbach et al. 23499* (MBM [photo]!, NY [photo]!, RFA, UPCB, US); *V.C. Souza & J.P. Souza 10927* (SPF!).

2. *Byttneria* Loefl., *Iter Hispan.*: 313. 1758. *nom. cons. vs. Butneria* P. Browne, Civ. Nat. Hist. Jam., 166: 490, 1756 *et Butneria* Duhamel, Traité Arbr. Arbust., 1: 113-114, t. 45. 1755 (?*Calycanthus* L. Syst. Nat. 10: 1053. 1759). Type: *Byttneria scabra* L., Syst. Nat., 10(2): 939. 1759.

Shrubs erect to decumbent or lianas; branches with simple and stellate trichomes, cylindrical, sometimes quadrangular or pentagonal, unarmed, or aculeate. Leaves simple, alternate, estipulate, leaf petiolate or (sub-)sessile; margin entire or partially to totally serrate; abaxial side with 1-5 extrafloral nectaries, each one with a linear cavity or with various apertures, located near the leaf base, on the midvein, main veins or on the junction of the blade to the petiole; primary venation actinodromous, major secondary veins semicraspedodromous to eucamptodromous or brochidodromous. Inflorescence axillary cymes, 3-9 flowers, with small bracts; peduncle usually very short to almost absent; bracteoles 1-2 per flower, usually persistent until the anthesis. Flowers bisexual, actinomorphic, dichlamydeous and heterochlamydeous; calyx symsepalous, sepals lobate, elliptical to filiform, valvar aestivation, corolla choripetalous, petals unguiculate, divided in a lower stalk-like portion (= claw), fleshy or membranous, glabrous or pubescent, more or less narrowed, in which the petal sticks into the flower; a median winged portion ("hood", which is herein considered as part of the claw – check Dorr (1999) for a discussion on such terminologies); and an upper portion (= petal lamina), the latter also fleshy or membranous, cylindrical, rarely flat, glabrous or pubescent, equal or up to 5 times longer than the claw; stamens 5, opposite to petals, with connate filaments forming a campanulate to urceolate staminal tube; anthers bithecae, divergent, sessile or subsessile; staminodes 5, fleshy, alternate to petals, free or connate at the base and to the staminal tube; gynoecium syncarpous, 5-carpelar and 5-locular; styles 5, connate almost up to the apex; stigma inconspicuous or capitate, with 5 globose lobes; ovules 2 per locule. Fruit a globose schizocarp, dehiscence septicidal or loculicidal, aculeate, with acute to acicular prickles, persistent or caducous; seeds ovoid, brown or black, smooth or tuberculate, not winged.

Byttneria is a Pantropical genus with *ca.* 130 species, mostly found in the Neotropics. In South America, there are *ca.* 70 species, found along the open seasonally dry areas of the Brazilian Cerrado and Caatinga, but with other representatives in other forested and riverine areas of the continent. In the last review of the group, Cristóbal (1976) recognized six sections, based solely on morphological characters. In South America, there are species from the sections (1) *B.* sect. *Byttneria* (21 species, all Neotropical), (2) *B.* sect. *Vahihara* (Pantropical; 61 species, 13 Neotropical), (3) *B.* sect. *Urticifolia* (15 species, all Neotropical) and (4) *B.* sect. *Crassipetala* (Paleotropical and Neotropical; 22 species, 19 from the Neotropics).

In the Atlantic Forest, fourteen species can be found in these four sections: three in *B.* sect. *Byttneria* (*B. hatschbachii*, *B. pedersenii* and *B. scabra*), four in *B.* sect. *Crassipetala* (*B. australis*, *B. beyrichiana, B. cristobaliana* and *B. filipes*), five in *B.* sect. *Urticifolia* (*B. abutiloides*, *B. gracilipes*, *B. implacabilis*, *B. triadenia* and *B. urticifolia*) and two from *B.* sect. *Vahihara* (*B. catalpifolia* and *B. gayana*). Brazil has records for all species from the Atlantic Forest, but species occurring in the Southern portion of the Atlantic Forest can also occur in ecotone areas in Argentina, Paraguay and Uruguay.

Byttneria can be distinct from its allied genus *Ayenia* for bearing an extrafloral nectary (sometimes more than one, reaching three up to five) on the abaxial side of the leaf blade, usually located on the base of the midveins. Nectary morphology is quite variable (Fig. 3 and 4), as this structure may contain one or more apertures (*i.e.*, it is uni or multiapertured) with variable pubescence and distribution. The nectary region is usually visible to the naked eye, but the nectary cavity of one aperture can only be seen when the nectary is uniaperturate (Fig. 4E-F). In species with

multiaperturate nectaries (Fig. 4A-D), that region can be found at naked eye or under a stereomicroscope, but each aperture is microscopic, only visible under magnification (check Arbo 1977 and Cristóbal 1960 for more anatomical and micromorphological details on these structures).

Byttneria has no conspicuous androgynophore (while *Ayenia* has), with two thecae (unlike *Ayenia*), and the length of the petal claw is smaller than or equal to the petal lamina (in *Ayenia*, the claw is much longer than the lamina). Further diagnostic characters are mostly vegetative, related to life form, leaf features, occurrence and size of the shoot prickles. Nevertheless, floral characters such as indumentum, size and form of the petal lamina and claw are also variable (Figs. 3 and 5), and thus important for infrageneric delimitation.

Byng & Christenhusz (2018) have proposed to synonymize all *Byttneria* to *Ayenia*, probably based on published phylogenies for the group (Whitlock *et al.* 2001; Whitlock & Hale 2011). However, most branches on the phylogenies hitherto published are weakly supported to allow any consistent taxonomical recircumscriptions. In fact, current efforts on systematics of *Ayenia* are revealing an alternative scenario in the classification of the group (W. Sharber, pers. comm.), with *Byttneria* being paraphyletic with *Ayenia* nested in it. Therefore, in this study, we did not adopt Byng & Christenhusz's (2018) circumscription, maintaining the two genera as distinct until further notice.

2.1. *Byttneria abutiloides* A.St.-Hil. & Naudin, Ann. Sci. Nat., Bot. sér. 2, 18: 31. 1842. Type: BRAZIL, "*In montibus Serra dos Órgãos*" [Rio de Janeiro], 1838, *G. Gardner 326* (Holotype: K!; isotypes: BM [photo]!, G [photo]!, GH [photo]!, MO [photo]!, NY 2x [photo]!, P 2x [photo]!, S [photo]!, W [photo]!). (Fig. 2B).

