

RAINBIO: a mega-database of tropical African vascular plants distributions

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Abstract

The tropical vegetation of Africa is characterized by high levels of species diversity but is undergoing important shifts in response to ongoing climate change and increasing anthropogenic pressures. Although our knowledge of plant species distribution patterns in the African tropics has been improving over the years, it remains limited. Here we present RAINBIO, a unique comprehensive mega-database of georeferenced records for vascular plants in continental tropical Africa. The geographic focus of the database is the region south of the Sahel and north of Southern Africa, and the majority of data originate from tropical forest regions. RAINBIO is a compilation of 13 datasets either publicly available or personal ones. Numerous in depth data quality checks, automatic and manual via several African flora experts, were undertaken for georeferencing, standardization of taxonomic names and identification and merging of duplicated records. The resulting RAINBIO data allows exploration and extraction of distribution data for 25,356 native tropical African vascular plant species, which represents ca. 89% of all known plant species in the area of interest. Habit information is also provided for 91% of these species.

Keywords

Herbarium specimens, tropical forests, georeferencing, taxonomic backbone, habit, digitization, native species, cultivated species, biodiversity assessment

Introduction

Improving our understanding of the distribution of biodiversity has been suggested as “one of the most significant objectives for ecologists and biogeographers” (Gaston 2000). Indeed, fundamental understanding of biodiversity patterns and inference of conservation assessments leading to wise and sustainable management of biodiversity at various scales are heavily dependent on our knowledge of species distributions. For tropical regions especially, we have had an incomplete understanding of species distributions which causes a major problem for ecological and conservation research (Bini et al. 2006, Feeley and Silman 2011). There has been a global lack of tropical biodiversity data availability (Collen et al. 2008, Feeley and Silman 2011), although this is increasingly being improved (e.g., Enquist et al. 2009; <http://bien.nceas.ucsb.edu/bien/>, www.gbif.org, ter Steege et al. 2016). The tropical vegetation of Africa contains high levels of species diversity but is subject to important shifts in response to ongoing climate change and increasing anthropogenic pressures (Blach-Overgaard et al. 2015;

Hansen et al. 2013; Lewis et al. 2009; McClean et al. 2005). Even though our knowledge of plant species distribution patterns in the African tropics has been improving over the years (Linder et al. 2012; Stropp et al. 2016), it remains limited (Küper et al. 2006), which calls for initiatives to collate African biodiversity data.

Here, we present RAINBIO, a unique comprehensive database of georeferenced records of vascular plants (Tracheophyta) in sub-Saharan tropical Africa and north of Southern Africa, including Gulf of Guinea islands, Cape Verde and Zanzibar archipelagos (Fig. 1). Until recently, distribution data on tropical African plants were scattered among institutions and individual researchers and not compiled into a single comprehensive database. A recent analysis of African (including Madagascar) vascular plant species occurrences available via the Global Biodiversity Information Facility portal (GBIF, www.gbif.org) resulted in 934,676 herbarium records after data filtering for 57 countries (Stropp et al. 2016). However, over half of these specimens (512,680) belonged to South Africa alone, with Madagascar and Tanzania having the second and third most specimens, respectively (Stropp et al. 2016). This study underlined the lack of high quality data for tropical Africa, especially the forested regions. Several resources, often accessible via the internet, offer access to a large number of occurrences thanks to recent efforts to digitize and georeference herbarium specimens (e.g. TROPICOS, Oever and Gofferje 2012, Heerlien et al. 2014). Additionally, researchers on tropical African botany have created their own “working” datasets for their plant groups or regions of interest (e.g. Blach-Overgaard et al. 2010; Droissart et al. 2012; Wieringa and Sosef 2011). These datasets have the advantage of having updated specimen identifications and generally more accurate georeferencing compared to the larger institutional datasets. RAINBIO is a compilation of thirteen datasets and should be seen as a readily workable dataset because we applied several quality filters, checked the data quality (both georeferencing and taxonomy) and identified and merged duplicate records.

General description and purpose

The first target of the RAINBIO project (African RAIN forest community dynamics: implications for tropical BIOdiversity conservation and climate change mitigation) funded by CESAB (CEntre de Synthèse et d'Analyse sur la Biodiversité) of the FRB (Fondation pour la Recherche sur la Biodiversité, France), is to compile a state-of-the-art dataset on plant species distribution across tropical Africa. RAINBIO uses large publicly available datasets and smaller “non public”/private databases. The resulting RAINBIO mega database allows the exploration and extraction of distributional data for 25,356 species (29,664 taxa including infraspecific taxa: subspecies and varieties) across continental tropical Africa. It is the first step towards a standardization of plant occurrences in this region and also contributes towards achieving Target 1 of the first Objective of the Global Strategy for Plant Conservation, “*an online flora of all known plants*”, adopted by the Convention on Biological Diversity (Paton et al. 2008).

Datasets

Two datasets are provided in *csv* format as well as an *R.data* working space (<http://rainbio.cesab.org/>). For the latter, an R script is provided for exploring and mapping occurrences.

The database made available here represents a subset of available fields (see below). The actual RAINBIO database follows the Darwin Core standard (Wieczorek et al. 2012). Users interested in fields not provided here (see details in <http://rainbio.cesab.org/>) are invited to contact the first author or last author.

The RAINBIO database is subject to future updates. Users interested in having an updated version of the database are invited to contact the first or the last author.

Object name: RAINBIO occurrence database of tropical African vascular plants

Character encoding: UTF-8

Format name: CSV and R.data

Format version: 1.0

Distribution: <http://rainbio.cesab.org/>

Publication date of data: September 2016

Language: English

Metadata: <http://vmamapgn-test.mpl.ird.fr/geonetwork/srv/eng/search#|75cf4509-1797-481f-b03c-9dcce3c773f>

Licenses of use: This database is made available under license Open Data Commons Attribution: <http://www.opendatacommons.org/licenses/by/1.0/>

Elements:

- RAINBIO unique identifier.
- Unique identifier of the source dataset.
- Taxonomic information (order, family, genus, species and infra-specific taxa).
- Country.
- Geographical coordinates in decimal degrees.

