



Catalogue of the vascular epiphytic flora of Uruguay

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ABSTRACT

We provide an updated list of the vascular epiphytic flora occurring in native environments of Uruguay based on literature review, herbarium specimens, and fieldwork throughout the country. The catalogue provides standardized information for each species, including accepted name, synonyms used within Uruguay, epiphytic category, distribution within the country, habitat, conservation status, observations, and a voucher citation. The effort documented 73 species for the epiphytic flora of Uruguay (3 % of the flora), distributed among 29 genera and 12 families. Bromeliaceae was the richest family (17), followed by Polypodiaceae (16) and Orchidaceae (12). *Tillandsia* stood out as the most speciose genus with 15 species. Characteristic holoepiphytes was the most diverse ecological category. More than half of the epiphytic species documented for Uruguay (53 %) reach their southernmost geographic distribution in the country, whereas only two mostly epipetric species of *Tillandsia* — *T. arequitae* and *T. uruguayensis* — are endemic to the country. Almost half of the epiphytic species found are presently under categories of threat of extinction, with 60 % of them occurring in national protected areas. Both the richest epiphytic families and the predominance of characteristic holoepiphytes coincide with findings from floristic and ecological studies previously carried out in humid subtropical regions.

Keywords: conservation status, epiphytic category, geographic distribution, hemiepiphytes, holoepiphytes, subtropical forests, Uruguay, vascular epiphytes

Introduction

Epiphytes are plants that germinate and grow on other plants, phorophytes, where they survive without absorbing nutrients from the host plant and without being connected to the ground, at least during some stage of the life cycle (Mirbel 1815; Madison 1977; Benzing 1990). As epiphytes are sustained entirely by nutrients and water available in the canopy (Moffett 2000), parasitic and hemiparasitic plants are not included in this life-form (Benzing 1987), since they extract nutrients and water from the living tissues of the host plant (Moffett 2000).

The most recent estimation of vascular epiphytes in the world reports 27,614 species, distributed in 73 families and 913 genera. The number of species represents ca. 10 % of the diversity of vascular plants of the planet (Zotz 2013a). Vascular epiphytes occur widely across the whole spectrum of phylogenetic diversity, so that epiphytism represents a life-form with multiple independent origins (Gentry & Dodson 1987). Epiphytes are well-represented within lycophytes and ferns, and are especially numerous among angiosperms. In the latter, the largest diversity occurs in monocots, accounting for approximately 80 % of all epiphytic species, with a high concentration in Orchidaceae and Bromeliaceae (Zotz 2013a). Epiphytic eudicots are

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otherwise much less diversified, but occur in a larger number of families, such as the Cactaceae, Ericaceae and Gesneriaceae. Among all epiphytic families, Orchidaceae stands out with more than 18,800 species, representing 68% of the total of epiphyte flora (Zotz 2013a). This remarkable diversity places the orchids as the most successful plant lineage in canopy colonization (Benzing 1990). This family is only distantly followed by Bromeliaceae with 1,770 species, and Polypodiaceae with 1,252 species, the second and third epiphytic families in species number (Zotz 2013a).

The epiphytic life-form has been reported as a characteristic component of wet and moist forests in tropical regions (Kreft *et al.* 2004; Kersten 2010; Menini Neto *et al.* 2016). Several authors documented the contribution of epiphytes to species richness, biological diversity maintenance, primary production and structure of these ecosystems (Gentry & Dodson 1987; Benzing 1990; Kersten 2010; Freitas *et al.* 2016). Despite being a typical component of tropical wet forests, vascular epiphytes also occur in subtropical moist forests (Waechter 1998; Rogalski & Zanin 2003; Giongo & Waechter 2004; Machado *et al.* 2016) and to a lesser extent in temperate moist forests (Zotz 2005; San Martín *et al.* 2008; Pincheira-Ulbrich 2011). Additionally, some species could even be found in arid and semi-arid environments (Gentry & Dodson 1987).

Uruguay is classified as a subtropical country mostly covered with grasslands, and thus is expected to have a relatively poor vascular epiphytic flora. However, several distinct forest types occur in this country, varying from moist forests along riversides to dry inland thorn forests (Alonso-Paz & Bassagoda 2002). A relatively high abundance and diversity of epiphytes are considered to be a defining feature for at least one particular forest type, the moist-hillside forest (Alonso-Paz & Bassagoda 2002; Brussa & Grela 2007). Nevertheless, there are no studies concerning the entire epiphytic flora of Uruguay and the relationships of this flora with forest types. Most of the present knowledge on vascular epiphytes is addressed in taxonomic studies of families or groups containing epiphytic species, such as ferns (Osten & Herter 1925; Herter 1928; 1939; 1949; Legrand & Lombardo 1958; Marchesi 1964; 1979; Mai 2014), peperomias (Trelease [1939]1941; Trelease & Herter 1952; Marchesi 1968; Mai *et al.* 2016), orchids (Izaguirre 1972; 1985; 2013; Rossado *et al.* 2014), bromeliads (Smith 1933; 1972; Marchesi 1965; Smith & Downs 1977; Brito & Llano 2008; Rossado 2018; Rossado *et al.* 2018a; b; 2019), tradescantia (Pellegrini 2018), ficus (Herter 1940; Brussa & Grela 2007) and cacti (Herter 1930; Lombardo 1946; 1964; Eggli *et al.* 2008; Berazategui *et al.* 2010).

The main objective of this study is to provide a complete and up to date list of the vascular epiphytic flora occurring in Uruguay in the form of a catalogue containing additional information on ecological category, eco-geographical distribution, and conservation status for each species.

Materials and methods

Study area

Uruguay is typical subtropical country, extending between 30°–35°S and 53°–58°W (Fig. 1). Climate is humid and warm-temperate, with high air humidity throughout the year and hot summers, corresponding to the *Cfa* type according to the Köppen-Geiger classification system (Kottek *et al.* 2006). The mean annual temperature is approximately 17.7 °C, with values decreasing from northwest to southeast of the country; the mean annual precipitation varies from 1200 mm in the southwest to 1600 mm in the northeast (Castaño *et al.* 2011).

Grasslands are the predominant vegetation type in Uruguay and they occupy approximately 70 % of the territory (Puerto 1987), while forests only cover approx. 5.2 %, occurring especially along floodplains of rivers and streams, hillsides, and ravines (MGAP 2018). Native forests are classified by the local conditions where they occur or by the dominant tree species. In this sense, based on Alonso-Paz & Bassagoda (2002) and Brussa & Grela (2007), we considered the following seven forest types: 1) *Butia* palm forest (*palmar*), an open forest or a wooded savanna where the tree layer is dominated by the palms *Butia odorata* (Barb. Rodr.) Noblick or *Butia yatay* (Mart.) Becc.; 2) hydrophilous forest (*bosque hidrófilo*) occurs in temporarily or permanently flooded areas; 3) open thorn forest (*bosque parque*) develops in flat plains of western Uruguay, as a type of wooded savanna dominated by xeric species as *Aspidosperma quebracho-blanco* Schltdl., *Prosopis affinis* Spreng., *Prosopis nigra* (Griseb.) Hieron. and *Vachellia caven* (Molina) Seigler & Ebinger; 4) psammophilous forest (*bosque psamófilo*) occurs on sandy soils, between dunes in wind protected areas along the coast; 5) riverside forest (*bosque ribereño*) occurs on floodplains of rivers; 6) xeric hillside forest (*bosque serrano*) occurs on dry, stony and shallow soils of hill slopes; 7) moist hillside forest (*bosque serrano húmedo*) also occurs on hill slopes, steep slopes, sheltered ravines or deep and narrow valleys, where high air moisture and more stable temperatures allow the development of relatively species-rich forests.

Data collection

The first step in preparing this catalogue was the compilation of a list of species cited in published literature and herbarium specimens deposited at MVFA, MVFQ, MVHC, MVJB and MVM. In addition, specimens of bromeliads and peperomias from Uruguay deposited at BA, CTES, LP and SI were included (herbaria acronyms follow Thiers 2018). This preliminary list was checked, edited and enlarged with the information collected in the field.

Extensive fieldwork was carried out as the second step for this study. Field excursions were planned based on

the analysis of collection sites given on the herbarium specimens. All the specimens were geo-referenced and mapped, allowing the detection of those regions in the country with no or a low number of collections. Fieldwork was then focused on these regions and carried out from September 2012 to December 2017, including 149 localities throughout all the 19 departments of Uruguay (Fig. 1). In the selected sites, a combination of ground-based techniques (direct observation, binoculars) and climbing methods (Flores-Palacios & García-Franco 2001) were used to assess the occurrence of epiphytic species. Specimens from all epiphytic species observed at each site were collected and deposited at MVJB or MVFA; whenever needed, sterile live collections were cultivated until flowering for identification purposes. Taxa were identified by studying species types and protologues, by the use of keys and descriptions in taxonomic literature and by the revision of herbarium specimens previously identified by specialists.

Catalogue data

The systematic classification adopted follows APG (Stevens 2017) for angiosperms and Smith *et al.* (2006) as modified by Christenhusz *et al.* (2011) for ferns. Species were named according to the website Flora do Brasil 2020 (2019). The catalogue includes all the species confirmed during fieldwork and with herbarium specimens stating the epiphytic habit and their occurrence in natural forests. In order to assess only epiphytic species naturally distributed in the country, species from urban environments were not included. For each confirmed species the following information was included: accepted name, synonyms previously used in publications of Uruguay, epiphytic category, distribution, habitat, conservation status, nomenclatural comments, observations, and a voucher specimen. For each species the specimen selected as a voucher corresponds with the oldest and most complete

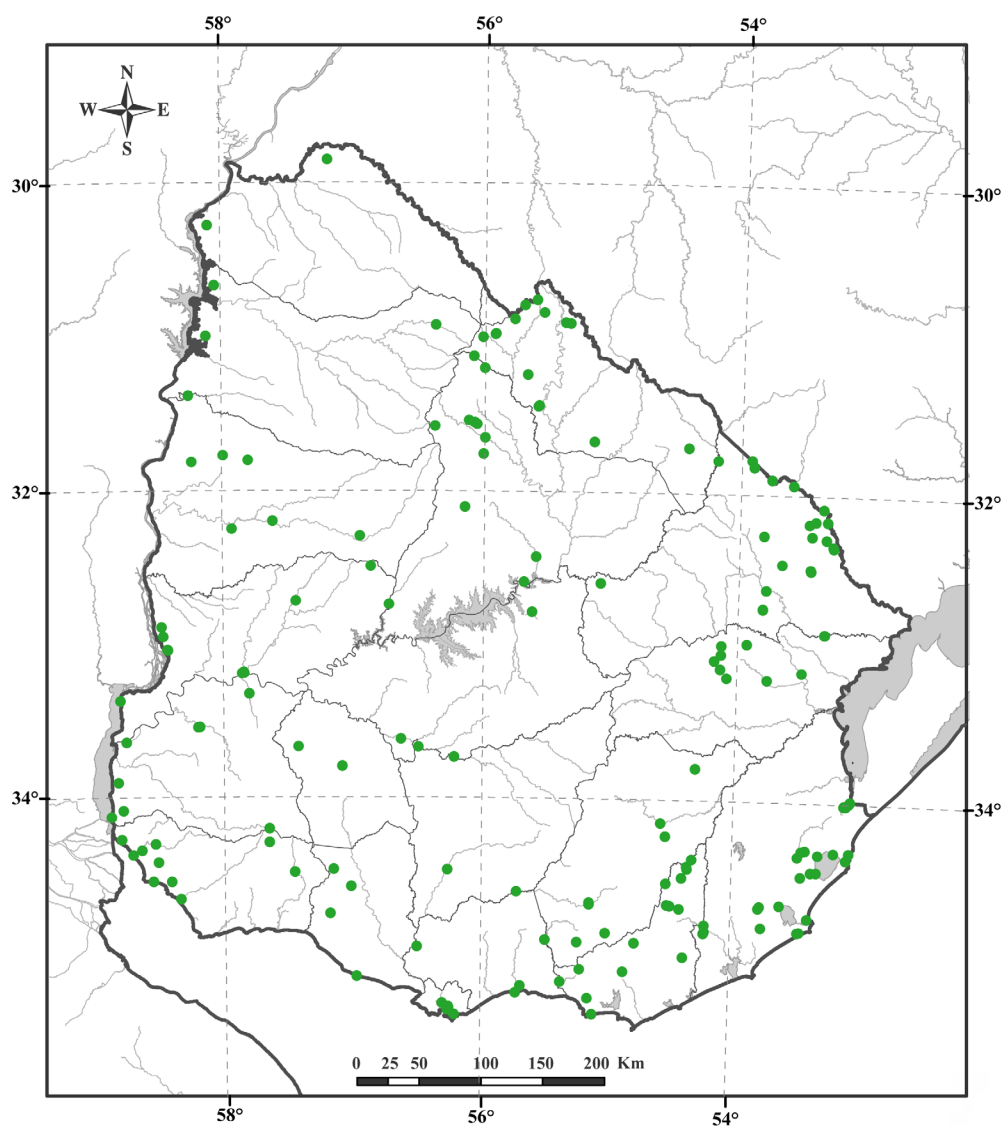


Figure 1. Distribution of sampled localities during fieldwork carried out in Uruguay (green dots).

specimen with epiphytic habit recorded in national herbaria.