Byttneria rivularis Gardner, London J. Bot. 2: 333. 1843, *nom. superfl.* Type: *G. Gardner 326* (Holotype: BM [photo]!; isotypes: K!, NY [photo]!, S [photo]!, W [photo]!).

Ayenia abutiloides (A.St.-Hil. & Naudin) Christenh. & Byng, Global Fl. 4: 134. 9 Feb 2018 [epublished].

Decumbent shrubs, branches cylindrical, aculeate. Leaves microphyllous (225–2,025 mm²), 10–15 × 6–10 cm, blade ovate, symmetrical, margin serrate, acute at the apex, cordate at the base; nectaries 3-5 per leaf, multiaperturate, dark, on the base of the midvein in the abaxial side; veins glabrous, primary venation actinodromous; major secondary veins semicraspedodromous. Flowers yellowish-green, petal claw membranous. Fruit spherical, densely aculeate.

Iconography – Cristóbal (1976), Fig. 44.

Distribution and Habitat – Brazil (Espírito Santo, Rio de Janeiro). Grows in humid areas near watercourses in ombrophyllous forests.

Preliminary conservation assessment – According to the IUCN preliminary categories, *B. abutiloides* should be considered as EN (Endangered). However, given the scarce, old collections, we believe it should be considered not as threatened, but as Possibly Extinct (EX).

Comments – *Byttneria abutiloides* is one of the few species bearing more than one nectary on the abaxial side of the leaf. Additionally, the slightly lanceolate petal lamina can also distinguish *B. abutiloides* from other species of the genus (check Cristóbal 1976). All examined specimens are outdated, from densely forested regions, with unprecise location.

Additional specimens examined–BRAZIL. Espírito Santo: Cachoeiro de Itapemirim, 5 May 1949, fl., *A.C. Brade 19762* (RB!, CTES).

2.2. *Byttneria australis* A.St.-Hil., Fl. bras. Merid. 1(4): 145. 1825. Type: BRAZIL, "*Province de Sainte-Catherine*" [Santa Catarina], 1816, *A. Saint-Hilaire s.n.* (Holotype: P [photo]!; isotype: F [photo]!). (Figs. 2A, 3D, 5A, B).

Solanum brevipes Dunal in A.DC., Prodr. Syst. Nat. Regni Vegetabilis 13(1): 203-204. 1852 (as Solanaceae). Type: BRAZIL. SANTA CATARINA: *Bacle s.n.* (Holotype: unknown; lectotype here designated MPU 012769, MPU [photo]!)

Ayenia australis (A.St.-Hil.) Christenh. & Byng, Global Fl. 4: 135. 9 Feb 2018 [epublished].

Erect shrubs, branches cylindrical, aculeate. Leaves microphyllous (225–2,025 mm²), usually 8 × 3 cm, blade oblanceolate, symmetrical, untoothed margin, acuminate at the apex, acute base; nectary 1 per leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins glabrous, primary venation pinnate; major secondary veins brochidodromous. Flowers yellowish-green, petal claw membranous, flat. Fruit globose, with small prickles.

Iconography – Cristóbal (1976), Figs. 5, 7 and 26; Cruz & Esteves (2009), pl. 1, p. 265.

Distribution and Habitat – Brazil (Paraná, São Paulo, Santa Catarina, Rio de Janeiro, Rio Grande do Sul). Mainly found in disturbed forested areas of the Southern portion of the Atlantic Forest, in moist environments, where it can be quite abundant. There are some records also in the grasslands of the Brazilian Pampas.

Preliminary conservation assessment – *Byttneria australis* is typical to the Southern portion of the Atlantic Forest of Brazil, but with a wide collection and several records inside protected areas. Thus, the IUCN criteria flags to be a "Least Concern" (LC) or "Near Threatened" (NT) taxon. Given it is an endemic species to Brazil, we belive the latter category—Near Threatened—may suit better.

Comments – Records of *Byttneria australis* are relatively abundant from its native areas. This species has a quite distinctive petal, with the bi-winged portions of hood and lamina both fleshy and the claw membranous.

Additional specimens examined–BRAZIL. Santa Catarina: Itajaí, 29 December 1958, fl., *R. Reitz 6065* (HBR,

NY, R!); Lomba Alta, 7 March 1949, fl., *F.K. Rawitscher s.n.* (SPF 80238) (SPF!); Botuverá, 1 April 2007, fr., *J.A. Fazini s.n.* (FURB 27342) (FURB [photo]!). **Rio Grande do Sul:** São Leopoldo, X.1941, *J.E. Leite 574* (NY [photo]!); Irai, Balneário Osvaldo Cruz, 23 January 1990, *A. Krapovickas & C.L. Cristóbal 43484* (K!; MO); Marcelino Ramos, 15 February 1993, fl., *J.A. Jarenkow 2320* (ESA [photo]!, FLOR, ICN, MBM). **Paraná:** Cianorte, 24 August 1967, fl., *G. Hatschbach et al. 16973* (MBM, NY [photo]!); São Mateus do Sul, 14 November 1988, fl., *G. Hatschbach et al. 52524* (F, MBM, US [photo]!, UPCB). **São Paulo:** São Pedro, 15 June 2000, *S. Gandolfi et al. s.n.* (ESA 4x [photo]!).

2.3. *Byttneria beyrichiana* K.Schum., in Mart., Fl. bras. 12(3): 96. 1886. Type: BRAZIL, Rio de Janeiro ("*Rio Janeiro*"), 1844, *H.K. Beyrich s.n.* (Holotype: F (destroyed), F [photo]!). (Figs. 3E, 5C, 2D).

Byttneria beyrichiana var. *glazioviana* K.Schum. in Mart., Fl. bras. 12(3): 96. 1886. Type: BRAZIL, "*Habitat in Brasiliae provincial Rio de Janeiro prope metropolin*" [Rio de Janeiro], 1877, *A.F.M. Glaziou 8571* (Syntypes: K 1213508! (lectotype here designated), R!, G [photo]!).

Ayenia beyrichiana (K.Schum.) Christenh. & Byng, Global Fl. 4: 135. 9 Feb 2018 [epublished].