Object name: RAINBIO species checklist of tropical African vascular plants

Character encoding: UTF-8

Format name: CSV and R.data

Format version: 1.0

Distribution: <http://rainbio.cesab.org/>

Publication date of data: September 2016

Language: English

Metadata: <http://vmamapgn-test.mpl.ird.fr/geonetwork/srv/eng/search#|d20604bc-ce2d-444f-b4b6-e73e55ad3ef2>

Licenses of use: This database is made available under license Open Data Commons Attribution: <https://creativecommons.org/licenses/by-nc/4.0/legalcode>

Elements:

- Taxonomic information (order, family, genus, species and infra-specific taxa).
- Habit type.

Collectors and owners of the data

RAINBIO is a compilation of thirteen datasets (more details on these sources at the end of the article) of three kinds: (i) extensive ‘public’ databases of several herbaria institutes (BR, BRLU, K, LISC, MO, and WAG (incl. AMD, L & U as well); acronyms according to Thiers (continuously updated), (ii) personal databases collated by individual researchers (focusing on a given taxonomic group or a given geographic area) and (iii) other sources of plant occurrences such as silica-gel collections or vegetation plot inventories. The WAG dataset includes a series of personal datasets (like ii) compiled for taxonomical revisions of over 35 genera in different families. Occurrences are thus supported by specimens deposited in herbaria (586,920 records), silica-dried specimens (13,510 records) or observations from plot inventories (13,443 records).

Methods of data collection

The workflow for building the database involved numerous steps of cleaning, standardizing and quality checks described below. These steps were essentially built up in Postgres and PostGis scripts. Several other cleaning and checking steps were run using the R statistical software (R Core Team 2015).

Georeferencing verification processes

We performed two quality control checks on the geographical coordinates of the records:

First we checked if the documented country of each record corresponds to the country in which the record is georeferenced (Fig. 2).

If false, we checked whether the georeferenced record fell within a country neighbouring the documented country (Fig. 2A). If true, the occurrence was classified as ‘*Neighbour*’ and the nearest distance between the occurrence and the border of the documented country was calculated. Records with a distance of more than 5 km were discarded while records with a distance less than 5 km were retained. The logic behind this is that records could well be from a country neighbouring the one provided by the coordinate, because either the map or the coordinate is not precise enough.

Second, we checked if the occurrence fell within an ocean (Fig. 2C).

If true, the nearest distance between the occurrence and the coastline was calculated. If the distance was greater than 5 km, the record was discarded. If the distance was less than 5 km the record was retained. Again, the logic behind this was that the coordinate or the map may not be precise enough.

If false, the record was discarded.

Taxonomic backbone and standardization of taxonomic names

To resolve problems such as spelling errors and/or synonymies linked to heterogeneous taxonomic datasets, we first relied on the taxonomic backbone table used by the Naturalis Biodiversity Center herbaria (AMD, L, U & WAG). The structure of this table provides links among taxa names allowing the standardization of species name spelling and synonyms.

We then submitted this taxon list (30,147 names) to the online “Taxonomic Name Resolution Service” (TNRS, Boyle et al. 2013). This tool compares submitted names to names from four different sources (TROPICOS (<http://www.tropicos.org/>), USDA (<http://plants.usda.gov>), the Global Compositae Checklist (www.compositae.org/checklist) and The NCBI Handbook (<http://www.ncbi.nlm.nih.gov/guide/taxonomy/>)). The program returns a name match with the taxonomic status (accepted or not) and an overall matching score (a value between 0 (no match) and 1 (perfect match)). From this, two lists were produced: one identifying misspelled names and one identifying potential synonyms. The first list was generated by filtering out names with a taxonomic status as “accepted”, an overall score below 1 and no partial match (i.e. both genus and species names are matched). The second list was created by filtering out (i) names with an overall score of 1 and whose submitted name was different from the accepted name, and (ii) names with an overall score under 1 and whose matched name was different from the accepted name. For both lists, we further screened the database names manually for the presence of the matched name (for the list of misspelled names) and for the presence of the accepted name (for the list of synonyms). The remaining and/or unresolved names were then scrutinized against the African Plant Checklist and Database (Klopper et al. 2007, African Plants Database 2015) and the World Checklist of Selected Plant Families (Govaerts et al. 2009) to assess their status.

Overall, if we consider records that passed the different georeferencing quality checks (see above), 3,114 species names (3806 taxa) were excluded from our database after these different standardization procedures.

Family names for angiosperms were standardized to following the Angiosperm Phylogeny Group III system (APG III 2009).

Workflow to identify and merge record duplicates

The database is a compilation of both extensive ‘public’ databases compiled by herbarium institutes and smaller personal databases focusing on either a given taxonomic group or a given geographic area. Despite their limited number of records, the latter have been compiled by experts and therefore the quality of georeferencing and identification are generally better. A major issue was that most records in personal databases were duplicated within large herbarium database. Likewise, there was overlap in specimen data among major herbarium databases because specimens have often

been collected in several duplicates that were later distributed among herbaria. It was important to identify and merge these duplicates because each could carry a different identification and/or georeference. Hence, the identification of duplicate records had to be carried out in order to select the most accurate information in cases where duplicate records contained conflicting data.

When duplicates with different identifications were encountered, the following procedure was followed to identify the most reliable record:

- if the identification varied between an institutional and a personal database, we chose the identification recorded in the personal database (see the description of the datasets below).
- if a personal database was not available, we chose the identification with the most recent date of identification.
- if identification dates were similar or not given, we chose the identification at the lowest taxonomic rank (e.g. genus, species, subspecies, etc.). For example, if one record was identified to the infra-specific level while another was identified to the genus level, then the former was chosen.
- if after these steps no one record was identified, a random one was chosen.

When duplicates with different coordinates were identified, several subsequent steps were undertaken to identify the most reliable georeferencing:

- if only one of the records passed the quality check for country described above, those coordinates were chosen.
- if the coordinates came from an institutional and a personal database, the chosen georeferencing was the one from a personal database (see the description of the datasets above).
- if none was chosen by the previous step, the chosen georeferencing was the one with the highest precision of the geographical coordinates using a precision code calculated for the project from 1 to 8 (see Table 1).
- if after these steps no one record was identified, a random one was chosen.

Identification of introduced and cultivated taxa

Because we want to work only with natural occurrences of indigenous species, we had to, as far as possible, identify and discard specimens collected from planted and/or cultivated individuals and those from introduced species.

The first step in this process was to screen the text in the locality field of the specimen records. We first built a preliminary list of locality descriptions by searching for a list of keywords (e.g. 'Botanical garden'). Of this preliminary list of 898 locality descriptions we selected 653 that most likely correspond to *ex situ* living collections. All records collected (1,427) from these localities were then discarded.