The epiphytic category was assigned according to the relationship with the phorophyte, based on observations carried out during fieldwork. The adaptive classification follows several authors (Benzing 1990; Moffett 2000; Kersten 2010) and distinguishes two main categories: I) holoepiphytes (HL) (permanent epiphytes): species that develop their whole life cycle on the phorophyte, and II) hemiepiphytes (HE) (temporary epiphytes) plants that spend part of their life as epiphytes and another part in contact with the ground. According with Moffett (2000) and Zotz (2013b) (who coined Schimper's (1903) terminology), we considered as HE only the species which germinate in tree crowns and later establish contact with the ground via aerial roots. The HL category was subdivided into: i) characteristic holoepiphytes (HLC) (obligate, true or habitual): species that always germinate, grow and reproduce in the canopy; (ii) facultative holoepiphytes (HLF) (casual): species that germinate and reproduce either on trees or in other substrates; (iii) accidental holoepiphytes (HLA): usually terrestrial, saxicolous, or epilithic species that occasionally grow on trees and are able to reproduce in the canopy. For the alternative or main habitat of the HLF and HLA terminology, we followed Barfuss *et al.* (2016): terrestrial, plants that grow on the ground and root into the substrate (tr); epilithic, plants which grow over bare rocks (el), and saxicolous, plants which root in rocks crevices or into the substrate accumulated between rocks (sx), respectively.

Geographic distribution data refers to the departments where the species were registered based on herbarium specimens and field observations, and is abbreviated as follows: Artigas: AR; Canelones: CA; Cerro Largo: CL; Colonia: CO; Durazno: DU; Flores: FS; Florida: FA; Lavalleja: LA; Maldonado: MA; Montevideo: MO; Pay: PA; Río Negro: RN; Rivera: RI; Rocha: RO; Salto: SA; San José: SJ; Soriano: SO; Tacuarembó: TA, and Treinta y Tres: TT. Additionally, the distribution in neighboring regions of Uruguay was investigated in order to detect the southernmost limit for each species; for this purpose we consulted several online databases (GBIF 2018; SPLink 2018; Flora do Brasil 2020 2019; IBODA 2019), publications concerning vascular epiphytes (Bauer & Waechter 2011; Perleberg *et al.* 2013; Carneiro *et al.* 2016; Gonzatti *et al.* 2016; Machado *et al.* 2016; Martínez *et al.* 2016; Guerrero & Cellini 2017; Pellegrini 2018), and in some cases data from herbarium labels. Habitat distribution follows the forest classification previously described (see Study area).

The assessment of the conservation status of each species follows the classification system proposed by IUCN (2012): Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN) and Critically Endangered (CR). The evaluation of IUCN categories at

the national level was based essentially on the geographic range criterion, through the assessment of Area of Occupancy (AOO) (IUCN 2012). We used AOO because most epiphytic species of Uruguay show a discontinuous geographic distribution. To assess it, we used the software GeoCAT-Geospatial Conservation Assessment Tool (Bachman *et al.* 2011) with a cell width of 15 km, except for a few species whose habitat has low surface and so a cell width of 10 km was used: *Asplenium gastonis* Fée, *Didymoglossum hymenoides* (Hedw.) Copel., *Niphidium crassifolium* (L.) Lellinger, *Pecluma paradiseae* (Langsd. & Fisch.) M.G. Price, *Polyphlebium angustatum* (Carmich.) Ebihara & Dubuisson, *Rhipsalis floccosa* Salm-Dyck ex Pfeiff., *Tillandsia arequitate* (André) André ex Mez, *T. loliacea* Mart. ex Schult. f. in Roem. & Schult., *T. tricholepis* Baker, *T. uruguayensis* Rossado and *T. xiphoides* Ker Gawl. For those species under any threatened category, the occurrence in national protected areas (SNAP) was evaluated.

Results

Vascular epiphytic flora of Uruguay

The epiphytic flora of Uruguay comprised 73 species, distributed in 29 genera and 12 families. Angiosperms were represented by 48 species, 16 genera and six families, whereas ferns by 25 species, 13 genera and six families. The richest families were Bromeliaceae (17 spp.), Polypodiaceae (16 spp.) and Orchidaceae (12 spp.), followed by Piperaceae (seven spp.) and Cactaceae (six spp.) (Fig. 2). On the whole, the three richest families constitute 62 % of the epiphytic flora of the country. *Tillandsia* stood out as the most speciose genus with 15 species, more distantly followed by *Peperomia* (seven spp.) and *Pleopeltis* Humb. & Bonpl. ex Willd. (five spp.).

Among the epiphytic categories (Fig. 3) characteristic holoepiphytes (Figs. 4, 5) were the most diversified, with 46 species (63 %); most of these species occur within Bromeliaceae, Polypodiaceae and Orchidaceae. Second were the accidental holoepiphytes (Fig. 6), represented by 16 species (22 %), followed by facultative holoepiphytes (Fig. 7), represented by nine species (12 %), in both cases belonging to different families. The two remaining species (3 %) occurred as hemiepiphytes (Fig. 8), both belonging to the genus *Ficus* L. (Moraceae).

All the species registered as epiphytes in natural environments are native to Uruguay, i.e., no alien species established in natural forests. Only two accidental epiphytic species of *Tillandsia* (Bromeliaceae) are endemic to the country, *T. arequitate* and *T. uruguayensis*. These species are essentially epilithic, but occasionally grow as epiphytes on trees close to the rocky surfaces, where they are abundant. Out of the non-endemic epiphytic species, slightly more than half (53 %) reached in Uruguay their southernmost limit of distribution.



The conservation status assessment indicated a high extinction risk concerning the epiphytic flora, with 33 species (45 %) classified as threatened; 16 species (22 %) as VU and 17 species (23 %) as EN. Another set with 40 species (55 %) were outside of any threat, being classified in the LC and NT categories. Among the species identified as threatened, 20 have been reported for national protected areas.

Species catalogue

Ferns

Aspleniaceae

Asplenium L.

Asplenium gastonis Fée, Crypt. Vasc. Brésil 1. 70 t. 19 f. 2. 1869.

= *Asplenium divergens* Mett. ex Baker in Mart., Fl. bras. 1(2): 445. 1870.
(Fig. 7D).

Epiphytic category: HLF (sx).

Distribution: CL, DU, RI, TA, TT. Uruguay is the southern limit of distribution.

Habitat: moist hillside forests, riverside forests and xeric hillside forests.

Conservation status: NT.

Observations: the species is common in the ravines of northeastern Uruguay, but scarce towards the east.

Voucher: Picasso & Scarlato s.n. (MVJB 21875).

Asplenium sellowianum C. Presl ex Hieron., Hedwigia 60: 222. 1918. ≡ *Asplenium ulbrichtii* Rosenst. var. *sellowianum* (Hieron.) Osten & Herter, A. Mus. Hist. Nat. 2 (1): 349. 1925.

≡ *Asplenium lunulatum* Sw. var. *sellowianum* Hieron., Bot. Jahrb. Syst. 22 (3): 377. 1896.

= *Asplenium ulbrichtii* Rosenst. var. *tenerrimum* (Hieron.) Osten & Herter, A. Mus. Hist. Nat. 2 (1): 349. 1925

≡ *Asplenium lunulatum* Sw. var. *tenerrima* Hieron., Bot. Jahrb. Syst. 22(3): 377-378. 1896.

– *Asplenium sellowianum* C. Presl., Tent. Pterid. 107. 1836, nom. nudum.

Epiphytic category: HLA (tr, sx).

Distribution: AR, CL, DU, MA, RI, SO, TA, TT.

Habitat: moist hillside forest, riverside forest and xeric hillside forest.

Conservation status: LC.

Observations: even when most herbarium records are from eastern Uruguay, it is a widely distributed species in Uruguay, possibly present throughout the country.

Taxonomic comment: there are different interpretations of the correct nomenclature for this species, but we follow Ganem *et al.* 2016 name proposal and lectotypification.

Voucher: Brussa *et al.* s.n. (MVJB 29867).

Asplenium ulbrichtii Rosenst., Hedwigia 43: 220. 1904.

= *Asplenium ulbrichtii* var. *major* Rosenst., Hedwigia 46: 99. 1906.

= *Asplenium ulbrichtii* var. *serrato-dentatum* Rosenst., Hedwigia 46: 99. 1906.

Epiphytic category: HLA (tr).

Distribution: AR, CA, CL, CO, DU, FA, LA, MA, PA, RI, SA, SJ, SO, TA, TT.

Habitat: moist hillside forests, riverside forests and xeric hillside forests.

Conservation status: LC.

Voucher: Berro 5214 (MVFA).

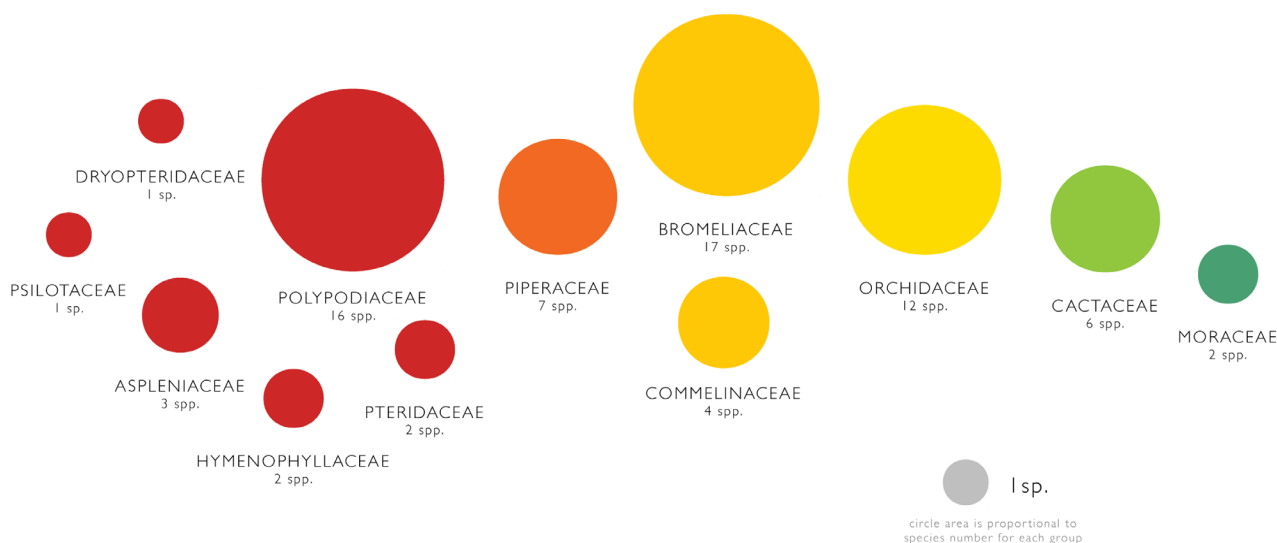


Figure 2. Number of epiphytic species per vascular families in the flora of Uruguay.