Decumbent shrubs, branches cylindrical, aculeate. Leaves notophyllous (2,025–4,500 mm²), 9–14 × 5–11 cm, blade ovate, symmetrical, margin slightly crenate to serrate, acuminate at the apex, truncate to concavo-convex at the base; nectary 1 per leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins hairy, primary venation actinodromous; major secondary veins semicraspedodromous. Flowers purplish, petal claw membranous, flat. Fruit subglobose, irregularly aculeate.

Iconography – Cristóbal (1976), Fig. 21.

Distribution and Habitat – Brazil (Rio de Janeiro), growing in the ombrophyllous forests in sites of "Serra da Pedra Branca".

Preliminary conservation assessment – This is a very narrow endemic species to Rio de Janeiro state, with its last collection from the early 1970s. Although according to the IUCN criterion B *B. beyrichiana* should be considered as EN (Endangered), given its population density (AOO = 16 km² and EOO = 2,481 km²), we believe it should be better suited as CR (Critically Endangered), given the old remaining collections at herbaria.

Comments – *Byttneria beyrichiana* resembles to another species from open or seasonally dry areas, *B. fernandesii* Cristóbal, which inhabits the Brazilian Caatinga, and to the widespread *B. filipes* Mart. ex K. Schum. Nevertheless, *B. beyrichiana* can be distinguished from *B. fernandesii* due to its aculeate branches (*vs.* unarmed branches in the latter) and its dehiscent fruit (*vs.* indehiscent). Conversely, the flowers of *B. beyrichiana* can be distinguished from *B. filipes* due to its glabrous petals (*vs.* pilose in the base in *B. filipes*). The variety of *B. beyrichiana* described by Schumann in *Flora brasiliensis* was later treated as a synonym by Cristóbal (1976). As this variety was based on continuous and variable characters (*i.e.*, small differences on the shape and density of the leaves indumentum and number of flowers per inflorescence), we followed Cristóbal's circumscription.

Additional specimens examined–BRAZIL. Rio de Janeiro: Rio de Janeiro, 3 March 1974, fl. & fr., *P. Carauta 1692* (CTES, MBM, NY [photo]!).

2.4. *Byttneria catalpifolia* Jacq., Pl. Rar. Hort. Schoenbr. 1: 21. 1797. Type: "*Crescit ad Caracas*", 1793, unknown collector (Holotype: W according to Cristóbal (1976), but not found in any online repository). (Figs. 2C, 3F, 5K-M).

Ayenia catalpifolia (Jacq.) Christenh. & Byng, Global Fl. 4: 135. 9 Feb 2018 [epublished].

Lianas, branches cylindrical, unarmed. Leaves varying in size, usually mesophyllous (4,500–18,225 mm²), rarely macrophyllous (18,225–164,025 mm²), blade widely ovate, symmetrical, margin untoothed, straight to slightly acuminate at the apex, base widely cordate; nectary 1 per leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins prominent, especially at the abaxial side, primary venation actinodromous, with 3-4 veins leaving the petiole; major secondary veins brochidodromous. Flowers whitish to pink, petal claw membranous, flat. Fruit variable in shape, size and prickle density, depending on the subspecies—see discussion below.

Iconography – Schumann in Martius (1886), v. XII, part. III, fasc. 96, pl. 20; Cristóbal (1976), Figs. 7, 87-88; Cruz & Esteves (2009), pl. 1, p. 265.

Distribution and Habitat – *Byttneria catalpifolia* is one of the most widespread species of *Byttneria* (Fig. 2C), occurring throughout the Neotropics and with disjunct populations in tropical Africa and French Polynesia.

Preliminary conservation assessment – Both subspecies are widespread, with numerous records; therefore, they can be categorized as LC (Least Concern), as suggested by the preliminary assessment of this study.

Comments – Cristóbal (1976) mentioned three subspecies of *B. catalpifolia*, two of them native to the Neotropics: *B. catalpifolia* Jacq. subsp. *catalpifolia* and *B. catalpifolia* subsp. *sidifolia* (A.St-Hil.) Cristóbal. *Byttneria catalpifolia* subsp. *catalpifolia* differs from the subsp. *sidifolia* due to the following characters: (1) leaf indumentum pubescent, usually with denser stellate trichomes (*vs.* less pubescent leaves, with scarcer stellate trichomes); (2) margin of the petal lamina erose to sub-erose (*vs.* untoothed), and (3) fruit spherical, flattened, smaller in dimensions but densely prickled, with prickles longer than fruit size (*vs.* not flattened fruit with a lobed equatorial portion, larger in dimensions but with smaller and less dense in prickles) (Fig. 5K-M). In the Atlantic Forest, *B. catalpifolia* subsp. *catalpifolia*

is more abundant in the northern portion, with most records in Bahia, Espírito Santo, and Pernambuco states. Conversely, *B. catalpifolia* subsp. *sidifolia* is more abundant in the Southern portion of the domain, with records especially in Rio de Janeiro, Paraná, and São Paulo states (Fig. 2C). The orthographical variation, "*B. catalpaefolia*", found in older studies and herbarium specimens, must be replaced in conformity with the Article 60.10 of the Shenzhen Code (Thurland *et al.* 2018).

Additional specimens examined–*Byttneria catalpifolia* subsp. *catalpifolia*–BRAZIL. Bahia: Ilhéus, *s.d.*, *J.S. Blanchet 2386*, (US); *J.S. Blanchet s.n.*, 1836 (NY 627561) (NY [photo]!). **Ceará:** Pacoti, "*mata da Serrinha*", 14 June 1957, fr., *T.N. Guedes s.n.* (RB 114220) (RB!). **Pernambuco:** Vicência, 30 July 1968, *D. Andrade-Lima* 68-5422 (IPA 18856) (IPA); Nazaré da Mata, 15 July 1953, fl. & fr., *J.C. Moraes 791*, (SPF!).

***Byttneria catalpifolia* subsp. *sidifolia*–ARGENTINA. Misiones:** Iguazú, fl. & fr., 27 March 1970, *A. Krapovickas et al. 15737* (CTES). **BRAZIL. São Paulo:** Araras, fl., 02 September 1984, *J.R. Pirani et al. 845* (SPF!); Limeira 1954, *W. Hoehne s.n.* [barcode: SPF15260] (SPF!); Timburi, fr., 14 June 1995, *J.Y. Tamashiro 1265* (SPF!). **Paraná:** Terra Boa, 14 May 1969, fr., *G. Hatschbach et al. 21480* (NY [photo]!).