Table 1. Accuracy code given to georeferenced records and corresponding uncertainty in degrees.

Criterion	Code
accurate to degree only (~110 km)	1
15 minutes precision (~30 km)	2
5 minutes precision (~10 km)	3
2 minutes precision (~4 km)	4
minute is exact (~ 2 km)	5
1/10 decimal minute exact (~ 200 m)	6
1/100 decimal minute exact (~ 20 m)	7
1/1000 decimal minute exact (~ 2 m)	8

In order to differentiate between native species and cultivated or other introduced taxa, the following procedure was adopted. We expected to find most cultivated or introduced taxa among those with few collections (these taxa are in fact rarely collected in the field). We therefore first extracted all species with fewer than eleven records. Then, GBIF occurrences were used to document the distribution outside of the area covered by the RAINBIO database: for each species, we verified whether occurrences were available on GBIF and if that was the case, we downloaded GBIF occurrences using the *rgbif* package (Chamberlain et al. 2016). Species appearing as mostly collected outside of the geographical coverage of the RAINBIO database were selected and manually checked to confirm they were truly introduced/cultivated, resulting in a list of 1,658 cultivated/introduced species. This list was further completed by using information provided by the African Plant Checklist and Database (Klopper et al. 2007) and the World Checklist of Selected Plant Families (Govaerts et al. 2009). The final list of cultivated/introduced species identified within the RAINBIO database comprised 1,635 species, which corresponds fairly well to the ca. 2100 naturalized non-African species in the whole of Africa as calculated by Kleunen et al. (2015). All records belonging to those taxa were discarded (but see <http://rainbio.cesab.org/> for the list of those species).

Geographic coverage

Records of the RAINBIO database are localized in continental Africa, excluding Madagascar and Indian Ocean islands, but including Gulf of Guinea islands, Cape Verde and Zanzibar archipelagos representing 51 different countries. All records fall within an area delimited between -34.8328 and 37.1094 degrees of latitude, and between -25.33 and 51.4 degrees of longitude.

The geographic coverage of the RAINBIO database i.e. where record density is significant, is a region broadly delimited by ecoregions (*sensu* Olson et al. 2001) south of the Sahel and north of Southern Africa. The most significant amount of data originates from the tropical forest regions (Fig. 1).

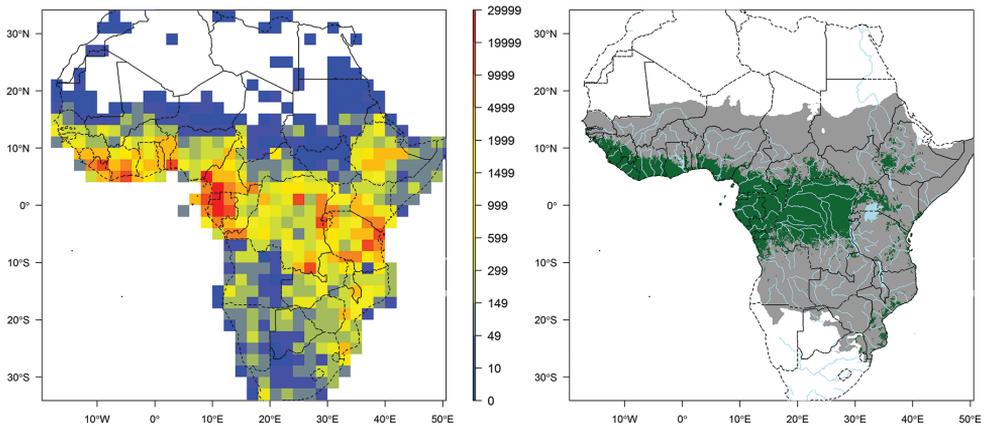


Figure 1. Left map: record density in $2^\circ \times 2^\circ$ cell including all georeferenced records that passed the quality checks. This map includes records that are identified or not to species level. Right map: main extent of RAINBIO geographical coverage from south of Sahel and north of Southern Africa (grey area); extent of tropical rain forest regions adapted from the land cover map published by Mayaux et al. (2004) (green area).

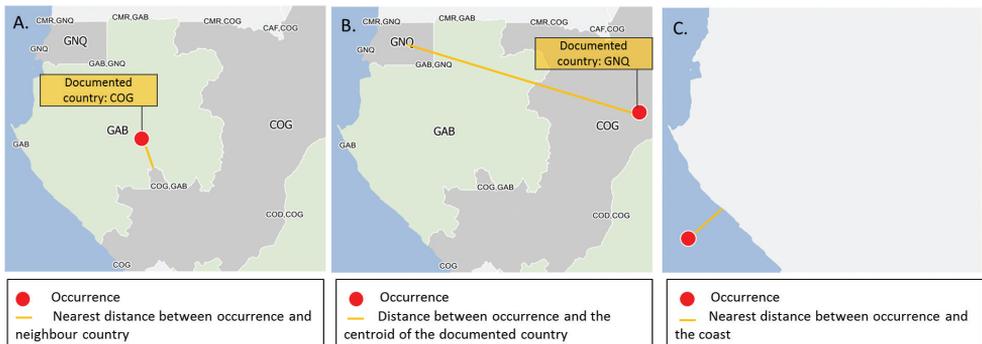


Figure 2. Examples of the georeferencing verification process. **a** The georeferenced record falls within a neighbouring country (here Gabon - GAB) of its documented country (here Republic of the Congo - COG). The nearest distance between the occurrence and the border of the documented country is computed **b** The georeferenced record falls within a non-neighbouring country (here Equatorial Guinea - GNQ) of its documented country (here Republic of the Congo). This record is classified as 'Error' and is discarded **c** The georeferenced record lies beyond the coastline. The nearest distance between the occurrence and the coastline of the documented country is computed.

Taxonomic coverage

The RAINBIO database comprises 25,356 species of vascular plants and 29,659 taxa (including subspecies and varieties), 3,158 genera and 273 families. The list of all taxa recorded in the RAINBIO database can be found in the Appendices.

Magnoliophyta are represented by 596,972 records and 24,770 species, Gymnosperms by 770 records and 40 species and Pteridophyta by 16,280 records and 546

species. The best represented families in Magnoliophyta are Rubiaceae, Fabaceae and Poaceae (Fig. 3A). Gymnosperms include eight families among which the Podocarpaceae is the most represented (Fig. 3B). Within Pteridophyta the most represented families are Polypodiaceae and Aspleniaceae (Fig. 3C).