Dryopteridaceae

Rumohra Raddi

Rumohra adiantiformis (G. Forst.) Ching, Sinensia 5: 70. 1934 = *Polystichum adiantiforme* (G. Forst.) J. Sm., Hist. Fil. 220. 1875 = *Polypodium adiantiforme* G. Forst., Fl. Ins. Austr. 82. 1786.

= *Aspidium capense* Willd. Sp. Pl., ed. 4, 5: 267. 1810, nom. illeg. non Swartz 1801.
(Fig. 6B).

Epiphytic category: HLA (tr).

Distribution: CA, CL, CO, DU, FS, FA, LA, MA, MO, RN, RI, RO, SJ, SO, TA.

Habitat: *Butia* palm forests, moist hillside forests, psammophilous forests, riverside forests and xeric hillside forests.

Conservation status: LC.

Voucher: *Delfino et al. s.n.* (MVJB 21194).

Hymenophyllaceae

Didymoglossum Desv.

Didymoglossum hymenoides (Hedw.) Copel., Philipp. J. Sci. 67: 77. 1938 = *Trichomanes hymenoides* Hedw., Fil. Gen. Sp. t. 3, f. 3d-e. 1799.

= *Trichomanes pabstianum* C. Mueller, Bot. Zeitung (Berlin) 12: 738. 1854.
(Fig. 6F).

Epiphytic category: HLF (el).

Distribution: CL, RO, TA. Uruguay is the southern limit of distribution.

Habitat: moist hillside forests and xeric hillside forests.

Conservation status: VU. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and occurs in the protected area 'Paisaje Protegido Paso Centurión y Sierra de Ríos'.

Observations: due to its small size, the species is probably under-represented in the national collections, and therefore information on current distribution and habitat occupied in Uruguay here presented could be under-estimated.

Voucher: *Mai et al.* 334 (MVJB).

Polyphlebium Copel.

Polyphlebium angustatum (Carmich.) Ebihara & Dubuisson, Blumea 51(2): 240. 2006. = *Trichomanes angustatum* Carmich., Trans. Linn. Soc. London 12: 513. 1819.

= *Trichomanes tenerum* Spreng., Syst. Veg. 4: 129. 1827. (Fig. 7A).

Epiphytic category: HLF (el).

Distribution: CL, DU, MA, RI, RO, TA, TT. Uruguay is the southern limit of distribution.

Habitat: moist hillside forests and xeric hillside forests.

Conservation status: VU. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and occurs in the protected area 'Paisaje protegido Valle del Lunarejo'.

Observations: the specimens with epiphytic habit were mainly collected over the arborescent fern *Dicksonia sellowiana* Hook, which coincides with reports from southern Brazil (Buzatto *et al.* 2008).

Voucher: *Brussa et al. s.n.* (MVJB 21196).

Polypodiaceae

Campyloneurum C. Presl.

Campyloneurum nitidum (Kaulf.) C. Presl., Tent. Pterid. 190. 1836. = *Polypodium nitidum* Kaulf., Enum. Filic. 92. 1824.

= *Campyloneurum major* (Hieron. ex Hicken) Lellinger, Amer. Fern J. 78: 26. 1988. = *Polypodium phyllitidis* L. fo. *major* Hieron. ex Hicken, Revista Mus. La Plata 15: 272. 1908.

– *Polypodium phyllitidis* auct. non. L.: Osten & Herter (1925); Herter (1928; 1939; 1949); Legrand & Lombardo (1958).

(Fig. 7E).

Epiphytic category: HLF (sx, el).

Distribution: AR, CL, DU, LA, MA, MO, RI, RO, TA, TT. Uruguay is the southern limit of distribution.

Habitat: moist hillside forest, riverside forest and xeric hillside forest.

Conservation status: LC.

Taxonomic comment: in Uruguay *Campyloneurum nitidum* was for a long time considered under the name *Polypodium phyllitidis* L. (= *C. phyllitidis* (L.) C. Presl.) (Osten & Herter 1925; Herter 1928; 1939; 1949; Legrand & Lombardo 1958). Lellinger (1988) argues that there has been

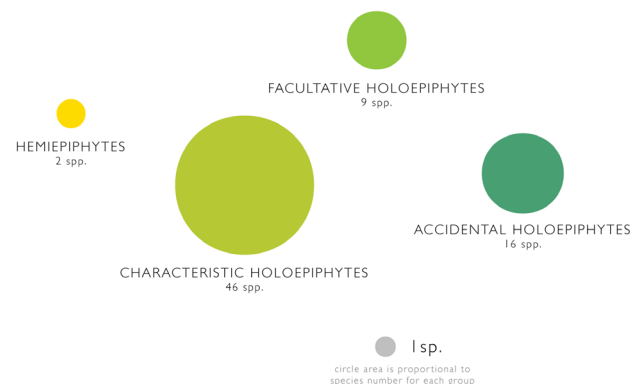


Figure 3. Number of epiphytic species in the vascular flora of Uruguay according to distinct adaptive categories.



Figure 4. Characteristic holoepiphytes: **A.** *Microgramma squamulosa*. **B.** *M. vacciniifolia*. **C.** *Pecluma sicca*. **D.** *Pleopeltis minima*. **E.** *Peperomia tetraphylla*. **F.** *P. psilostachya*. **G.** *P. catharinae*. **H.** *P. pereskiiifolia*.



Figure 5. Characteristic holopiphytes: **A.** *Lepismium lumbricoides*. **B.** *Rhipsalis cereuscula*. **C.** *Tillandsia ixiioides*. **D.** *Aechmea recurvata* and *T. aëranthos*. **E.** *T. aëranthos*. **F.** *T. usneoides*. **G.** *Gomesa bifolia*. **H.** *Acianthera sonderiana*. **I.** *Capanemia micromera*.



Figure 6. Accidental holoepiphytes: **A.** *Adiantum raddianum*. **B.** *Rumohra adiantiformis*. **C.** *Peperomia comarapana*. **D.** *P. increscens*. **E.** *Cyclopogon elatus*. **F.** *Cereus hildmannianus* subsp. *uruguayanus*. **G.** *Tillandsia arequitae*. **H.** *T. xiphioides*. **I.** *Tradescantia mundula*.



Figure 7. Facultative holoepiphytes: **A.** *Polyphlebium angustatum*. **B.** *Vittaria lineata*. **C.** *Pleopeltis lepidopteris*. **D.** *Asplenium gastonis*. **E.** *Campyloneurum nitidum*. **F.** *Didymoglossum hymenoides*. **G.** *Peperomia trineuroides*. **H.** *Billbergia nutans*.

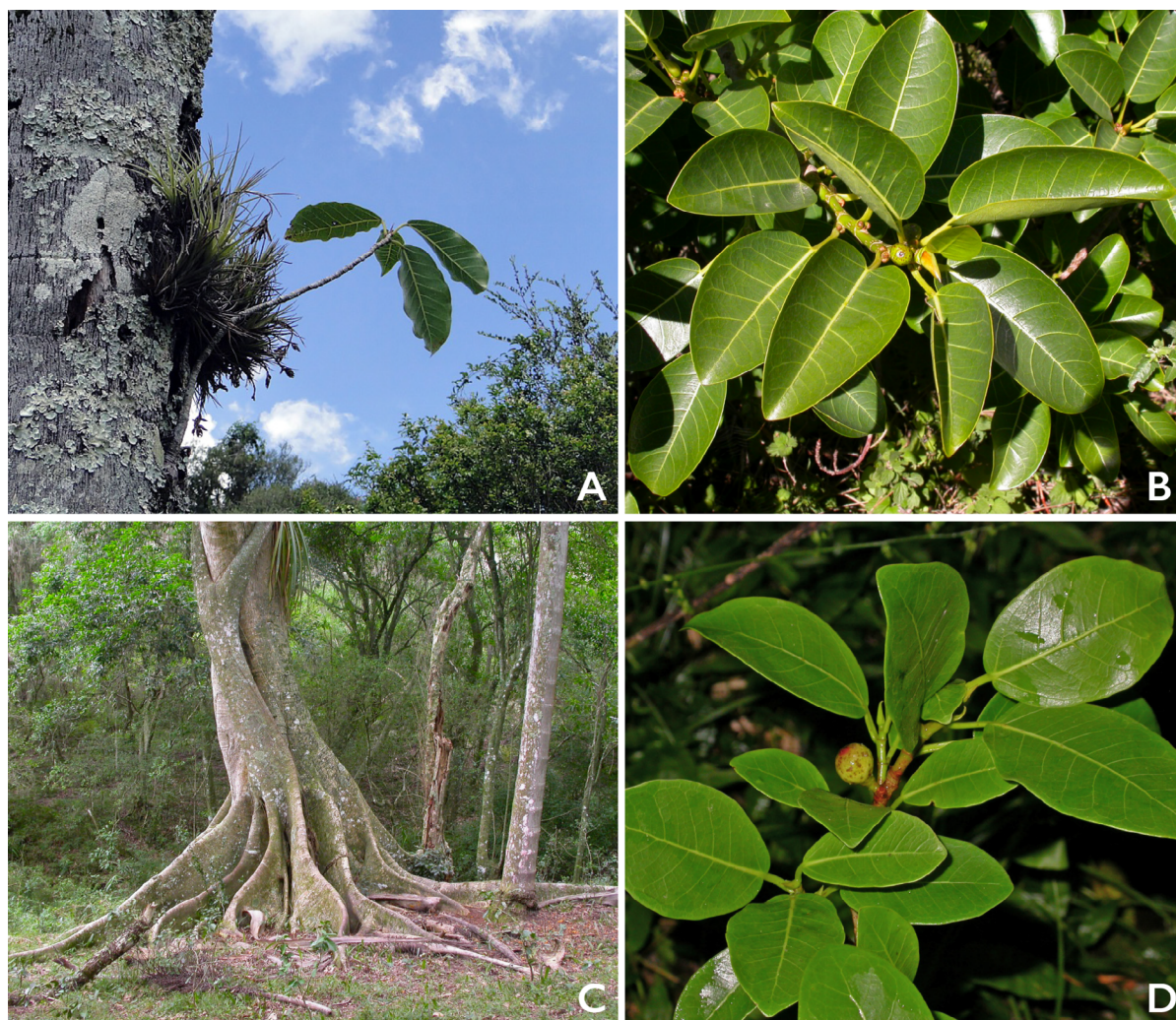


Figure 8. Hemiepipytes: **A, B.** *Ficus luschnathiana*. **C, D.** *F. cestrifolia*.

confusion between both species and discards the presence of *C. phyllitidis* in southern Brazil, Paraguay, Uruguay and Argentina, an opinion more recently also shared by Vasques & Prado (2011). We were able to corroborate that specimens deposited at national herbaria and identified as *C. phyllitidis* from a morphological standpoint correspond with *C. nitidum*. *Campyloneurum nitidum* exccicates were also studied at ICN, and the morphological characteristics observed there matched those of the Uruguayan specimens.