2.5. *Byttneria cristobaliana* Dorr, Kew Bull. 54(4): 991-992. 2000. Type: BRAZIL, Bahia, Buerarema, 1995, *J.G. Jardim 637* (Holotype: CEPEC; isotypes: NY [photo]!, US [photo]!, SP!, CTES [photo]!). (Fig. 2C).

Ayenia cristobaliana (Dorr) Christenh. & Byng, Global Fl. 4: 135. 9 Feb 2018 [epublished].

Decumbent shrubs, branches cylindrical, densely aculeate. Leaves microphyllous (225–2,025 mm²) (check Dorr 1999 for leaf dimensions), blade linear-lanceolate, symmetrical, margin untoothed, acuminate at the apex, cuneate to convex at the base; nectary 1 per leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins pubescent, the main vein bordered by a cinereous portion, different in color from the rest of the blade (see Dorr 1999); primary venation pinnate, major secondary veins brochidodromous. Flowers purple, petal claw membranous, flat. Fruit not seen.

Iconography – Dorr (1999), Figs. 1-2.

Distribution and Habitat – Brazil (Bahia). A species found mainly in disturbed areas or in secondary ombrophyllous forests of the Atlantic Forest.

Preliminary conservation assessment – The collection of the species is scarce, and there are no records inside any protected areas since the description by Dorr (1999). Hence, according to the IUCN criterium B (spatial parameters: AOO = 8 km², EOO = 17 km²), it should be categorized as EN (Endangered).

Comments – *Byttneria cristobaliana* was described by Dorr (1999), resembling *B. australis* and occurring in the Southern portion of the Atlantic Forest. However, *B. australis* differs from *B. cristobaliana* due to the adaxial side markedly maculate in *B. cristobaliana* (*vs.* non maculate in *B. australis*) and in the petiole length, smaller in *B. cristobaliana* than in *B. australis*. Full description accompanied by illustrations can be found in Dorr (1999).

Additional specimens examined – BRAZIL. Bahia: Itabela, 17 May 1971, fl., *T.S. Santos 1657* (CEPEC [barcode: CEPEC6871]).

2.6. *Byttneria filipes* Mart. ex K.Schum. in Mart., Fl. bras., 12(3): 95. 1886. Type: BRAZIL, Bahia, Jacobina ("*... ad Serra da Jacobina et Villa da Barra*"), 1995, *J.S. Blanchet 2660* (Lectotype: K! (Inadvertently designated by Cristóbal (1976)), E [photo]!; isolectotypes: BM [photo]!, F [photo]!, G [photo]!, GH [photo]!, LE, NY [photo]!, W). (Figs. 2C, 3G, 4C, 5D).

Byttneria martiana K.Schum. in Mart., Fl. bras. 12(3): 94. 1886. Type: BRAZIL, "*Habitat in Brasilia, loco haud indicato*: *C.F.P. Martius s.n.*" (Holotype: M).

Byttneria paraguayensis (Britton) Chodat ("*Buttneria paraguayensis*"), Bull. Herb. Boissier ser. 2, 1: 403. 1901. Type: ?BRAZIL, "*l'Assomption*" [?Asunción]: *T. Morong s.n.* (Holotype: PH [photo]!).

Byttneria filipes Mart. ex K.Schum. var. *puberula* Hassl., Trab. Mus. Farmacol 21: 86. 1909. Type: PARAGUAY, *T. Rojas 124* (Holotype: GH).

Ayenia filipes (Mart. ex K.Schum.) Christenh. & Byng, Global Fl. 4: 135. 9 Feb 2018 [epublished].

Decumbent shrubs, branches cylindrical, aculeate. Leaves microphyllous (25–2,025 mm²), 5–12 × 2–5 cm, blade ovate-lanceolate, symmetrical, margin untoothed, straight to slightly acuminate at the apex, convex at the base; nectary 1 per leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins glabrous, prominent, primary venation pinnate, major secondary veins brochidodromous. Flowers yellowish-green, petal claw membranous, flat. Fruit small, spherical, with irregular prickles.

Iconography – Cristóbal (1976), Figs. 6, 7 and 19.

Distribution and Habitat – Brazil (Alagoas, Bahia, Ceará, Maranhão, Mato Grosso, Mato Grosso do Sul, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, Sergipe). Also, in Argentina (Entre Ríos, Corrientes, Formosa), Paraguay (Amambay) and Bolivia (Santa Cruz). *Byttneria filipes* is remarkably disjunct, known from riverine forests or arboreal formations of Caatinga and Atlantic Forest, and from the western portion of Brazil, in swampy areas of Pantanal.

Preliminary conservation assessment – As this is a widespread species but with disjunct populations, we believe that *B. filipes* is likely to be suited as LC (Least Concern).

Comments – *Byttneria filipes* is easily distinct from other *Byttneria* by the shape, color and size of petal lamina, which is fleshy and green-yellowish rather than

membranous and purple (Fig. 5D; check also Cristóbal 1976 illustrations). Cristóbal (1976) mentioned the morphological range of variation among specimens of *B. filipes*, but she established no kins to the disjunct pattern of this taxon. Further assessment of herbarium collections and studies on population genetics should clarify the actual infraspecific circumscription of *B. filipes*. In the protologue, *B. filipes* had no holotype designated. Cristóbal (1976) also mentioned more than one type collection from Martius in her monograph and did not designate a lectotype. Thus, we designate the collection of *Blanchet 2660* in K as the lectotype.

Additional specimens examined – BRAZIL. Bahia: Itacaré, 3 October 1998, *J.G. Jardim 1849* (CEPEC; NY [photo! barcode: NY836715]); *ibid*, 4 March 2004, *J.G. Jardim 4213* (SPF! [barcode: SPF171593]); Conde, 18 August 1995, fl. & fr., *G. Hatschbach et al. 63138* (CEPEC, ESA [photo]!, FLOR, MBM [photo]!, MO, SPF!, SPSF, UPCB).

2.7. *Byttneria gayana* A.St.-Hil., Fl. bras. Merid. 1: 145-146. 1825. Type: BRAZIL, São Paulo, Lorena ("*Inveni in sylvis primaevis prope pagum disctum Pôrto da Caxueira, haud longe ab urbicula Lorena, província S. Paulo.*"), 1848, *A. Saint-Hilaire 596* (Holotype: P [photo]!; isotypes: P [photo]!, F [photo]!). (Figs. 2B, 3H, 5F).