In 2007, the total number of Angiosperm taxa in an area broadly corresponding to the geographic coverage of the RAINBIO database was estimated to be 32,424 by the African Plant Checklist and Database (Klopper et al. 2007, African Plants Database 2015). RAINBIO database comprises 29,013 angiosperm taxa. We can therefore estimate that the RAINBIO database includes information for approximately 89% of all known species in the area of interest.

Habit data

We provide habit for almost all species recorded in the RAINBIO database (available for 23,111 species or 91% of all species). Information was gathered at the species level and was initially taken from the Naturalis Herbarium Collections database.

This information was then completed by relying on the field description of herbarium specimens: keywords for seven specific habits (tree, shrub, herb, liana, epiphyte, mycoheterotroph and parasitic) were searched for in the description field of all specimens. For example, for the ‘tree’ habit, the key-words were “Tree”, “tree”, “Arbre”, “arbre”, “Arbor”, “arbor”. If one of these key-words was found in the description field of a specimen, the record was tagged for the ‘tree habit’. The tags for each habit were then summed for each species. This procedure resulted for example in twenty tags for the species *Acacia adenocalyx* among which nine of them concerned the ‘shrub’ category and seven the ‘liana’ category. For each species the habit with the highest number of tags was chosen. If this habit represented less than half of the tags, the second ranked habit was considered as a secondary habit. For *Acacia adenocalyx*, this procedure therefore resulted in the choice of ‘shrub’ habit as the primary habit and ‘liana’ habit as a secondary habit. Erect palm-like plants (e.g. Palms, *Dracaena*, *Pandanus*) are included as ‘shrub’ or ‘tree’ according to literature.

The results obtained through this procedure were compared to the information obtained through the Naturalis Herbarium Collections database. Results were mostly congruent, validating our procedure. Mismatches between both sources and species with missing habit were finally manually checked and added by using information provided by the African Plant Checklist and Database (Klopper et al. 2007, African Plants Database 2015), the World Checklist of Selected Plant Families (Govaerts et al. 2009) and by checking specimens of such species.

Temporal coverage

Collecting years range from 1782 to 2015.

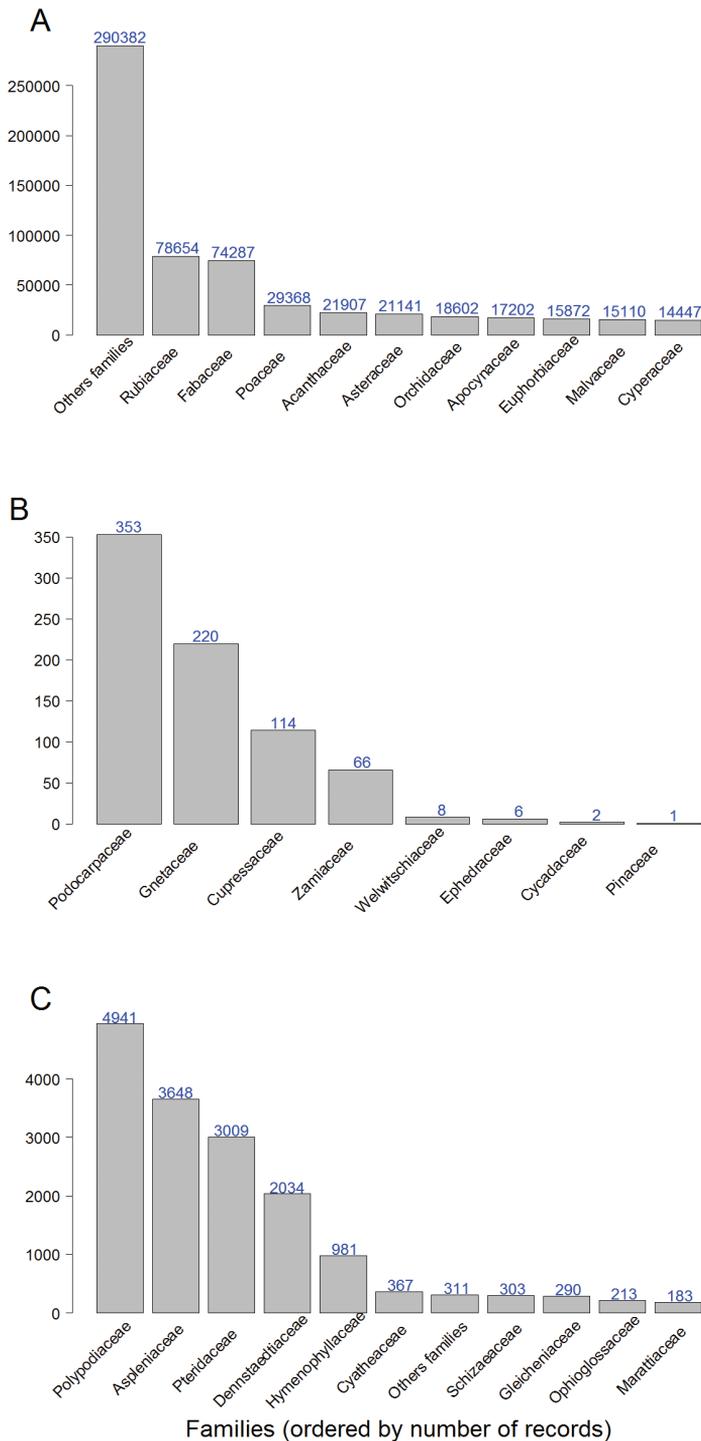


Figure 3. Most represented families (sorted by number of records) for each of the three divisions of vascular plants represented in the RAINBIO database. **A** Magnoliophyta **B** Gymnosperms **C** Pteridophyta.

Description of the thirteen datasets

The thirteen datasets that contributed to the RAINBIO are described below and sorted according to the total number of record provided.