Voucher: Brussa & Grela s.n. (MVJB 26612).

Microgramma C. Presl.

Microgramma mortoniana de la Sota, Am. Fern. J. 63: 64. 1973.

Epiphytic category: HLC.

Distribution: AR, CO, PA, RN, SO.

Habitat: *Butia* palm forests, hydrophilous forests, open thorn forests, psammophilous forests, riverside forests and xeric hillside forests.

Conservation status: NT.

Observations: the species is only present in the west of the country, and most records are concentrated in a few localities of the southwest.

Voucher: Rosengurtt et al. 10503 (MVFA).

Microgramma squamulosa (Kaulf.) de la Sota, Opera Lilloana 5: 59, f. 2, 3, 6, 7. 1960. \equiv *Marginaria squamulosa* (Kaulf.) Herter, Revista Sudamer. Bot. 6: 131. 1940. \equiv *Polypodium lycopodioides* L. var. *squamulosum* (Kaulf.) Baker, Fl. Bras. (Martius) 1(2): 534. 1870. \equiv *Pleopeltis squamulosa* (Kaulf.) C. Presl., Tent. Pterid. 193. 1836. \equiv *Polypodium squamulosum* Kaulf., Enum. Filic. 89. 1824.

– *Polypodium lycopodioides* auct. non. L.: Legrand & Lombardo (1958).

(Fig. 4A).

Epiphytic category: HLC.

Distribution: AR, CA, CL, CO, DU, FA, LA, MA, MO, PA, RN, SA, SJ, SO, TA, TT. Uruguay is the southern limit of distribution.

Habitat: hydrophilous forest, moist hillside forest, psammophilous forest, riverside forest and xeric hillside forest.

Conservation status: LC.

Observations: this is one of the most common and widely distributed epiphytic species.

Voucher: *Arechavaleta s.n.* (MVM 415).

Microgramma vacciniifolia (Langsd. & Fisch.) Copel., Gen. Fil. 185. 1947. \equiv *Marginaria vacciniifolia* (Langsd. & Fisch.) C. Presl, Tent. Pterid. 188. 1836. \equiv *Polypodium vacciniifolium* Langsd. & Fisch., Pl. Voy. Russes Monde 8, pl. 7. 1810.

(Fig. 4B).

Epiphytic category: HLC.

Distribution: AR, CA, CL, DU, FA, MA, MO, PA, RI, RN, RO, SA, SJ, TA.

Habitat: hydrophilous forests, moist hillside forests, psammophilous forests, riverside forests and xeric hillside forests.

Conservation status: LC.

Voucher: *Del Puerto & Marchesi 3623* (MVFA).

Niphidium J. Sm.

Niphidium crassifolium (L.) Lellinger, Amer. Fern J. 62: 106 - 107. 1972. \equiv *Polypodium crassifolium* L., Sp. Pl. 2: 1083. 1753.

Epiphytic category: HLF.

Distribution: CL. Uruguay is the southern limit of distribution.

Habitat: moist hillside forest.

Conservation status: EN. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and occurs in the protected area 'Paisaje Protegido Paso Centurión y Sierra de Ríos'.

Observations: the species has been poorly sampled in the country (three herbarium specimens). All the specimens were collected in moist hillside forests in eastern Uruguay where they grow preferentially on cliffs, and only one epiphytic plant was recorded and collected over a big *Luehea divaricata* Mart. tree, on large branches forming a circular population.

Voucher: *Mai et al. 331* (MVJB).

Pecuma M.G. Price.

Pecuma filicula (Kaulf.) M.G. Price, Am. Fern. J. 73(4): 114. 1983. \equiv *Polypodium filiculum* Kaulf. Enum. Filic. 275. 1824.

Epiphytic category: HLC.

Distribution: RI. Uruguay is the southern limit of distribution.

Habitat: moist hillside forests.

Conservation status: EN. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), but is absent in national protected areas.

Observation: we include *P. filicula* in the epiphytic flora of Uruguay because within its natural range and in neighboring areas of Uruguay it grows as holoeiphyte (Evans 1969; Márquez *et al.* 2006; Cervi & Borgo 2007; Torres *et al.* 2013; Martínez *et al.* 2016). However, only two exsiccates of this species exists in the country (MVM 4195 and MVFA 27662), of which one of them (MVM 4195) is ancient and lacks collection data (date, environment and locality); therefore, information about this species is limited. We hypothesize that this species must occur in Uruguay in well preserved, isolated and remote habitats, which have kept the species from being gathered by recent collectors.

Voucher: *Bonifacino et al. s.n.* (MVFA 27662).

Pecuma paradiseae (Langsd. & Fisch.) M.G. Price, Am. Fern. J. 73(4): 115. 1983. \equiv *Polypodium paradiseae* Langsd. & Fisch., Pl. Voy. Russes Monde 11, pl. 11. 1810.

Epiphytic category: HLC.

Distribution: RI, TA.

Habitat: moist hillside forests.

Conservation status: EN. The species is not included as a priority for conservation in Uruguay by Marchesi *et al.* (2013). The species occurs in the protected area 'Paisaje protegido Valle del Lunarejo'. Therefore, we consider it relevant to add *P. paradiseae* to the list of species considered as priority for conservation in Uruguay.

Observations: the species has been collected in only two nearby localities in northeastern Uruguay.

Voucher: *Brussa et al. s.n.* (MVJB 28285).

Pecuma pectinatiformis (Lindm.) M.G. Price, Am. Fern. J. 73 (4):115. 1983. \equiv *Polypodium pectinatiforme* Lindm., Hedwigia 43: 309. 1904.

Epiphytic category: HLC.

Distribution: RI.

Habitat: moist hillside forest. It occurs exclusively in ravines in northeastern Uruguay.

Conservation status: EN. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and occurs in the protected area 'Paisaje protegido Valle del Lunarejo'.

Voucher: *Picasso & Scarlato s.n.* (MVJB 21404).

Pecuma sicca (Lindm.) M.G. Price, Am. Fern. J. 73(4): 115. 1983. \equiv *Polypodium siccum* Lindm., Ark. Bot. 1: 234, pl. 11, f. 4. 1903.

(Fig. 4C).

Epiphytic category: HLC.

Distribution: AR, CL, MA, RI. TA. TT. Uruguay is the southern limit of distribution.

Habitat: moist hillside forests and xeric hillside forests.

Conservation status: NT; nevertheless, it is still a species that is considered as a priority for conservation in the country (Marchesi *et al.* 2013).

Voucher: *Marchesi s.n.* (MVFA 1072).

Pleopeltis Humb. & Bonpl. ex Willd.

Pleopeltis hirsutissima (Raddi) de la Sota, Darwiniana 45 (2): 239. 2007. \equiv *Polypodium hirsutissimum* Raddi., Opusc. Sci. 3: 286. 1819.

= *Polypodium rufulum* C. Presl., Delic. Prag. 1: 164. 1822

Epiphytic category: HLC.

Distribution: AR, CL, MA, RI. RO, RN, TA, TT. Uruguay is the southern limit of distribution.

Habitat: *Butia* palm forest, moist hillside forest and xeric hillside forest.

Conservation status: LC.

Voucher: *Herter s.n.* (*Herb. Osten* 18595, MVM).

Pleopeltis lepidopteris (Langsd. & Fisch.) de la Sota, Darwiniana 45 (2): 239. 2007. \equiv *Polypodium lepidopteris* (Langsd. & Fisch.) Kunze., Linnaea 13: 132. 1839. \equiv *Acrostichum lepidopteris* Langsd. & Fisch., Pl. Voy. Russes Monde 5, pl. 2. 1810.

(Fig. 7C).

Epiphytic category: HLF (sx, el).

Distribution: AR, CL, DU, LA, MA, RI, RO, TA, TT. Uruguay is the southern limit of distribution.

Habitat: moist hillside forests, psammophilous forests and xeric hillside forests.

Conservation status: LC.

Voucher: *Marchesi* 583 (MVFA).

Pleopeltis macrocarpa (Bory ex Willd.) Kaulf., Berlin. Jahrb. Pharm. Verbundenen Wiss. 21: 41. 1820. \equiv *Polypodium macrocarpum* Bory ex Willd., Sp. Pl. Editio quarta 5(1): 147. 1810.

= *Marginaria lanceolata* (L.) Herter, Revista Sudamer. Bot. 6: 131. 1940. \equiv *Pleopeltis lanceolata* (L.) Kaulf. Enum. Filic. 245. 1824 \equiv *Polypodium lanceolatum* L. Sp. Pl. 2: 1082. 1753.

Epiphytic category: HLC.

Distribution: MA, RO.

Habitat: hydrophilous forest, moist hillside forest, psammophilous forest, riverside forest and xeric hillside forest.

Conservation status: NT; nevertheless it is a species considered as a priority for conservation in the country (Marchesi *et al.* 2013).

Voucher: *Arechavaleta s.n.* (MVM 4199).

Pleopeltis minima (Bory) J. Prado & R.Y. Hirai, Am. Fern. J. 100 (4): 191. 2010. \equiv *Polypodium polypodioides* (L.) Watt var. *minimum* (Bory) Kuhlmann & Kuhn, Fl. Distr. Ibiti: 22. 1948 \equiv *Polypodium minimum* (Bory) Herter, Anales Mus. Nac. Montevideo, ser. 2, 1: 368, tab. 28. 1925, *nom. illeg.* non Aublet 1775 \equiv *Marginaria minima* Bory., Dict. Class. Hist. Nat. 10: 177. 1826.

= *Polypodium polypodioides* (L.) Watt var. *minus* (Fée) Weath., Contr. Gray Herb. 124: 31. 1939.

= *Pleopeltis squalida* (Vell.) de la Sota., Hickenia 3(46): 196. 2003 \equiv *Polypodium incanum* Sw. var. *squalidum* (Vell.) Baker., Fl. Bras. 1(2): 526. 1870 \equiv *Polypodium squalidum* Vell. Arch. Mus. Nac. Rio de Janeiro 5: 449. 1881.

= *Marginaria dielsii* Herter, Revista Sudamer. Bot. 6: 130. 1940.

= *Marginaria microlepis* (Fée) Herter, Revista Sudamer. Bot. 6: 130. 1940. \equiv *Polypodium microlepis* Fée, Mém. Foug. 238. 1850.

(Fig. 4D).

Epiphytic category: HLC.

Distribution: AR, CL, CO, DU, FA, PA, RN, RI, RO, SA, SO, TA.

Habitat: moist hillside forests, open thorn forests, riverside forests and xeric hillside forests.

Conservation status: LC.

Voucher: *Zúñiga s.n.* (*Herb. Gibert*, MVM 4201).

Pleopeltis pleopeltifolia (Raddi) Alston, Bol. Soc. Brot. Sér. 2 30: 21. 1956. \equiv *Polypodium pleopeltifolium* Raddi, Opusc. Sci. 3: 286. 1819.

= *Polypodium angustum* (Humb. & Bonpl. ex Willd.) Liebm., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 5, 1: 186. 1849 \equiv *Pleopeltis angusta* Humb. & Bonpl. ex Willd. Sp. Pl. Editio quarta 5(1): 211. 1810.

Epiphytic category: HLC.

Distribution: AR, CL, CO, DU, FA, LA, MA, PA, RN, RI, RO, SA, SJ, SO, TA, TT.

Habitat: hydrophilous forest, moist hillside forest, riverside forest and xeric hillside forest.