Byttneria laevigata Schott ex Pohl, Pl. bras. 2: 70-71, t. 145. 1830. Type: BRAZIL, Rio de Janeiro ("*Habitat inter frutices, cirea Metropolim Rio de Janeiro*"), 1830, *H.W. Schott 5378* (lectotype [inadvertently designated by Cristóbal 1976]: W0026559 (second-step lectotypification here made) [photo]!; isolectotype: W0026560 [photo]!).

Ayenia gayana (A.St.-Hil.) Christenh. & Byng, Global Fl. 4: 136. 9 Feb 2018 [epublished].

Lianas, branches cylindrical, unarmed. Leaves notophyllous (2,025–4,500 mm²), 8–13 × 4–7 cm, blade ovate to elliptic, symmetrical, margin untoothed, acuminate at the apex, convex at the base; nectary 1 per leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins glabrous, flat, primary venation pinnate, major secondary veins brochidodromous. Flowers yellowish-green, petal claw membranous, flat. Fruit small, with small, sparse prickles.

Iconography – Cristóbal (1976), Fig. 100.

Distribution and Habitat – Brazil (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro). A species endemic to Brazil, mostly found in ombrophyllous forests of the Atlantic Forest, also occurring in the Southern portion of the Chapada Diamantina Plateau. Within the Atlantic Forest domain, four clustered populations can be recognized: one in Southern Bahia, and other three in, respectively, Espírito Santo, Rio de Janeiro, and Minas Gerais states.

Preliminary conservation assessment – According to the IUCN criterium B, *B. gayana* can be considered as NT or LC (Near Threatened or Least Concern), given its wide distribution through southeastern Brazil and Bahia. However, as each disjunct population have aggregated individuals, this species might be considered as LC rather than NT.

Comments – *Byttneria gayana* resembles *B. catalpifolia*, but the leaves of the first are glabrous (*vs.* tomentose in the latter), and the petal lamina is glabrous (*vs.* pillose in *B. catalpifolia*). Examination of materials from the four known disjunct populations revealed no significant morphological distinction among them. Nonetheless, further assessment is required towards checking a potential lack of genetic flow among those four apparently clustered populations.

Additional specimens examined – BRAZIL. Bahia: Porto Seguro, 8 March 1974, *W.W. Thomas et al. 12018* (CEPEC, MO, US [photo]!); **Rio de Janeiro:** Magé, March 1978, fl., *P. Occhioni 8362* (MBM [photo]!); Rio de Janeiro, 21 February 1879, fl. & fr., *A. Glaziou 10330* (P 3x [photo!, R!); **Espírito Santo:** Linhares, 20 February 1986, *L.A. Mattos-Silva 2008* (CEPEC, CVRD, RB [photo]!).

2.8. *Byttneria gracilipes* Baill. ex Cristóbal, Adansonia 2: 167. 1861-62. Type: unknown location, unknown collector, *s.n.* (Holotype: (designated by Cristóbal 1976): P2286191 [photo]!; isotype: F [photo]!). (Figs. 2A, 3I, 5E).

Byttneria gracilipes Baill. Adansonia 9: 336. 1870. [*nom. illeg.*]

Byttneria gracilipes Le Maout & Decne. Traite Gen. Bot. 343. 1868 [*nom. illeg.*]

Ayenia gracilipes (Decne. ex Baill.) Christenh. & Byng, Global Fl. 4: 136. 9 Feb 2018 [epublished].

Lianas, branches cylindrical, unarmed. Leaves notophyllous to mesophyllous (2,025–18,225 mm²), variable in dimensions, 9–17 × 5–9 cm, blade ovate, symmetrical, margin serrate, straight to slightly acuminate at the apex, convex to slightly rounded at the base; nectary 1 per leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins glabrous, only the first mid-veins prominent in the abaxial side, primary venation pinnate, with two basal secondary veins, major secondary veins semicraspedodromous. Flowers purple to yellowish-green, petal claw fleshy, flat. Fruit small, densely aculeate with small, caducous prickles.

Iconography – Baillon (1861), p. 167; Le Maout & Decaisne (1868), p. 343; Cristóbal (1976), Figs. 5, 55-56; Cruz & Esteves (2009), pl. 1, p. 265.

Distribution and Habitat–Brazil (Paraná, Rio Grande do Sul, São Paulo) and Argentina (Misiones, Corrientes). *B. gracilipes* is restricted to the Southern portion of the Atlantic Forest, in ombrophyllous forests. In Brazil, it likely occurs in Santa Catarina state too.

Preliminary conservation assessment – According to the IUCN criterium B, this species may be considered as NT or LC (Near Threatened or Least Concern) due to

its wide range (AOO = 136 km² and EOO = 297,684 km²). The category NT ("Near Threatened") may more suitable due to its occurrence in areas of the Southern portion of the Atlantic Forest.

Comments – *Byttneria gracilipes* is sympatric with *B. urticifolia* and they are often confused in herbaria (Cristóbal 1976). The two taxa can be distinct by the notable presence of prickles on the leaf veins of *B. urticifolia*, absent in *B. gracilipes*. Besides, the fruit of *B. urticifolia* is much more densely aculeate than in *B. gracilipes*, which has smaller and sparser prickles.

Typification and authorship of *B. gracilipes* is problematic. Baillon (1861; 1870) first mentioned this name when describing the floral development of *Byttneria*, but it consists of a *nomen nudum*. Nevertheless, he mentioned that a specimen of *B. gracilipes* was cultivated at the National Museum of Natural History of France, in Paris, where he developed most of his studies (Stafleu & Cowan 1976). In fact, there is a voucher in P [barcode: P2286191] from 1849 that might be from such specimen, but it has never been clearly designated as the type of *B. gracilipes*. Later, Le Maout & Decaisne (1868) again mentioned *B. gracilipes*, now under an original illustration of *Byttneria* (Traite Gen. Bot.: 343), but also as a *nomen nudum*. Only one century later, Cristóbal (1976) provided a complete description of *B. gracilipes*, mentioning as holotype the preserved specimen of P mentioned by Baillon beforehand. Concurrently, Cristóbal herself assigned a very fragmented material—a voucher of a leaf fragment with no label—from Field Museum (barcode: F73511F) as an isotype of a name that had no valid designation. This information, however, is missing in her monograph of *Byttneria*, and she is the true author who inadvertently validated "*B. gracilipes*" in her study. The precedence of the isotype designated by Cristóbal, however, remains dubious, and we could not check the physical collection of P to properly evaluate that.