- **Naturalis Herbarium Collections database (WAG, L, U, AMD)**
 Origin: Naturalis Biodiversity Center, Leiden, The Netherlands
 References: Wieringa and Sosef (2011), Oever and Gofferjé (2012); <http://herbarium.naturalis.nl>
 Metadata: <http://vmamapgn-test.mpl.ird.fr/geonetwork/srv/eng/search#|8fa7bdc6-69a6-4ccd-a3c9-ea8a1836ac0e>
 Access date: first extract in 10/2014, followed by an update in 08/2015.
 Type: herbarium specimens
 Query: Africa, excluding some countries (Madagascar & north African countries)
 Number of records included: 519,623
- **Missouri Botanical Garden database (MO)**
 Origin: TROPICOS database, Missouri Botanical Garden, Saint Louis, U.S.A.
 References: <http://www.tropicos.org>
 Metadata: <http://vmamapgn-test.mpl.ird.fr/geonetwork/srv/eng/search#|513617b3-9d01-4c0d-8909-f965ff3eed53>
 Access date: 7/11/2014
 Type: herbarium specimens
 Query: excluding several African countries (South Africa, Madagascar, North African countries). The tag 'is_cultivated' was False.
 Number of records included: 147,520
- **Meise Botanic Garden database (BR)**
 Origin: Botanic Garden Meise, Meise, Belgium
 References:
<http://www.br.fgov.be/RESEARCH/COLLECTIONS/HERBARIUM/advancedsearch.php>
 Metadata: <http://vmamapgn-test.mpl.ird.fr/geonetwork/srv/eng/search#|b5e8416d-d742-4cef-99be-75e646cfb041>
 Access date: October 2014
 Type: herbarium specimens
 Number of records included: 132,771
- **Université Libre de Bruxelles herbarium database (BRLU)**
 Origin: database of the Herbarium of the Université Libre de Bruxelles, Brussels, Belgium
 References: <http://herbarium.ulb.ac.be/>

Metadata: <http://vmamapgn-test.mpl.ird.fr/geonetwork/srv/eng/search#|87177d1b-54f4-4ca2-a7de-a5db91f8b605>

Access date: November 2014

Type: herbarium specimens

Number of records included: 62,380

- **Royal Botanic Gardens, Kew (K)**

Origin: downloaded from gbif.org.

References: <http://www.gbif.org/dataset/cd6e21c8-9e8a-493a-8a76-fbf7862069e5>

Metadata: <http://vmamapgn-test.mpl.ird.fr/geonetwork/srv/eng/search#|ac585ae5-b331-4855-873c-f78a92919f5c>

Access date: 9/12/2014

Type: herbarium specimens

Query: only georeferenced records in African countries

Number of records included: 55,919

- **Collection of African plant samples dried in silica-gel**

Origin: Evolutionary Biology and Ecology Unit, Université Libre de Bruxelles, Brussels, Belgium.

Metadata: <http://vmamapgn-test.mpl.ird.fr/geonetwork/srv/eng/search#|e43766e7-e734-487d-98f4-a45188d99edd>

Access date: November 2014

Type: leaves dried in silica-gel (no voucher)

Number of records included: 14,510

- **Instituto de Investigação Científica Tropical (LISC), University of Lisbon**

Origin: downloaded from gbif.org

References and metadata: <http://www.gbif.org/dataset/231c5bcf-1b56-4905-a398-6d0e18f6de1a>

Access date: 24/7/2015

Type: herbarium specimens

Query: only georeferenced records in African countries

Number of records included: 14,301

- **Occurrences from tree plot data**

Origin: Evolutionary Biology and Ecology Unit, Université Libre de Bruxelles, Brussels, Belgium

References: (Dauby 2012; Dauby et al. 2014)

Metadata: <http://vmamapgn-test.mpl.ird.fr/geonetwork/srv/eng/search#|a7e8a9d5-1cfe-4ee1-a16a-ffa81dd34bf>

Access date: November 2014

Type: Inventory tree data.

Number of records included: 12,874

- **African Palms**

Origin: database collated by Anne Blach-Overgaard

References: (Blach-Overgaard et al. 2010; Blach-Overgaard et al. 2013; Blach-Overgaard et al. 2015)

Metadata: <http://vmamapgn-test.mpl.ird.fr/geonetwork/srv/eng/search#|f20ff0ad-94a5-450f-9ea2-28af706a1b40>

Access date: November 2014

Type: herbarium specimens

Number of records included: 5,567

- **Rubiaceae endemic to Atlantic Central Africa**

Origin: database collated by Bonaventure Sonké and Vincent Droissart

References: (Droissart et al. 2011)

Metadata: <http://vmamapgn-test.mpl.ird.fr/geonetwork/srv/eng/search#|1bd345aa-a9eb-4be9-8cc4-1c5869118105>

Access date: November 2014

Type: herbarium specimens

Number of records included: 4,529

- **Dzanga-Sangha vascular plant database**

Origin: database collated by David J. Harris in the Dzanga-Sangha region (Central African Republic)

References: (Harris 2002)

Metadata: <http://vmamapgn-test.mpl.ird.fr/geonetwork/srv/eng/search#|07425bb4-f412-4961-9ac0-34c3445027f9>

Access date: November 2014

Type: herbarium specimens

Number of records included: 3,571

- **Orchidaceae endemic to Atlantic Central Africa**

Origin: database collated by Vincent Droissart and Tariq Stévant

References: (Droissart 2009; Droissart et al. 2011)

Metadata: <http://vmamapgn-test.mpl.ird.fr/geonetwork/srv/eng/search#|1aea0fd6-f074-4274-878c-38d755a278b4>

Access date: November 2014

Type: herbarium specimens

Number of records included: 2,054

- **African *Berlinia* (Caesalpinioidea)**

Origin: database collated by Barbara Mackinder

References: (Mackinder and Harris 2006, Mackinder and Pennington 2011)

Metadata: <http://vmamapgn-test.mpl.ird.fr/geonetwork/srv/eng/search#|05579478-47d2-421e-94fa-b1476a39a133>

Access date: November 2014

Type: herbarium specimens

Number of records included: 1,596

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Two new non-spiny *Solanum* (Solanaceae) from the Gran Chaco Americano and a key for the herbaceous glandular-pubescent solanums from the region

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Abstract

The Gran Chaco Americano is a major savanna woodland system in South America that harbours great plant and animal diversity. Two new herbaceous species of the Morelloid clade of *Solanum* (largely corresponding to the traditional *Solanum* section *Solanum*) are described here from the Bolivian Chaco. Both species are morphologically similar to a group of related species with glandular pubescence and enlarged, foliaceous calyces that includes *S. atriplicifolium* Gillies ex Nees, *S. nitidibaccatum* Bitter, *S. physalifolium* Rusby, *S. sarrachoides* Sendtn. and *S. tweedianum* Hook. *Solanum woodii* Särkinen & S.Knapp, **sp. nov.** is unusual in the Morelloid clade in having tapering anthers on short filaments, and is superficially similar to the unrelated *S. anomalostemon* S.Knapp & M.Nee from dry forests in Peru. *Solanum michaelis* Särkinen & S.Knapp, **sp. nov.** is distinct in its enlarged calyx with a short tube and long lobes that apparently reflex at fruit maturity. Both new taxa are illustrated, their conservation status assessed, and their distributions mapped. We also provide a key to the glandular-pubescent herbaceous *Solanum* species of the Chaco vegetation to aid in identification of these taxa.