Conservation status: LC.

Observations: this is one of the most common and widely distributed epiphytic species in Uruguay.

Voucher: *Osten* 3100 (MVM).

Serpocaulon A.R. Sm.

Serpocaulon catharinae (Langsd. & Fisch.) A.R. Sm., Taxon 55 (4): 928. 2006. \equiv *Polypodium catharinae* Langsd. & Fisch., Pl. Voy. Russes Monde 1, pl. 9. 1810.

Epiphytic category: HLC.



Distribution: CA, MA, RO, SJ, TT. Uruguay is the southern limit of distribution.

Habitat: *Butia* palm forests, hydrophilous forests, moist hillside forests, riverside forests and xeric hillside forests.

Conservation status: LC.

Voucher: *Del Puerto & Marchesi 6107* (MVFA).

Serpocaulon latipes (Langsd. & L. Fisch.) A.R. Sm., Taxon 55 (4): 928. 2006. \equiv *Polypodium latipes* Langsd. & Fisch., Pl. Voy. Russes Monde 1, pl. 10. 1810.

Epiphytic category: HLC.

Distribution: LA, MA, RO. Uruguay is the southern limit of distribution.

Habitat: *Butia* palm forests, moist hillside forests and riverside forests.

Conservation status: NT.

Observations: in the region (Argentina and Brazil) this species is generally terrestrial. However, in Uruguay most specimens grew as epiphytes, and for this reason it is assigned the HLC category.

Voucher: *Brussa et al. s.n.* (MVJB 27279).

Pteridaceae

***Adiantum* L.**

Adiantum raddianum C. Presl., Tent. Pterid. 158. 1836.

= *Adiantum cuneatum* Langsd. & Fisch., Ic. Fil.: 23, t. 26. 1810, *nom. illeg. non Forst.* 1786. (Fig. 6A).

Epiphytic category: HLA (tr).

Distribution: AR, CA, CL, CO, DU, FA, LA, MA, MO, PA, RN, RI, RO, SA, SJ, SO, TA, TT.

Habitat: moist hillside forest, riverside forest and xeric hillside forest.

Conservation status: LC.

Voucher: *Mai 149* (MVJB).

***Vittaria* Sm.**

Vittaria lineata (L.) Sm., Mém. Acad. Roy. Sci. (Turin) 5 (1790–1791): 421, pl. 9, f. 5. 1793. \equiv *Pteris lineata* L., Sp. Pl. 2: 1073. 1753. (Fig. 7B).

Epiphytic category: HLF (el, sx).

Distribution: CL, LA, MA, RI, RO, TA. Uruguay is the southern limit of distribution.

Habitat: *Butia* palm forests, moist hillside forests, riverside forests and xeric hillside forests.

Conservation status: LC.

Voucher: *Marchesi s.n.* (MVFA 14008).

Psilotaceae

***Psilotum* Sw.**

Psilotum nudum (L.) P. Beauv., Prodr. Aethéogam. 106, 112 (1805) \equiv *Lycopodium nudum* L., Sp. Pl. 2: 1100–1101. 1753.

Epiphytic category: HLC.

Distribution: RI, RO.

Habitat: *Butia* palm forest, moist hillside forest and riverside forest.

Conservation status: VU. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and occurs in the protected area 'Paisaje protegido Valle del Lunarejo'.

Observations: this fern occurs in two disjunct areas in Uruguay, in the northeast and in the east of the country.

Voucher: *Marchesi s.n.* (MVFA 14026).

Angiosperms

Bromeliaceae

***Aechmea* Ruiz & Pav.**

Aechmea recurvata (Klotzsch) L.B.Sm., Contr. Gray Herb. 98: 5. 1932. \equiv *Macrochordium recurvata* Klotzsch, Allg. Gartenzeitung 24: 393. 1856.

= *Aechmea legrelliana* (Baker) Baker, 17: 236. 1879. \equiv *Hohenbergia legrelliana* Baker, Refug. Bot. 4: t. 285. 1871. = *Aechmea ampullacea* Mez, Monogr. Phan. 9: 257. 1896. (Fig. 5D).

Epiphytic category: HLC or HLF (sx).

Distribution: CL, RI, RO, TA, TT. Uruguay is the southern limit of distribution.

Habitat: *Butia* palm forests, hydrophilous forests, riverside forests, xeric hillside forests and moist hillside forests.

Conservation status: LC.

Observations: the epiphytic category of this species depends on the environment. In *Butia* palm forest, hydrophilous and riverside forest the species grows exclusively as an epiphyte (HLC), whereas in hillside forests it grows both as an epiphyte and as saxicolous (HLF).

Voucher: *Berro 2054* (MVFA).

***Billbergia* Thunb.**

Billbergia nutans H. Wendl. ex Regel, Gartenflora 18: 162, t. 617. 1869.

(Fig. 7H).

Epiphytic category: HLF (sx).
Distribution: AR, CL, RI, TA.
Habitat: moist hillside forest and riverside forest.
Conservation status: NT.
Voucher: *Marchesi 999* (MVFA).

***Tillandsia* L.**

Tillandsia aëranthos (Loisel.) L.B. Sm. Lilloa 9: 200. 1943.
≡ *Pourretia aëranthos* Loisel. Herb. Gén. Amat. 5: t. 304. 1821.
= *Tillandsia dianthoidea* G. Rossi, Cat. Pl. Hort. Modoet. Ed. 2, 79: t. 1. 1825 [1826].
= *Tillandsia bicolor* Brongn., Voy. Monde 2: 185: t. 36. 1829 [1834].
= *Tillandsia microxiphion* Baker, Bot. Mag. 119: t. 7320. 1893.
(Fig. 5D; 5E).

Epiphytic category: HLC.
Distribution: AR, CA, CL, CO, DU, FA, FS, LA, MA, MO, PA, RN, RI, RO, SA, SJ, SO, TA, TT.
Habitat: *Butia* palm forests, hydrophilous forests, moist hillside forests, open thorn forests, psammophilous forests, riverside forests and xeric hillside forests.
Conservation status: LC.
Observations: it is one of the most frequent and widely distributed epiphytic species in Uruguay.
Voucher: *Osten 2880* (MVM).

Tillandsia arequitae (André) André ex Mez, Monogr. Phan. 9: 814. 1896. ≡ *Tillandsia xiphioides* var. *arequitae* André, Rev. Hort. 65: 156. 1893.
(Fig. 6G).

Epiphytic category: HLA (el).
Distribution: LA, MA.
Habitat: xeric hillside forests.
Conservation status: VU. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), but is absent in national protected areas.
Observations: the species is an endemic species of Uruguay, with a distribution restricted to the southeast of the country. It is rarely found as an epiphyte on trees close to the rocky surfaces where it is more abundant.
Voucher: *Rossado 402* (MVFA).

Tillandsia bandensis Baker, J. Bot. 25: 234. 1887.

Epiphytic category: HLC or HLA (el).
Distribution: AR, CL, CO, RN, SA, SO, TT.
Habitat: hydrophilous forest, open thorn forest, xeric hillside forests.
Conservation status: NT.
Observations: the species presents two subspecies in two disjunct areas of Uruguay; *T. bandensis* subsp. *grandipetala*

Rossado occurs in eastern Uruguay, while the typical one occurs in the west of the country near the Uruguay River (Rossado *et al.* 2019). The epiphytic category varies in relation to these two areas, behaving as a HLC in the west and as HLA (el) in the east.
Voucher: *Berro 4179* (MVFA).

Tillandsia duratii Vis., Nuovi Saggi Imp. Regia Accad. Sci. Padova 5: 271, t. 29. 1840.

Epiphytic category: HLC.
Distribution: AR, PA, SA.
Habitat: open thorn forests, riverside forests.
Conservation status: VU. The species is not included as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and is absent in national protected areas. Additionally, the species is found in few localities within Uruguay, mainly associated with open thorn forest which is an endangered habitat in the country, therefore we consider it relevant to add *T. duratii* to the list of species considered as a priority for conservation in Uruguay.
Voucher: *Berro 1328* (MVFA).

Tillandsia geminiflora Brongn., Voy. Monde 2: 186. 1829 [1834].

Epiphytic category: HLC.
Distribution: CL, LA, RO, TT. Uruguay is the southern limit of distribution.
Habitat: hydrophilous forests, moist hillside forests, psammophilous forests, riverside forests and xeric hillside forests.
Conservation status: NT.
Voucher: *Berro 2416* (MVFA).

Tillandsia ixioideis Griseb. Abh. Königl. Ges. Wiss. Göttingen 24: 333. 1879.
(Fig. 5C).

Epiphytic category: HLC.
Distribution: AR, PA, RN, SJ.
Habitat: open thorn forest.
Conservation status: VU. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), but is absent in national protected areas.
Voucher: *Berro 1657* (MVFA).

Tillandsia loliacea Mart. ex Schult. f. in Roem. & Schult., Syst. Veg. 7(2): 1204. 1830.

Epiphytic category: HLC.
Distribution: AR. In the region, northern Uruguay and southern Corrientes (Argentina) represents the southern limit of distribution.
Habitat: open thorn forests.



Conservation status: EN. The species is not included as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and is absent in national protected areas. Therefore, we consider it relevant to add *T. loliacea* to the list of species considered as a priority for conservation in Uruguay, as it was suggested in Rossado *et al.* (2018b).

Observations: the species has been found only in one locality in Uruguay.

Voucher: Villagrán *et al.* s.n. (MVJB 30693).

Tillandsia myosura Griseb. ex Baker, J. Bot. 16: 240. 1878.

Epiphytic category: HLC.

Distribution: CO, LA, MA, RN, SA, SJ, SO.

Habitat: riverside forest, psammophilous forest, xeric hillside forest.

Conservation status: NT.

Taxonomic comment: some specimens collected in Uruguay have been misidentified and cited for the country under the name of *T. crocata* (E. Morren) Baker (Smith 1933; Marchesi 1965; Smith 1972; Smith & Downs 1977).

Voucher: Osten 3055 (MVM).

Tillandsia recurvata (L.) L., Sp. Pl. (ed. 2) 1: 410. 1762. \equiv *Renalmia recurvata* L., Sp. Pl. 1: 287. 1753.

Epiphytic category: HLC.

Distribution: AR, CA, CL, CO, DU, FA, FS, LA, MA, MO, PA, RI, RN, RO, SA, SJ, SO, TA, TT.

Habitat: hydrophilous forests, moist hillside forests, open thorn forests, psammophilous forests, riverside forests and xeric hillside forests.

Conservation status: LC.

Voucher: Osten 2943 (MVM).

Tillandsia recurvifolia Hook., Bot. Mag. 87: t. 5246. 1861.

– *Tillandsia meridionalis* auct. non Baker: Smith (1972); Smith & Downs (1977).

Epiphytic category: HLC.

Distribution: AR, SA.

Habitat: open thorn forests.

Conservation status: EN. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), but is absent in national protected areas.

Observations: the species is restricted to northwestern Uruguay.

Taxonomic comment: the species has been erroneously identified as *Tillandsia meridionalis* Baker.

Voucher: Klappenbach s.n. (MVM 2948).

Tillandsia stricta Sol. ex Sims, Bot. Mag. 37: t. 1529. 1813.

Epiphytic category: HLC.

Distribution: CL, RO, TT. Uruguay is the southern limit of distribution.

Habitat: moist hillside forest, riverside forest.

Conservation status: VU. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and occurs in the protected area 'Paisaje Protegido Paso Centurión y Sierra de Ríos'.

Voucher: Berro 2417 (MVFA).

Tillandsia tricholepis Baker, J. Bot. 16: 237. 1878.

Epiphytic category: HLC.