Additional specimens examined – ARGENTINA. Misiones: Cainguás, 30 July 1987, fr., *R. Vanni et al. 875* (SPF!). **BRAZIL. Paraná:** Cerro Azul, 3 May 1977, *G. Hatschbach et al. 39887* (MBM, NY [photo]!, MO); **São Paulo:** Águas da Prata, 21 March 1994, fl., *A.B. Martins et al. 31477*, (UEC [photo]!); Corumbataí, 21 August 1995, fl., *O. Cesar 599*, (SPF!).

2.9. *Byttneria hatschbachii* Cristóbal, Bonplandia 4: 307-310. Type: BRAZIL, Paraná, Arapoti, 1968, *G. Hatschbach et al. 20042* (Holotype: CTES [photo]!). (Figs. 2A, 3J, 5G).

Ayenia hatschbachii (Cristóbal) Christenh. & Byng, Global Fl. 4: 136. 9 Feb 2018 [epublished].

Erect subshrubs, branches pentagonal, unarmed. Leaves mesophyllous (4,500–18,225 mm²), 4–14 × 0.5–1.5 cm, blade linear, symmetrical, margin untoothed, straight at the apex, with a small apiculous, cuneate at the base; nectary 1 per leaf, uniaperturate, located on the base of the midvein in the abaxial side; veins glabrous, yellow, very prominent in the abaxial side of a greenish leaf, primary venation pinnate, major secondary veins hemieucamptodromous. Flowers purple to yellowish-green, petal claw membranous, petal lamina with minute hair in its lower portion. Fruit small, aculeate, caducous prickles.

Iconography – Cristóbal (1976), Figs. 7 and 77; Cruz & Esteves (2009), pl. 1, p. 265.

Distribution and Habitat – Brazil (Paraná, Rio Grande do Sul, Santa Catarina, São Paulo). A species endemic to Brazil, found at the Southern portion of the Atlantic Forest, occurring from São Paulo to Rio Grande do Sul states, reaching the Brazilian Pampas. It inhabits in open or forested moist areas. In the Atlantic Forest, *B. hatschbachii* is common in transitional areas of disturbed sites, particularly in Paraná and São Paulo states.

Preliminary conservation assessment – The wide distribution of *B. hatschbachii* through its native area of occurrence classifies it as NT or LC (Near Threatened or Least Concern) according to the IUCN criterium B.

Comments – *Byttneria hatschbachii* can be easily confused to *B. scalpellata* and *B. pedersenii*, as mentioned by Cristóbal (1976). The distinction among them relies mainly on the petiole length and leaf blade. *Byttneria hatschbachii* has the petiole lower than the length of the leaf blade, *vs.* almost the same length in *B. scalpellata*. Also, leaf blade is rounded in *B. hatschbachii vs.* attenuate in *B. pedersenii*. Lastly, in *B. pedersenii* there are some axillary inflorescences with minute flowers, while in *B. hatschbachii*, the inflorescence is terminal.

Additional specimens examined – BRAZIL. Paraná: Sengés, 16 October 1997, fl., *G. Hatschbach et al. 67111* (ALCB, ESA [photo]!, MBM [photo]!, MO); Araucária, 28 October 1972, fl., *G. Hatschbach et al. 30570* (MBM [photo]!, NY); Curitiba, 13 November 1993, *A. Bidá 705* (NY, UPCB [photo]!); **São Paulo:** Itapeva, *V.C. Souza 7047* 2002 (ESA 2x [photo! barcodes: ESA26623, ESA21284], SPF! [barcode: SPF108063], SJRP [barcode: SJRP13032]); **Santa Catarina:** Lages, 22 October 2004, fl., *G. Hatschbach et al. 78348* (HUCS, UPCB).

2.10. *Byttneria implacabilis* Cristóbal, Bonplandia 4: 190-191. 1976. Type: BRAZIL, Santa Catarina, Garubá, 1973, *A. Krapovickas 23074* (Holotype: CTES [photo]!; isotypes: RB!, P [photo]!, MO [photo]!, US [photo]!, SI, S [photo]!). (Fig. 2B).

Ayenia implacabilis (Cristóbal) Christenh. & Byng, Global Fl. 4: 136. 9 Feb 2018 [epublished].

Erect subshrubs, branches pentagonal, fistulose and densely aculeate, prickles regularly spread over minor stem branches. Leaves notophyllous (2,025–4,500 mm²), 10–16 × 3–9 cm, blade ovate, symmetrical, margin serrate, acuminate apex, convex to rounded base; nectary 1-3 per

leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins hairy, flat, primary venation pinnate, major secondary veins semicraspedodromous. Flowers yellowish-green, petal claw fleshy, lamina cylindrical, widely pubescent, with long trichomes equally spaced on the lamina margin. Fruit small, aculeate, with acute prickles.

Iconography – Cristóbal (1976), Fig. 46.

Distribution and Habitat – Brazil (Paraná, Santa Catarina). A narrow endemic species to the Southern portion of the Brazilian Atlantic Forest, occurring in the coastal region of Paraná up to the northern coast of Santa Catarina. It grows mainly on the understory of forested formations.

Preliminary conservation assessment – According to the IUCN criterium B, *B. implacabilis* should be categorized as EN (Endangered). Our proposition of such categorization relies on its endemism in a forested area that, although being under anthropic pressure, has a fair sampling effort and collection periodicity (the last collections date from 2006).

Comments – *Byttneria implacabilis* is distinct mainly by its prominent and dense prickles. It is different from the remaining species due to the presence of multiaperturate nectary on the leaf blade, as well as by the aculeate and angulose branches, an unusual association of characters in *Byttneria*.

Additional specimens examined – BRAZIL. Paraná: Morretes, 18 March 1909, fr., *P. Dusén 8262* (MO [photo]!), *ibid.*, 24 January 1979, fl., *G. Hatschbach et al. 41947* (MBM [photo]!, NY, SPF!), Guaratuba, 10 March 1963, fl., *G. Hatschbach et al. 9771*, (MBM [photo]!, US). **Santa Catarina:** São Francisco do Sul, 08 September 2006, *B. Mehlhaff 150* (JOI [barcode: JOI2169]).

2.11. *Byttneria pedersenii* Cristóbal, Bonplandia 4: 271-275. 1976. Type: PARAGUAY, San Pedro, "*36 km N de San Estanislao*", 1968, *A. Krapovickas 13953* (Holotype: CTES [photo]!). (Figs. 2B, 4E, 5H).