Resumen

El Gran Chaco americano es un ecosistema importante en América del Sur de bosques de sabana que alberga una gran diversidad de plantas y animales. Se describen aquí dos especies nuevas de plantas herbáceas del chaco boliviano pertenecientes al clado Morelloid de *Solanum* (en gran parte correspondiente a la tradicional *Solanum* sección *Solanum*). Ambas especies son morfológicamente similares a un grupo de especies relacionadas, que poseen pubescencia alargada y glandular, además de cálices foliáceos que incluye *S. atriplicifolium* Gillies ex Nees, *S. nitidibaccatum* Bitter, *S. physalifolium* Rusby, *S. sarrachoides* Sendtn.

y *S. tweedianum* Hook. *Solanum woodii* Särkinen & S.Knapp, **sp. nov.** es inusual en el clado Morelloid en poseer anteras cónicas y filamentos cortos, además es superficialmente similar a la no relacionada *S. anomalostemon* S.Knapp & M.Nee de los bosques secos de Perú. *Solanum michaelis* Särkinen & S.Knapp, **sp. nov.** es distinta en el cáliz alargado con un tubo corto y lóbulos largos que aparentemente se doblan hacia atrás en la madurez del fruto. Se presentan aquí ilustraciones de las dos nuevas especies, se evalúa su estado de conservación, y se proporcionan mapas de su distribución. También se proporciona una clave para las especies herbáceas de *Solanum* del Chaco con pubescencia glandular para contribuir a la identificación de estas especies.

Keywords

Bolivia, chaco woodlands, endemism, Morelloid clade, South America, Solanaceae, *Solanum* section *Solanum*

Palabras clave

Bolivia, bosques del chaco, endemismo, clado Moreloide, Sudamerica, Solanaceae, *Solanum* sección *Solanum*

Introduction

Solanum L. is one of the most species-rich vascular plant genera in South America (Jørgensen et al. 2011), where many new species continue to be described (e.g., Anderson et al. 2006; Stern 2014; Stern and Bohs 2010; Knapp 2010 a,b; Farruggia and Bohs 2010; Tepe and Bohs 2009; Tepe et al. 2012; Särkinen et al. 2013a, 2015a, 2015b). Within South America, the tropical Andes represent one of the main centres of species diversity for *Solanum* for both spiny (Leptostemonum clade, see Stern et al. 2011) and non-spiny clades (Weese and Bohs 2007; Särkinen et al. 2013b). Other centres of diversity include dry regions such as the Atacama desert (Regmandra clade, Bennett 2008), and seasonally dry tropical forests including the Gran Chaco Americano (Cyphomandropsis clade, Bohs 2001; Dulcamaroid clade, Knapp 2013; Geminata clade, Knapp 2002, 2008; section *Gonatotrichum*, Stern et al. 2013; section *Erythrotrichum*, Agra 2008).

The Gran Chaco Americano is the most extensive dry forest complex in the Americas and the second largest forested lowland area in South America after the Amazon (Galera and Ramella 1997, Olson et al. 2000). The ecoregion covers 1,100,000 km² in eastern Bolivia (19% of the total area of Gran Chaco) and northern Argentina (46%), all of western Paraguay (34%), and a small portion of Brazil (1%) (Galera and Ramella 1997; Olson et al. 2000). Two sub-regions can be recognized: a) the Dry Chaco where the dominant vegetative structure is xerophytic deciduous forest with multiple layers including a canopy, sub-canopy, shrub and herbaceous layer; and b) the Humid Chaco composed of seasonally flooded plains covered by wetlands and palm tree savannas. Some authors distinguish seasonally dry tropical forests from Chaco vegetation per se (Pennington et al. 2006), but here we are using a more inclusive categorization. The Chaco represents one of the last great undisturbed areas of habitat in South America outside Amazonia, but recent rates of habitat conversion are alarmingly high (Huang et al. 2009; Hoyos et al. 2013; Yanosky 2013). The region is poorly

explored, but rich in diversity that has been shown to be in rapid decline (Periago et al. 2014). Plant collections from the Chaco region are poorly represented relative to other habitats in the relevant countries; for example, of the 17,961 Paraguayan plant specimens held in the collections of the Natural History Museum (BM), only 0.6% are from the Chaco ecoregion. New collections made from the region are of interest not only for documenting the diversity of this under-collected and highly threatened area (see Galera and Ramella 1997, <http://www.worldwildlife.org/ecoregions/nt0210>), but also because novelties are likely to be found.

The Morelloid clade is a group of ca. 75 species most of which are endemic to the tropical Andes (Bohs 2005; Särkinen et al. 2015c). The clade includes five major groups traditionally recognised at the sectional level (sections *Solanum*, *Campanulisolanum* Bitter, *Parasolanum* A.Child pro parte, *Chamasarachidium* Bitter, and *Episarcophyllum* Bitter), which are in the process of re-circumscription based on molecular results (Särkinen et al. 2015c). Section *Solanum* is the largest of these with ca. 52 species and ca. 580 published names and is the only group to occur outside of the Americas. Section *Solanum* is distinguished by its herbaceous or sub-shrubby habit, inflorescences usually positioned along the internodes, small flowers and fruits, and the usual possession of stone cells in the fruits (Bitter 1911), which appear as small, seed-like structures that are usually white and spherical rather than flattened and brown or yellowish brown like the seeds. These stone cells are derived from accretions of sclerenchyma in the mesocarp (Bitter 1911, 1914; Danert 1969). Although some studies have been done to clarify the taxonomy of the Old World and North American species of the Morelloid group (Edmonds 1977, 1978; Schilling 1981), monographic study is needed to aid species identification and to clarify synonymy, especially in Andean South America where most of the species diversity is found (Edmonds 1972; Barboza et al. 2013) and where the Morelloid clade is amongst the most diverse groups of *Solanum*.