Distribution: AR.

Habitat: open thorn forests.

Conservation status: EN. The species is not included as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and is absent in national protected areas. Therefore, we consider it relevant to add *T. tricholepis* to the list of species considered as a priority for conservation in Uruguay.

Observations: the species was recently found in natural environments only in the department of Artigas. In Uruguayan herbaria, there are also specimens from suburban sites around the cities of Salto and Tacuarembó, and so they were not assessed in distribution and conservation status.

Voucher: Villagrán *et al.* s.n. (MVM 23003).

Tillandsia uruguayensis Rossado, Phytotaxa 345 (2): 134–137. 2018.

Epiphytic category: HLA (el).

Distribution: AR, RI, TA. The species is endemic to Uruguay with a restricted distribution in the northeast of the country, but could also occur in nearby Brazil.

Habitat: moist hillside forest, xeric hillside forest.

Conservation status: VU; due to its recent discovery (Rossado *et al.* 2018a) the species is not included as a priority for conservation in Uruguay by Marchesi *et al.* (2013). We consider it relevant to add *T. uruguayensis* to the list of species considered as priority for conservation in Uruguay. The species occurs in the protected area 'Paisaje protegido Valle del Lunarejo'.

Observations: the species is rarely found as an epiphyte in xeric hillside forest on trees close to the rocky surfaces where it is abundant.

Voucher: Rossado & Bonifacino 418 (MVFA, WU).

Tillandsia usneoides (L.) L., Sp. Pl. (ed. 2) 1: 411. 1762. \equiv *Renalmia usneoides* L., Sp. Pl. 1: 287. 1753. (Fig. 5F).

Epiphytic category: HLC.

Distribution: AR, CL, DU, FA, LA, MA, RI, RO, RN, SA, SO, TA, TT.

Habitat: hydrophilous forests, moist hillside forests,

psammophilous forests and riverside forests.

Conservation status: LC.

Observation: the species probably has a wider distribution, so the current distribution is underrepresented due to low sampling.

Voucher: *Osten 3121* (MVM).

Tillandsia xiphioides Ker Gawl., Bot. Reg. 2: t. 105. 1816.
(Fig. 6H).

Epiphytic category: HLA (el).

Distribution: CL, SJ.

Habitat: xeric hillside forest.

Conservation status: EN. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), but is absent in national protected areas.

Observations: the species occurs only in two localities in Uruguay, distant from one another. *Tillandsia xiphioides* is rarely found as an epiphyte on trees, close to the rocky surfaces where it is more abundant.

Voucher: *Rossado et al. 24* (MVJB).

Cactaceae

Cereus Mill.

Cereus hildmannianus Schum. **subsp. *uruguayanus*** (Kiesling) Taylor, Cactaceae Consensus Init. 6: 15. 1998.

= *Cereus uruguayanus* Ritter ex Kiesling, Darwiniana 24: 448-450, 1982

– *Cereus peruvianus* auct. non Miller: Herter (1930); Lombardo (1946; 1964).

(Fig. 6F).

Epiphytic category: HLA (tr).

Distribution: AR, CA, CL, CO, MA, RI, RO, SA, SO, TA, TT.

Habitat: moist hillside forests, psammophilous forests, riverside forests and xeric hillside forests.

Conservation status: not estimated, due to the small number of collections available.

Observations: the species is notably underrepresented in local collections due to the inherent difficulties associated with herborization. The data presented for this species were obtained from herbarium specimens and field observations.

Taxonomic comment: in the region there are different interpretations with regard to the name of this species. We follow the taxonomic criteria of Flora do Brasil 2020 (2019). However, IBODA (2019) interpret the species present in Uruguay as *Cereus uruguayanus*. Additionally, another name used for this taxon in the region is *C. alacriportanus* Pfeiff. (Bauer & Waechter 2006), which has several interpretations (Leuenberger 2004; Hunt *et al.* 2006); therefore, it lacks a taxonomic consensus.

Voucher: *Legrand 3223* (MVM).

Lepismium Pfeiff.

Lepismium aculeatum (F.A.C. Weber) Barthlott, Bradleya 5: 99. 1987 ≡ *Rhipsalis aculeata* F.A.C. Weber, Rev. Hort. 64: 428, 1892.

Epiphytic category: HLC.

Distribution: AR.

Habitat: open thorn forest.

Conservation status: EN. The species is not included as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and is absent in national protected areas. Therefore, we consider it relevant to add *L. aculeatum* to the list of species considered as priority for conservation in Uruguay.

Observations: the species was collected only in one locality in Uruguay.

Voucher: *Berazategui & Duarte s.n.* (MVM 21051).

Lepismium cruciforme (Vell.) Miq., Bull. Sci. Phys. Nat. Néerl. 1838: 49.1838 ≡ *Rhipsalis cruciforme* (Vell.) A. Cast., Anales Mus. Nac. Hist. Nat. Buenos Aires. Ser. 3 32: 496. 1925 ≡ *Cactus cruciformis* Vell., Fl. Flumin. 207. 1825 [1829].

= *Rhipsalis myosurus* (Salm-Dyck ex DC.) Foerster., Handb. Cact. 455, 1846.

Epiphytic category: HLC.

Distribution: AR, CL, RO, TT. Uruguay is the southern limit of distribution.

Habitat: riverside forests and moist hillside forests.

Conservation status: VU. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and occurs in the protected area 'Paisaje Protegido Paso Centurión y Sierra de Ríos'.

Observations: the species is known from two areas in the country, one in northern Uruguay and the other in the east of the country.

Voucher: *Del Puerto 2060* (MVFA).

Lepismium lumbricoides (Lem.) Barthlott, Bradleya 5: 99. 1987 ≡ *Rhipsalis lumbricoides* (Lem.) Lem. ex Salm-Dyck, Ill. Hort. 6: misc. 88. 1859 ≡ *Cereus lumbricoides* Lem. Cact. Gen. Sp. Nov. 60. 1839.

(Fig. 5A).

Epiphytic category: HLC.

Distribution: AR, CL, CO, FA, MA, PA, RN, RI, RO, SA, SJ, SO, TA, TT.

Habitat: hydrophilous forests, open thorn forests, psammophilous forests, riverside forests, moist hillside forests and xeric hillside forests.

Conservation status: LC.

Observations: it is the most widely distributed epiphytic cactus in Uruguay, present throughout the country.

Voucher: *Berro 2144* (MVFA).

***Rhipsalis* Gaertn.**

Rhipsalis cereuscula Haw., Philos. Mag. Ann. Chem. 7: 112. 1830.

= *Rhipsalis saglionis* (Lem.) Otto, Repert. Bot. Syst. 2: 936. 1843.

(Fig. 5B).

Epiphytic category: HLC.

Distribution: AR, TA.

Habitat: riverside forests.

Conservation status: VU. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and occurs in the protected area 'Área de Manejo de Hábitats y/o Especies Rincón de Franquía'.

Observations: most records are from northwestern Uruguay. However, two recent collections from Tacuarembó (Brussa & Álvarez *s.n.* MVJB 30298, MVJB 30300), expand the distribution of this species to central Uruguay.

Voucher: *Anonymus* (Herb. Osten 17328, MVM).

Rhipsalis floccosa Salm-Dyck ex Pfeiff., Enum. Diagn. Cact. 134. 1837.

Epiphytic category: HLC.

Distribution: RI.

Habitat: moist hillside forests.

Conservation status: VU. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013) and occurs in the protected area 'Paisaje protegido Valle del Lunarejo'.

Voucher: *Bayce et al. s.n.* (MVFA 17322).

Commelinaceae

***Tradescantia* L.**

Tradescantia crassula Link & Otto, Icon. Pl. Rar. 2: 13, pl. 7. 1828.

Epiphytic category: HLA (sx).

Distribution: CL, MA, RO, TT. Uruguay is the southern limit of distribution.

Habitat: moist hillside forests and xeric hillside forests.

Conservation status: NT.

Voucher: *Mai & Abreu s.n.* (MVJB 29773).

Tradescantia fluminensis Vell., Fl. Flumin. 3: 140, pl. 152. 1825.

= *Tradescantia albiflora* Kunth, Enum. Pl. 4: 84. 1843.

Epiphytic category: HLA (tr).

Distribution: AR, CA, CL, CO, FA, MA, MO, RI, RN, RO, SA, SO, TT.

Habitat: hydrophilous forest and riverside forest.

Conservation status: LC.

Voucher: *Mai & Rossado 189* (MVJB).

Tradescantia mundula Kunth, Enum. Pl. 4: 83. 1843. (Fig. 6I).

Epiphytic category: HLA (tr).

Distribution: CL, LA, RI, RO, TT.

Habitat: hydrophilous forests, moist hillside forests and riverside forests.

Conservation status: NT

Voucher: *Rosengurtt & Del Puerto s.n.* (MVFA 10762).

Tradescantia tenella Kunth, Enum. Pl. 4: 83. 1843. = *Tradescantia anagallidea* Seub., Fl. Bras. 3(1): 249. 1871.

Epiphytic category: HLA (tr).

Distribution: AR, CL, FA, LA, MA, RI, RO, SJ, SO, TA, TT.

Habitat: hydrophilous forests, moist hillside forests, open thorn forests, riverside forests and xeric hillside forests.

Conservation status: LC.

Voucher: *Izaguirre et al. s.n.* (MVFA 21083B).

Moraceae

***Ficus* L.**

Ficus cestrifolia Schott, Syst. Veg. [Sprengel] editio decima sexta 4(App.): 409. 1827.

(Fig. 8 C;D).

Epiphytic category: HE.

Distribution: RO. Uruguay is the southern limit of distribution.

Habitat: moist hillside forest and psammophilous forest.

Conservation status: EN. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), but is absent in national protected areas.

Taxonomic comment: there is no present consensus regarding the names *Ficus cestrifolia* and *F. organensis* Miq. Some authors interpret the names as synonyms (Berg & Villavicencio 2004; IBODA 2019), while others regard them as two different species (Pelissari & Romaniuc Neto 2013; Romaniuc Neto *et al.* 2015). More work needs to be done to solve this taxonomic problem. For this publication, we use *F. cestrifolia*, because the Uruguayan specimens agree with the protologue and it is also the oldest name.

Observations: the species is only represented by three collections in national herbaria, all from nearby localities in southeastern Uruguay.

Voucher: *Brussa & Gago s.n.* (MVJB 28367).

Ficus luschnathiana (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi. 3: 298. 1867 \equiv *Urostigma luschnathianum* Miq. Fl. Bras. 4 (1): 101. 1853.

= *Ficus monckii* Hassl., Annuaire Conserv. Jard. Bot. Genève 21: 127. 1919.

= *Ficus monckii* Hassl. var. *san-martinianus* Parodi, Darwiniana 6: 165, f. 5, t. 10. 1943.

= *Ficus diabolica* Herter, Revista Sudamer. Bot. 6: 150, f. p. 152. 1940.
(Fig. 8A, B).

Epiphytic category: HE.

Distribution: AR, CL, CO, RN, RI, RO, SA, SO, TA, TT. Uruguay is the southern limit of distribution.

Habitat: riverside forest and xeric hillside forests.

Conservation status: LC.

Observations: the species is the most widely distributed hemiepiphytic species of the country, but it is scarcely represented in national herbaria.

Voucher: *Lombardo 2454* (MVJB).

Orchidaceae

Acianthera Scheidw.

Acianthera hygrophila (Barb. Rodr.) Pridgeon & M.W. Chase, Lindleyana 16(4): 244. 2001. \equiv *Pleurothallis hygrophila* Barb. Rodr., Gen. Sp. Orchid. 1: 7. 1877.

Epiphytic category: HLC.