Ayenia subsessilis (Cristóbal) Christenh. & Byng, Global Fl. 4: 137. 9 Feb 2018 [epublished].

Decumbent subshrubs, branches angulose, ribbed and fistulose, unarmed. Leaf subsessile, with a small winged and ribbed petiole inserted in the stem, notophyllous (2,025–4,500 mm²), 11 × 0.5 cm, blade linear to slightly lanceolate, symmetrical, margin untoothed, straight apex, cuneate base; nectary 1 per leaf, uniaperturate, located on the base of the midvein in the abaxial side; veins yellow-greenish to ochraceous, prominent in the abaxial side, primary venation pinnate, major secondary veins hemieucamptodromous. Flowers yellowish-green to purple, petal claw membranous, lamina cylindrical, fleshy, and pubescent only in its lower portion. Fruit small, densely aculeate, with small prickles.

Iconography – Cristóbal (1976), Figs. 1 and 79.

Distribution and Habitat – Argentina (Misiones); Brazil (Mato Grosso do Sul); Paraguay (Caaguazú). Like *B. gracilipes* and *B. urticifolia*, *B. pedersenii* is also common to the ecotone areas among the Atlantic Forest, the Pampas and the Chaco.

Preliminary conservation assessment – According to the IUCN criterium B, the species should be categorized as NT or LC (Near Threatened or Least Concern; AOO = 152 km², EOO = 201,563 km²).

Comments – *Byttneria pedersenii* resembles *B. hatschbachii*, but the former has axillary inflorescences with small flowers (*vs.* terminal inflorescences), and the base of its leaf blade is attenuate (*vs.* rounded, expanded in *B. hatschbachii*).

Additional specimens examined – ARGENTINA. MISIONES: Apóstoles, 01 February 1961, fl., *R.M. Crovetto 9360* (P [photo]!), Posadas, *Ekman 193* 1907 (NY [photo! barcode: NY222222]). **BRAZIL. MATO GROSSO DO SUL**. Bela Vista, 16 November 2002, fl., *G. Hatschbach et al. 74289* (MBM [photo]!, K!).

2.12. *Byttneria scabra* L., Syst. Nat., 10(2): 939. 1759. Type: VENEZUELA, Bolívar, Alto Caroni, "*alrededores de Sta. Elena de Uairén*", 1946, *T. Lasser 1445* (Neotype (designated by Dorr & Wieserma (2010)): US [photo]!; isoneotypes: NY, VEN). (Fig. 2C).

Byttneria longifolia Turcz. Bull. Soc. Imp. Naturalistes Moscou 25(2): 154. 1852. Type: VENEZUELA, Caracas, *N. Funck 156* (Syntypes: P2286217 [photo]! (lectotype here designated), P2286218 [photo]!, W).

Byttneria salicifolia Roem. & Schult., Syst. Veg, 5: 470. 1819. Type: VENEZUELA, Caripe, "*Couvent de Capucins entre les Ind. Chaymas*", *A. Bonpland 306*, Holotype: LZ [destroyed] (isotype: P2286219 [photo]! (here designated as lectotype)).

Byttneria scabra var. *brasiliensis* K.Schum. in Mart., Fl. bras. 12(3): 87. 1886. Type: BRAZIL, "*In Brasiliae prov. S. Paulo*" [São Paulo], *W.J. Burchell 4262* (Syntypes: BR [photo]! (lectotype here designated); "*In Brasilia australi, locis haud accuratius addictis*", *Sello 3457* (P1900225 [photo]!).

Byttneria scabra var. *dentata* A.St-Hil. & Naud., Fl. bras. Merid. 1(4): 144. 1825. Type: BRAZIL, "*In prov. Goyaz ad Rio Pilloens*", *J.B.E. Pohl s.n.* (Holotype: M [photo]!).

Byttneria scabra var. *hastata* K.Schum. in Mart., Fl. bras. 12(3): 87. 1886. Type: BRAZIL, Minas Gerais, Caldas ("*In prov. Minas Geraes apud Caldas*"), *G.A. Lindberg 287a* (Syntypes: BR [photo]! (lectotype here designated), S [photo]!).

Byttneria scabra var. *latissima* K.Schum. in Mart., Fl. bras. 12(3): 87-88. 1886. Type: BRAZIL, Minas Gerais, Caldas ("*In provincia Minas Geraes prope Caldas*"), *A.F. Regnell III-282* (Syntypes: S12-17524 [photo]! (lectotype here designated), S12-17525 [photo]!, S12-17526 [photo]!, S12-17531 [photo]!, S12-17532 [photo]!, P [photo]!).

Byttneria scabra. var. *serrata* K.Schum. in Mart., Fl. bras. 12(3): 87. 1886. Type: BRAZIL, "*In prov. S. Paulo et Minarum apud Ypanema, Serra da Lapa, in campis S. Joao d"el*

Rey et Camapuam" [São Paulo], *C.F.P. Martius 657* (Syntypes: M [photo]!; "*prope Ytú*" (Itu), *L. Riedel 1967*, P1900224 (lectotype here designated) [photo]!).

Ayenia scabra (L.) Christenh. & Byng, Global Fl. 4: 136. 9 Feb 2018 [epublished].

Decumbent subshrubs, branches angulose, aculeate, ribbed. Leaves microphyllous (225–2,025 mm²), blade variable in shape and dimensions, but usually linear to slightly lanceolate, symmetrical, margin usually untoothed, sometimes dentate only in the apex, convex apex, rounded base; nectary 1 per leaf, uniaperturate, located on the base of the midvein in the abaxial side; veins white-yellowish, prominent especially in the abaxial side, primary venation pinnate, major secondary veins semicraspedodromous. Flowers pinkish to purple, petal claw membranous, almost glabrous, with few trichomes on the hood, lamina cylindrical, almost glabrous, with sparse trichomes in the lower portion. Fruit small, subspherical, with densely sparse caducous prickles.

Iconography – Schumann in Martius (1886), v. XII, part. III, fasc. 96, pl. 19; Cristóbal (1976), Figs. 5, 6, 60-61 and 75; Cruz & Esteves (2009), pl. 1, p. 265; Colli-Silva *et al.* (2019), Fig. 2.