Recent taxonomic work focusing on delivering a global monographic treatment of the Morelloid clade has resulted in the description of various new species from the tropical Andes (Särkinen et al. 2013a, 2015a, 2015b). A further two new species are here described based on morphological and preliminary molecular data from Bolivian Chaco woodlands. A total of six species of *Solanum* from the Morelloid clade are now known to occur in the Chaco region, and we provide a key for the identification of similar glandular-pubescent herbaceous non-spiny solanums from the Gran Chaco Americano.

Materials and methods

Descriptions are based on field work and examination of herbarium specimens from K, LPB, MO, and NY (acronyms follow Index Herbariorum; <http://sweetgum.nybg.org/science/ih/>). Many more duplicates of the specimens cited collected by M. Nee and J.R.I. Wood are expected to be found in Bolivian (USZ for Nee, BOLV and USZ for Wood) and other herbaria deposited under *Solanum* sp. or *Solanum phyalidicalyx* Bitter.

Specimens with coordinates were mapped directly and those lacking coordinates were located using Google Earth and gazetteers. Extent of Occurrence (EOO) and Area of Occupancy (AOO) were calculated using GeoCat (www.geocat.kew.org) with a 2 km cell width for AOO calculation. The preliminary conservation status of each species was assessed using the IUCN (2014) criteria based on the GeoCat analyses (Bachman et al. 2011) combined with field knowledge. All specimens are cited in the text, and full data is provided in the Suppl. material 1 and on Solanaceae Source (www.solanaceaesource.org).

Taxonomic treatment

Solanum michaelis Särkinen & S.Knapp, sp. nov.

urn:lsid:ipni.org:names:77158524-1

Fig. 1

Diagnosis. Like *Solanum sarrachoides* Sendtn. and *S. physalifolium* Rusby but differing in having larger anthers 2.5–3.2 mm long, and similar to *Solanum tweedianum* Hook. in having long calyx lobes but differing in having a shorter calyx tube in both flower (0.8–1.3 mm) and fruit (2.0–2.5 mm).

Type. BOLIVIA. Tarija: Prov. Gran Chaco, 44.5 km (by rd) W from upper bridge over Rio Pilcomayo and 17.7 NE of Palos Blancos, on rd from Villa Montes to Palos Blancos, 21°27'S, 63°40'45"W, 815 m, 21 Mar 2007 (fl, fr), *M. Nee & R. Flores S. 54821* (holotype: LPB; isotypes: BM [BM001211859], MO [sheet number 6073914, barcode MO-2113149], NY [NY00853628], UT [UT-126715]; [records indicate that duplicates were sent to CAS, CORD, G, MEXU, NSW, SI, USZ, US, UT, WIS]).

Description. Decumbent to erect subwoody herb to 1 m tall, spreading to up to 2 m in diameter. Stems 3–4 mm in diameter at base, spreading or erect, terete, straw coloured, glabrescent; new growth densely glandular-papillate and pubescent with a mixture of patent, simple, uniseriate eglandular and glandular trichomes, the trichomes of several lengths, 1-celled to 17-celled, 0.2–2 mm long, translucent, if glandular then with a terminal gland (this often breaking off). Sympodial units difoliate, not geminate. Leaves simple, (2.4–)4.0–7.6 cm long, (1.4–)2.3–3.0(–4.0) cm wide, ovate; adaxial surface moderately pubescent with both eglandular and glandular hairs along lamina and veins; abaxial surface more densely pubescent along veins; major veins 3–5 pairs; base truncate to rounded; margins entire to shallowly and unevenly lobed (mostly near the base); apex acute; petiole (0.7–)1.5–2.0 cm long, pubescent with spreading eglandular and glandular hairs like those on the stem. Inflorescences 2.5–3.5 cm long, lateral, internodal to leaf-opposed, simple, racemose, with (6–)7–10(–12) flowers, pubescent with both eglandular and glandular trichomes like those on stem; peduncle 1.4–3.3 cm long; pedicels spaced 0–1 mm apart, 6–10 mm long, ca. 0.2 mm in diameter at base and apex, straight and spreading at anthesis, articulated at the base. Buds ellipsoid, white or purple-tinged, densely pubescent with

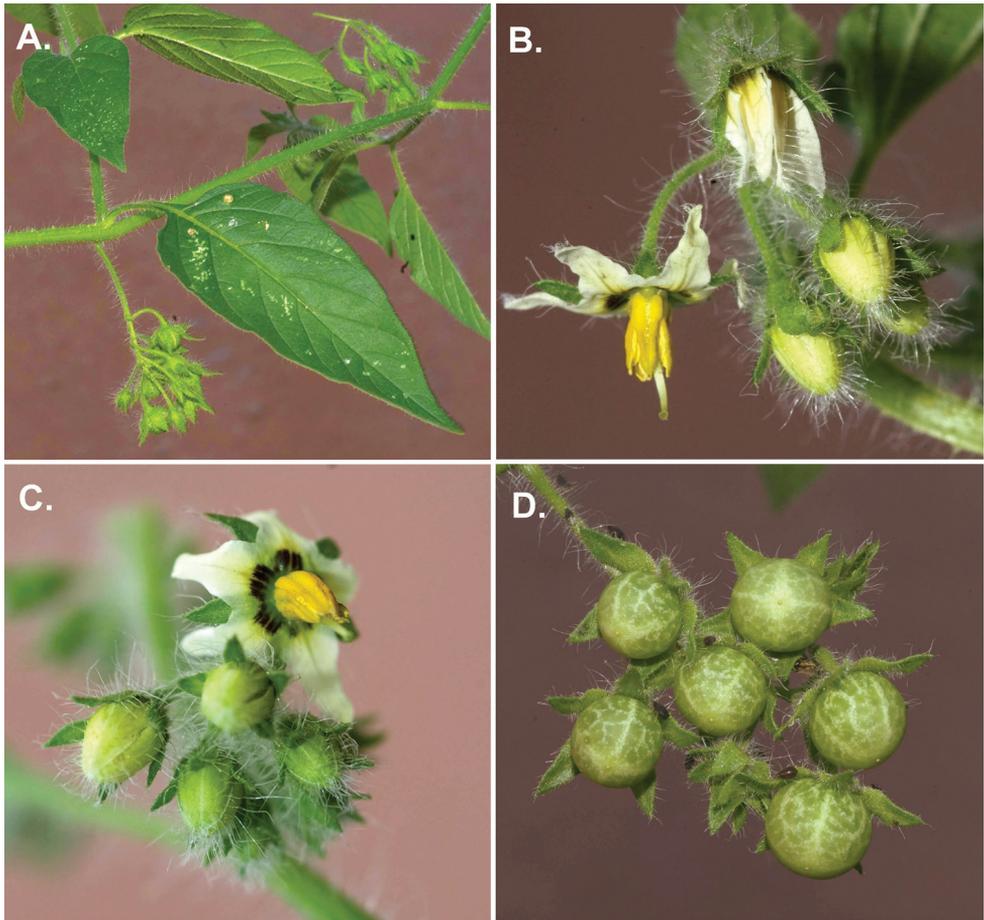


Figure 1. *Solanum michaelis*. **A** Fruiting stem **B** Inflorescence with details of indumentum of simple, multi-cellular eglandular and glandular trichomes along the stem, calyx and corolla **C** Flower at full anthesis with buds **D** Maturing fruit (**A–D** Nee & Flores 54821; photos by Michael Nee).