Distribution: CL. Uruguay is the southern limit of distribution.

Habitat: riverside forests.

Conservation status: EN. The species was cited for Uruguay some years ago (Rossado *et al.* 2014) so, it is not included as a priority for conservation in Uruguay by Marchesi *et al.* (2013). As it was previously suggested in Rossado *et al.* (2014), we consider it relevant to add *A. hygrophila* to the list of species considered as a priority for conservation in Uruguay.

Observations: the species was collected only in one locality in Uruguay. The species occurs in the protected area 'Paisaje Protegido Paso Centurión y Sierra de Ríos'.

Voucher: *Rossado et al. 178* (MVFA, MVJB).

Acianthera pubescens (Lindl.) Pridgeon & M. W. Chase, Lindleyana 16(4): 245. 2001. \equiv *Pleurothallis pubescens* Lindl., Companion Bot. Mag. 2: 355. 1836.

= *Pleurothallis riograndensis* Barb. Rodr., Gen. Sp. Orchid. 2: 28. 1882.

Epiphytic category: HLC.

Distribution: CL, RO. Uruguay is the southern limit of distribution.

Habitat: hydrophilous forests.

Conservation status: EN. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), but is absent in national protected areas.

Observations: the species shows a restricted distribution in eastern Uruguay.

Voucher: *Brescia et al. s.n.* (MVFA 16348).

Acianthera sonderiana (Rchb. f.) Pridgeon & M. W. Chase, Lindleyana 16(4): 246. 2001. \equiv *Pleurothallis sonderiana* Rchb. f., Linnaea 22: 830. 1849 [1850].
(Fig. 5H).

Epiphytic category: HLC.

Distribution: CL. Uruguay is the southern limit of distribution.

Habitat: hydrophilous forests, moist hillside forests and riverside forests.

Conservation status: VU. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and occurs in the protected area 'Paisaje Protegido Paso Centurión y Sierra de Ríos'.

Observations: the species shows a restricted distribution in the east of the country.

Voucher: *Izaguirre et al. s.n.* (MVFA 21093B).

Campylocentrum Benth.

Campylocentrum aromaticum Barb. Rodr., Contr. Jard. Bot. Rio de Janeiro 4: 103. 1907.

Epiphytic category: HLC.

Distribution: CL, TT. Uruguay is the southern limit of distribution.

Habitat: moist hillside forests and riverside forests.

Conservation status: VU. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and occurs in the protected area 'Paisaje Protegido Paso Centurión y Sierra de Ríos'.

Voucher: *Izaguirre et al. s.n.* (MVFA 19156).

Capanemia Barb. Rodr.

Capanemia micromera Barb. Rodr., Gen. Sp. Orchid. 1: 138. 1877.
(Fig. 5I).

Epiphytic category: HLC.

Distribution: CL, RI, RO, TA, TT. Uruguay is the southern limit of distribution.

Habitat: moist hillside forest and riverside forest.

Conservation status: LC. The species is considered as



a priority for conservation in Uruguay by Marchesi *et al.* (2013). We consider that its presence in the country has been underestimated for a long time, due to the small size of the plants. In recent years, records for this species have increased considerably.

Voucher: *Izaguirre et al. s.n.* (MVFA 19099).

Capanemia superflua (Rchb. f.) Garay, Bot. Mus. Leaflet. 21: 261. 1967. \equiv *Oncidium superfluum* Rchb. f., Ann. Bot. Syst. 6: 721. 1861.

Epiphytic category: HLC.

Distribution: CL, LA, MA. Uruguay is the southern limit of distribution.

Habitat: riverside forests.

Conservation status: EN. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and occurs in the protected area 'Paisaje Protegido Paso Centurión y Sierra de Ríos'.

Observations: this species shows two distribution areas in eastern Uruguay, with few records in either one.

Voucher: *Duarte & Berazategui s.n.* (MVM 21160).

Cyclopogon C. Presl

Cyclopogon elatus (Sw.) Schltr. Repert. Spec. Nov. Regni Veg. Beih. 6: 53. 1919. \equiv *Spiranthes elata* (Sw.) Rich., De Orchid. Eur. 37. 1817. \equiv *Satyrium elatum* Sw., Prodr. 119. 1788.

(Fig. 6E).

Epiphytic category: HLA (tr, sx).

Distribution: AR, CA, CL, FA, LA, MA, RN, RI, RO, SA, SJ, TA, TT.

Habitat: hydrophilous forests, moist hillside forests, psammophilous forests, riverside forests and xeric hillside forests.

Conservation status: LC.

Observations: the species possibly has a wider distribution in Uruguay, and it is underrepresented in the national herbaria.

Voucher: *Del Puerto & Marchesi* 5267 (MVFA).

Gomesa R. Br.

Gomesa barbata (Lindl.) M.W. Chase & N.H. Williams, Ann. Bot. (Oxford) 104(3): 395. 2009. \equiv *Oncidium barbatum* Lindl., Coll. Bot. t. 27. 1821.

Epiphytic category: HLC.

Distribution: CL. Uruguay is the southern limit of distribution.

Habitat: moist hillside forests.

Conservation status: EN. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013) under the name *Gomesa ciliata* (Lindl.) M.W. Chase

& N.H. Williams, and occurs in the protected area 'Paisaje Protegido Paso Centurión y Sierra de Ríos'.

Observations: the species shows a restricted distribution in the east of the country.

Voucher: *Ziliani et al. s.n.* (MVFA 20350).

Gomesa bifolia (Sims) M.W. Chase & N.H. Williams, Ann. Bot. (Oxford) 104(3): 396. 2009. \equiv *Oncidium bifolium* Sims, Bot. Mag. 36: t.1491. 1812. (Fig. 5G).

Epiphytic category: HLC.

Distribution: AR, CL, CO, DU, LA, MA, PA, RN, RI, RO, SJ, SO, TA, TT.

Habitat: moist hillside forests, psammophilous forests, riverside forests and xeric hillside forests.

Conservation status: LC.

Observations: the species is the most frequent and widely distributed epiphytic orchid in Uruguay.

Voucher: *Osten* 2836 (MVM).

Gomesa uniflora (Booth ex Lindl.) M.W. Chase & N.H. Williams, Ann. Bot. (Oxford) 104(3): 398. 2009. \equiv *Oncidium uniflorum* Booth ex Lindl., Edwards's Bot. Reg. 29: t. 43. 1843.

\equiv *Gomesa longipes* (Lindl.) M.W. Chase & N.H. Williams, Ann. Bot. (Oxford) 104(3): 397. 2009. \equiv *Oncidium longipes* Lindl., Paxt. Fl. Gard. 1:46. 1850.

Epiphytic category: HLC.

Distribution: CL, TT. Uruguay is the southern limit of distribution.

Habitat: moist hillside forests and riverside forests.

Conservation status: EN. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and occurs in the protected area 'Paisaje Protegido Paso Centurión y Sierra de Ríos'.

Voucher: *Firpo s.n.* (MVFA 33751).

Hapalorchis Schltr.

Hapalorchis lineatus (Lindl.) Schltr. Beih. Bot. Centralbl., Abt. 2. 37(2): 363. 1920. \equiv *Spiranthes lineata* Lindl., Gen. Sp. Orchid. Pl. 471. 1840.

Epiphytic category: HLA (sx, tr).

Distribution: CA, CL, MA, RO. Uruguay is the southern limit of distribution.

Habitat: moist hillside forest, psammophilous forest and xeric hillside forest.

Conservation status: VU. The species is not included as a priority for conservation in Uruguay by Marchesi *et al.* (2013), and occurs in the protected area 'Paisaje Protegido Paso Centurión y Sierra de Ríos'.

Observations: due to its small size, possibly the species

is underrepresented in national herbaria and could have a wider distribution in eastern and southeastern Uruguay.

Voucher: *Rossado & Pinelli 458* (MVFA).

Trichocentrum Poepp. & Endl.

Trichocentrum pumilum (Lindl.) M.W. Chase & N.H. Williams, *Lindleyana* 16(2): 138. 2001. \equiv *Oncidium pumilum* Lindl., *Bot. Reg.* 11: t. 920. 1825.

Epiphytic category: HLC.

Distribution: CL, RO, TT. Uruguay is the southern limit of distribution.

Habitat: moist hillside forests, psammophilous forests and riverside forests.

Conservation status: VU. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), but is absent in national protected areas.

Voucher: *Berro 2858* (MVM).

Piperaceae

Peperomia Ruiz & Pav.

Peperomia catharinae Miquel, *Syst. Piperac.* 127. 1843.
= *Peperomia herteri* Trelease, *Rev. Sudamer. de Bot.* 6: 66. 1941.
= *Peperomia uruguayana* Trelease, *Rev. Sudamer. de Bot.* 6: 66. 1941.
(Fig. 4G).

Epiphytic category: HLC.

Distribution: CL, LA, MA, RI, RO, TT. Uruguay is the southern limit of distribution.

Habitat: hydrophilous forests, riverside forests, moist hillside forests and xeric hillside forests.

Conservation status: LC.

Voucher: *Arechavaleta 408* (MVM).

Peperomia comarapana C. DC., *Meded. Rijks-Herb.* 27: 8. 1915.
(Fig. 6C).

Epiphytic category: HLA (tr).

Distribution: AR, PA, RN.

Habitat: open thorn forests.

Conservation status: VU. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), but is absent in national protected areas.

Voucher: *Berazategui et al. s.n.* (MVM 23008).

Peperomia increscens Miquel, *Linnaea* 20: 124. 1847.
= *Peperomia blanda* var. *pseudodindygulensis* (C. DC.) Yunc., *Lilloa* 27: 218. 1953. \equiv *Peperomia pseudodindygulensis* C. DC., *Mém. Soc. Phys. Genève* 27(2): 307. 1882.

(Fig. 6D).

Epiphytic category: HLA (el, tr).

Distribution: AR, CL, PA, RI, RO, TA. Uruguay is the southern limit of distribution.

Habitat: moist hillside forests and xeric hillside forests.

Conservation status: NT

Observations: the species is distributed in eastern Uruguay, however a recent record from western Uruguay (Muñoz & Diaz *s.n.* MVJB 30518), has extended considerably the distribution for this species in the country.

Voucher: *Mai et al. 289* (MVJB).

Peperomia pereskiifolia (Jacq.) Kunth, *Nov. Gen. Sp.* (quarto ed.) 1: 68, [1815] 1816. ("pereskiaefolia") \equiv *Piper pereskiifolium* Jacq., *Collectanea* 4: 126. 1790.
(Fig. 4H).

Epiphytic category: HLC.

Distribution: MA, RO. Uruguay is the southern limit of distribution.

Habitat: moist hillside forest, psammophilous forest

Conservation status: EN. The species is considered as a priority for conservation in Uruguay by Marchesi *et al.* (2013), but is absent in national protected areas.

Observations: the species has a restricted distribution in southeastern Uruguay and up to date has been only registered in three localities. Voucher: *Alonso Paz 4680* (MVFQ).

Peperomia psilostachya C. DC., *Mém. Soc. Phys. Genève* 32 (2): 9, pl. 54, f. 6–9, 1893.
(Fig. 4F).

Epiphytic category: HLC.

Distribution: CL, RI. Uruguay is the southern limit of distribution.

Habitat: moist hillside forests and riverside forests.

Conservation status: EN. The species was cited for Uruguay few years ago (Mai *et al.* 2016) so, it is not included as a priority for conservation by Marchesi *et al.* (2013). Therefore, we consider it relevant to add *P. psilostachya* to the list of species considered as priority for conservation in Uruguay, as it was suggested in Mai *et al.* (2016). The species occurs in the protected area 'Paisaje Protegido Paso Centurión y Sierra de Ríos'.