Distribution and Habitat – Brazil (Amapá, Amazonas, Bahia, Distrito Federal, Goiás, Mato Grosso do Sul, Mato Grosso, Paraná, Rio Grande do Sul Roraima, São Paulo); with disjunct records from Colombia (Guainía, Vichada), Venezuela (Bolívar, Guárico), in the Guianas and in Trinidad and Tobago. *Byttneria scabra* is one of the most widespread species of the genus, occurring mainly in open or seasonally dry areas of Cerrado, the Páramos and the *campo rupestre* vegetations, but also growing within forests in the Amazonian region and reaching the Southernmost Brazilian states. In the Atlantic Forest, it is common in transitional zones with the Chaco, as well as in some forested or disturbed areas of Paraná, Minas Gerais, and São Paulo states.

Preliminary conservation assessment – The species should be categorized as LC (Least Concern), considering its widespread distribution.

Comments – *Byttneria scabra* is the type species of the genus and can be easily distinct from its allies of *Byttneria* sect. *Byttneria* by having both aculeate and angular branches. Several alternate names of *B. scabra* have been proposed through time, including half a dozen varieties recognized by Schumann in *Flora Brasiliensis*. All of these, however, were later synonymized to *B. scabra* on Cristóbal's (1976) monograph, based on an extensive study of variability of shape, size and indumentum of hundreds of leaves. Still, further studies on population genetics of this widespread and complex taxon would allow a reliable evaluation of its current taxonomic circumscription.

Additional specimens examined–BRAZIL. Mato Grosso do Sul: Mundo Novo, 10 December 1982, fl., *G. Hatschbach et al. 45843* (MBM [photo]!, MO); **Minas Gerais:** Poços de Caldas 19 January 1980, fl., *A. Krapovickas et al. 35373* (MBM [photo]!, MO); **Paraná:** Curitiba, "Capão da Imbuia", 05 November 1974, *L.T. Dombrowski 5429* (HCF); Guai, 15 January 1971, fl. & fr., *G. Hatschbach et al. 25963* (MBM [photo]!, NY, RFA, US); **Rio Grande do Sul:** Soledade, 27 November 2013, fl., *E. Pasini 982* (HUCS, ICN); **São Paulo:** Patrocínio Paulista, 1893, fl., *A. Loefgren 2151* (SP!).

2.13. *Byttneria triadenia* Cristóbal, Bonplandia 4: 194-197. 1976. Type: BRAZIL, Paraná, Paranaguá, 1969, *G. Hatschbach et al. 22866* (Holotype: CTES [photo]!; isotype MBM). (Figs. 2B, 3K, 4D, 5I).

Ayenia triadenia (Cristóbal) Christenh. & Byng, Global Fl. 4: 137. 9 Feb 2018 [epublished].

Decumbent shrubs, branches cylindrical, aculeate. Leaves microphyllous (225–2,025 mm²), 9–13 × 4–6 cm, blade oblanceolate, symmetrical, margin serrate with small teeth, straight apex, obtuse base; nectaries 3 per leaf, multiaperturate, sometimes only visible in stereomicroscope, located on the base of the midvein in the abaxial side; veins prominent in the abaxial side, primary venation pinnate, major secondary veins brochidodromous. Flowers yellowish-green and purple, petal claw purple, linear, cylindrical, glabrous; lamina cylindrical, fleshy, pubescent. Fruit small, spherical, densely covered by small pubescent prickles.

Iconography – Cristóbal (1976), Fig. 47.

Distribution and Habitat – Brazil (Paraná). *Byttneria triadenia* occurs sympatrically with *B. implacabilis,* both endemic to the costal Southern portion of the Atlantic Forest, with records throughout all coastal region of Paraná state. Cristóbal (1976) also mentioned the occurrence in Santa Catarina state, but the location of these vouchers is unprecise. It grows mainly in forested and moist formations of the ombrophyllous forests (Fig. 2B).

Preliminary conservation assessment – According to the IUCN criterium B, *B. triadenia* should be categorized as EN (Endangered).

Comments – Besides co-occurring with *B. implacabilis* and other Byttnerieae in the Southern coastal portion of the Atlantic Forest, *B. triadenia* is distinct from the remaining *Byttneria* due to the presence of more than one nectary on the base of the midvein, as well as due to its prominent prickles and leaves and branches remarkably pubescent.

Additional specimens examined – BRAZIL. Paraná: Guaratuba 20 March 2002, fl., *J.M. Silva 3577* (ALCB 2x, ESA [photo]!, HUCS, HUEFS [photo]!, MBM [photo]!, SPSF, SPF!).

2.14. *Byttneria urticifolia* K.Schum. in Mart., Fl. Bras. 12(3): 98. Type: BRAZIL, "*In silvis primaevis Brasiliae meridionalis, loco haid indicato*", *s.a.*, *F. Sellow 1123* (Holotype: F [photo]!). (Figs. 2B, 3L, 5J).

Ayenia urticifolia (Cristóbal) Christenh. & Byng, Global Fl. 4: 137. 9 Feb 2018 [epublished].

Decumbent subshrubs, branches slightly angulose, densely aculeate, ribbed, with canaliculate aculeate projections. Leaves microphyllous (225–2,025 mm²), 8–13 × 4–10 cm, blade ovate, symmetrical, margin serrate, straight to acuminate apex, subcordate to cordate base; nectary 1 per leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins glabrous, midribs with prickles, primary venation acrodromous, major secondary veins craspedrodomous. Flowers purple to yellowish-green, petal claw fleshy to linear, lamina membranous. Fruit small, spherical, densely covered by small pubescent prickles.

Iconography – Cristóbal (1976), Figs. 1, 5, 7, 54-55.

Distribution and Habitat – Brazil (Rio Grande do Sul), and neighboring areas of Argentina (Misiones). A species distributed in the Southern area of the Atlantic Forest, although more commonly found on dry grasslands and in transitional areas between forests and grasslands, in Rio Grande do Sul state and in Misiones, Argentina.

Preliminary conservation assessment – According to the IUCN criterium B, this species should be considered as NT or LC (Near Threatened or Least Concern).

Comments – *Byttneria urticifolia* resembles *B. gracilipes* but has prickles on their leaf veins (absent in the latter), and its fruit is much more densely aculeate than in *B. gracilipes*, with smaller and sparser prickles.

Additional specimens examined – ARGENTINA. Misiones: Concepción, *s.a.*, *H.A. Keller s.n* (CTES [CTES342419]); Cerro Azul, *s.a.*, *A. Krapovickas s.n* (CTES 32512).

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