Observations: there are only two records for this species in Uruguay.

Voucher: *Mai et al. 205* (MVJB).

Peperomia tetraphylla Hooker & Arnott, *Bot. Beechey Voy.* 97. 1832.
= *Peperomia reflexa* (L. f.) A. Dietrich, *Sp. Pl.* (ed. 6) 1: 180. 1831., *nom. illeg. non Kunth* (1815 [1816]: 70) \equiv *Piper reflexum* Linnaeus f., *Suppl. Pl.* 91. 1781.



= *Peperomia berroi* Trelease. Revista Sudamer. Bot. 6: 67. 1941.

= *Peperomia tacuariana* Trelease, Revista Sudamer. Bot. 6: 66. 1941.

= *Peperomia americana* (Miq.) Herter, Revista Sudamer. Bot. 10 (2): 46. 1952. ≡ *Peperomia reflexa* (L. f.) A. Dietrich fo. *americana* Miq., Syst. Piperac. 173. 1843.

= *Peperomia arechavaletae* var. *minor* Herter in Marchesi, Boletín Facultad de Agronomía 104: 10. 1968. – *Peperomia arechavaletae* var. *minor* Herter, Revista Sudamer. Bot. 10 (2): 45. 1952., nom. inval.

(Fig. 4E).

Epiphytic category: HLC.

Distribution: CL, MA, RI, RO, TT. Uruguay is the southern limit of distribution in America.

Habitat: moist hillside forests, hydrophilous forests and riverside forests.

Conservation status: LC.

Voucher: Berro 1213 (MVFA).

Peperomia trineuroides Dahlst. Kongl. Svenska Vetensk. Acad. Handl. 33(2): 198, t. 8, f. 2. 1900.

= *Peperomia arechavaletae* C. DC, Notizbl. Königl. Bot. Gart. Berlin 6: 466. 1917.

– *Peperomia arechavaletae* var. *minor* auct. non Herter: Marchesi (1968, p.p.)

(Fig. 7G).

Epiphytic category: HLF (sx).

Distribution: CL, RI, RO, TA, TT. Uruguay is the southern limit of distribution.

Habitat: moist hillside forests.

Conservation status: NT.

Voucher: Berro 1915 (MVFA).

Discussion

The epiphytic flora of Uruguay corresponds to 3.04 % of the total native flora of the country, whereas woody species represent 13 % (Haretche *et al.* 2012), based on the 2400 confirmed native species (Marchesi *et al.* 2013). As epiphytes and woody species are intrinsically associated with forests, these are significant values, especially when considering that most of the territory is dominated by grasslands, and that native forests cover only 5.2% of total surface (MGAP 2018). Although restricted in space, the quite distinct and widely distributed Uruguayan forest types represent a great importance for the conservation of the epiphytic flora. The absence of exotic epiphytes in natural environments indicates a well-preserved condition of these communities.

The richest epiphytic families in Uruguay are Bromeliaceae, Polypodiaceae and Orchidaceae, which are all highly specialized for canopy life, and are also among

the most diversified vascular families in the worldwide epiphytic flora (Benzing 1990; Zotz 2013a). Additionally, all the three families show several essential adaptations to survive in dry environments or with intermittent moisture availability (Benzing 1987; Gentry & Dodson 1987). These conditions are typical for a subtropical country like Uruguay, where the summer months can be relatively dry due to increased evaporation rates, and the winter months can be cold (Castaño *et al.* 2011), especially for many vascular epiphytes. These limiting factors might also explain why some common tropical families, such as Araceae and Gesneriaceae, do not extend with epiphytic habit southward into Uruguay.

The richest epiphytic families in Uruguay also match overall those found in epiphytic communities of humid subtropical areas in northeastern Argentina (Cabral & Salas 2008; Martín 2014), eastern Paraguay (Basualdo *et al.* 2005) and southern Brazil (Gonçalves & Waechter 2003; Giongo & Waechter 2004; Buzatto *et al.* 2008; Staudt *et al.* 2012; Perleberg *et al.* 2013; Matos *et al.* 2017; Ramos *et al.* 2019). However, in Uruguay Orchidaceae shows a lower contribution when compared with these studies, where it stands as the richest plant family. The lower orchid richness recorded in our study is in accordance with the strong north to south decrease of species and genera in eastern subtropical South America (Waechter 1998), extending from Paraná state (Brazil) to Buenos Aires province (Argentina). The same decreasing tendency was reported for epiphytic cacti (Bauer & Waechter 2011) and ferns (Gonzatti *et al.* 2016; Machado *et al.* 2016), and might also be explained by the decrease in average precipitation and temperature, and the concomitant increase of water deficit and number of frost days south of 30°S (Barros *et al.* 2006).

Tillandsia stands out as the richest epiphytic genus in Uruguay, and furthermore represents an overwhelming amount of atmospheric against urn or tank bromeliads (in the rate 15:2). In moist tropical regions, this proportion is commonly inverse, i.e., there are more bromeliads with water-containing rosettes of the genera *Aechmea* or *Vriesea* (Fontoura *et al.* 2012; Ramos *et al.* 2019). The combination of a dense cover of water-absorbing trichomes, the water-retention in narrow and succulent leaves and the reflective surfaces of plants given by grayish tones, positions several *Tillandsia*-species among the most xerophytic epiphytes, allowing their occurrence in dry or enduring water-deficit environments (Benzing 1987; 1990). Additionally, this genus includes both shade-tolerant species that inhabit closed and humid forests (e.g. hydrophilous forests and moist hillside forests) as well as light-demanding species adapted to open environments (e.g. open thorn forests), resulting in a wider distribution in Uruguay. Characteristic holoeiphytes (HLC) are by far the most diversified life-form in the Uruguayan epiphytic flora, as can be expected, because they also belong for the most part to the richest and well-adapted families occurring in epiphytic environments.



The predominance of this category has been often reported for epiphytic communities in moist subtropical climates (Gonçalves & Waechter 2003; Barbosa *et al.* 2015; Machado *et al.* 2016). Facultative holoepiphytes (HLF) represent a diverse taxonomic group, commonly varying according to the environmental characteristics, such as the abundance of rocky outcrops (walls or boulders) inside or adjacent to forests. Several facultative epiphytes eventually are more abundant and achieve bigger sizes on rocks than on trees (e.g.: *Asplenium gastonis*). Accidental holoepiphytes (HLA) occur under two quite distinct exposure conditions; one comprises those plants which are more abundant on the forest floor and can be found as epiphytes (e.g.: *Tradescantia fluminensis*, *Asplenium ulbrichtii*), or on shaded rocks inside the forest (e.g.: *Peperomia increscens*, *Billbergia nutans*); another group comprises those plants which typically occur on sun-exposed cliffs, and accidentally reach the nearby trees (e.g.: *Tillandsia arequitate*, *T. uruguayensis*, *T. xiphioides*). Accidental epiphytism is also favoured by phorophyte traits, such as more horizontal branches, presence of cavities in the trunks, and a thick fissured bark, as in *Pouteria salicifolia* (Spreng.) Radlk; the persistent leaf sheaths in palms such as *Butia* spp. also favors accidental epiphytes. Hemiepiphytes are the less diversified group in Uruguay, comprising only two species of *Ficus* (Moraceae). *Ficus luschnathiana* is widespread throughout the country and both young epiphytes and adult stranglers are commonly found in forests and on isolated trees. *Ficus cestrifolia* is otherwise restricted to a few localities in southeastern Uruguay, where the species grows both as a terrestrial and epiphytic plant.

Regarding the assessment of conservation status, almost half the epiphytic flora of Uruguay fits into some threatened category. All the species identified as Endangered occur in only a few sites and generally have small populations. In some cases, the habitats are severely fragmented (e.g. for *Acianthera hygrophila*, *Tillandsia loliacea*, *T. recurvifolia*) or are naturally restricted (e.g. for *Niphidium crassifolium*, *Pecluma paradiseae*, *P. pectinatifolium*, *Peperomia psilostachya*). The species circumscribed as Vulnerable generally have a wider geographical range, and usually with more than one distribution area within Uruguay; some of them have a low number of records (less than 10) or the records are concentrated in few localities. However, some of these cases could be a result of under-sampling, mainly because of small-sized plants which are easily overlooked (e.g. *Didymoglossum hymenoides*, *Hapalorchis lineatus*). Although more than half (60 %) of the threatened species (EN and VU) are included in national protected areas, the rest of them remain in an endangered situation. The risk of extinction is particularly critical for those species with restricted distribution, because they are much more threatened by habitat loss or degradation resulting from different anthropic activities.

The catalogue comprises several species which typically occur in rain forests and seasonal forests of the Atlantic

and Paranean biogeographic provinces (*sensu* Cabrera & Willink 1973). The Atlantic forest is often reported as one of the world's biodiversity hotspots (Galindo-Leal & Câmara 2003), showing high richness and endemism rates of vascular epiphytes (Martinelli *et al.* 2008; Menini Neto *et al.* 2016; Freitas *et al.* 2016). Several epiphytic species of these northern tropical and subtropical biogeographic provinces extend southwards into Uruguay. The relatively wide systematic participation of the Uruguayan epiphytes evidences that their occurrence is present in different taxonomic groups, such as ferns (e.g. *Campyloneurum*, *Niphidium*, *Pecluma*, *Pleopeltis*, *Psilotum*, *Serpocaulon*, and *Vittaria*) and angiosperms (e.g.: *Peperomia*, *Lepismium*, *Rhipsalis*), where it is especially relevant in orchids (e.g.: *Acianthera*, *Capanemia*, *Gomesa*). Besides this more tropical forest epiphytic flora, Uruguay also contains species extending from the dry and open forests and woodlands of the Chaco and Espinal biogeographic provinces, occurring mostly in northern Argentina (Cabral & Salas 2008; Martín 2014; Arnesi *et al.* 2018; IBODA 2019) and western Paraguay (IBODA 2019). These species occur exclusively in western Uruguay, and also belong to different families and genera (e.g.: *Lepismium aculeatum*, *Peperomia comarapana*, *Tillandsia duratii*, *T. ixiioides* and *T. recurvifolia*).

Among vascular epiphytes it is interesting to note that around half (52 %) of the non-endemic species reach their southernmost distribution in Uruguay. This southern limit is remarkable to orchids (10 of 12 species), ferns (13 of 25 species), and to the genus *Peperomia* (six of seven species) and *Ficus* (all the species in the country). This distributional trait of epiphytes was previously reported for orchids (Waechter 1998; Rossado *et al.* 2014) and peperomias (Mai *et al.* 2016), and is furthermore shared with many terrestrial woody species (Grela & Brussa 2003; 2005; Brussa & Grela 2007; Delfino *et al.* 2011; Haretche *et al.* 2012; Brussa 2016). The epiphytic examples given above reinforce the transitional nature of the Uruguayan flora, despite a single biogeographic province (Pampean) is commonly assigned to the entire country. Actually, the Uruguayan territory covers a remarkable combination of floristic elements from Atlantic, Paranean and Chacoan forests, as reported in previous works (Chebataroff 1942; Alonso-Paz & Bassagoda 2002; Brussa & Grela 2007; Haretche *et al.* 2012).

In conclusion, we hope that this updated list of vascular epiphytes of Uruguay will encourage other botanists and ecologists to study the epiphytic flora in more focused approaches, especially in population, community, and conservation ecology. The scientific contributions in these fields are essential at a time when the fate of many species is at risk, largely due to the shifting land use that Uruguay is currently experiencing. Continued fieldwork, especially in the northern and western scarcely studied areas can both increase the floristic list given in this catalogue and additionally expand the distribution range of the already known species.



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