spreading, multicellular hairs (see under calyx), the corolla not strongly exerted from the calyx, exceeding the calyx lobes by less than $\frac{1}{2}$ of their lengths before anthesis. Flowers 5-merous, all perfect. Calyx tube 0.8–1.3 mm long, the lobes 1.4–3.7 mm long, 0.6–1.0 mm wide, triangular with long-acuminate apices, densely pubescent with both eglandular and glandular trichomes, the eglandular trichomes 1.5–3.5 mm long. Corolla 0.7–1.3 cm in diameter, white with a green-black basal central star, stellate, lobed $\frac{1}{2}$ way to the base, the lobes 2.5–3.2 mm long, 1.5–2.5 mm wide, reflexed at anthesis, later spreading, sparsely pubescent abaxially with multicellular simple spreading eglandular uniseriate trichomes to 0.5 mm long, densely papillate on the tips and margins. Stamens equal; filament tube 0.1–0.25 mm long; free portion of the filaments 0.2–0.3 mm long, adaxially pubescent with tangled eglandular simple uniseriate trichomes; anthers 2.5–3.2 mm long, 0.9–1.1 mm wide, ellipsoid,

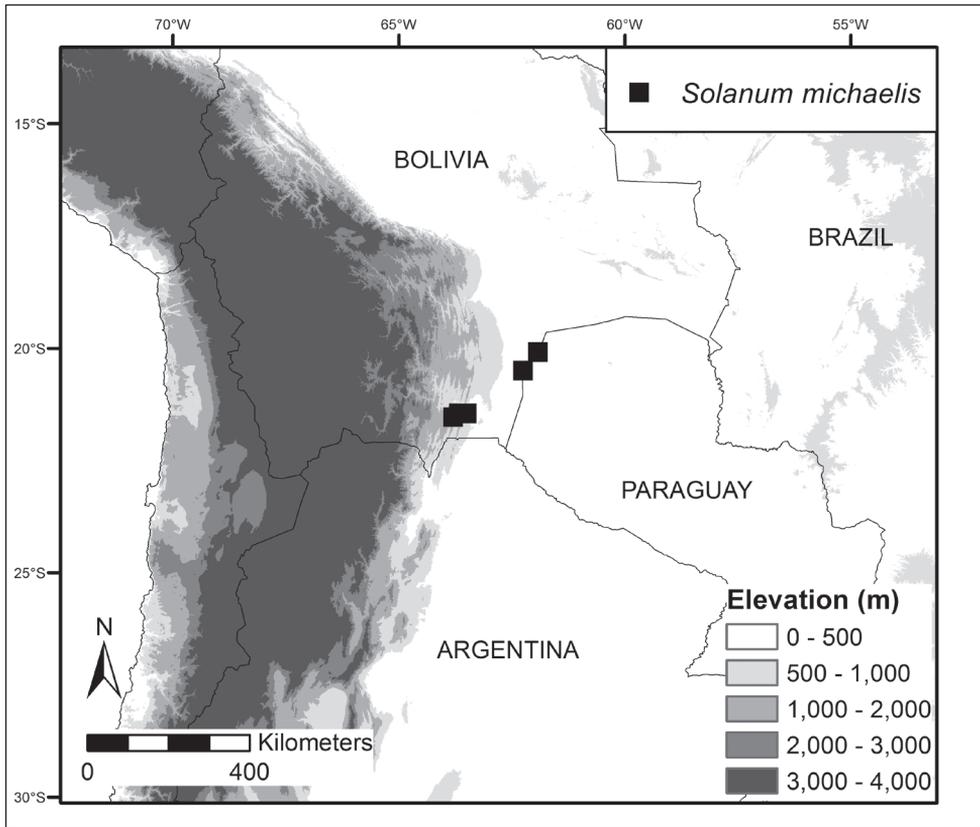


Figure 2. Distribution map of *Solanum michaelis*.

yellow, poricidal at the tips, the pores lengthening to slits with age. Ovary subglobose, glabrous; style 4–5 mm long, exerted 1.5–2.0 mm beyond the anther cone, densely pubescent with 4-celled simple uniseriate trichomes in the basal $\frac{1}{2}$ or $\frac{3}{5}$ where included in the anther cone; stigma capitate, the surface minutely papillate. Fruit a subglobose berry, slightly flattened, 5–12 mm in diameter, green and mottled with white vein-like reticulations (black when ripe fide *Fuentes & Navarro 2607*), the surface of the pericarp shiny; fruiting pedicels 1.6–2.0 mm long, ca. 0.5 mm in diameter at the base, ca. 1.0 mm in diameter at the apex, spaced 1–2 mm apart, strongly recurving, dropping off with the fruit leaving raised pedicels scars to 0.1 mm high; fruiting calyx tube 2.0–2.5 mm long, the lobes 5–8 mm long and 3.0–3.5 mm wide, spreading to reflexed. Seeds 15–25 per berry, 1.7–2.0 mm long, 1.1–1.5 mm wide, tear-drop shaped, pale brown, the surface minutely pitted, the hilum positioned subapically, the testal cells pentagonal in outline. Stone cells absent.

Distribution (Figure 2). Endemic to Bolivia in the Departments of Tarija and Santa Cruz; although the species is to be expected in adjacent Paraguay. *Solanum michaelis* grows in dry Chaco vegetation and in lower inter-Andean valleys, along slopes in sandy soils in mostly unshaded dry creek beds on bare soil, often in areas

that have been burned, or in more humid Chaco vegetation at the edge of “palmares” (stands of *Copernicia alba* Morong) between 300–900 m elevation.

Ecology. Flowering in March and between June and September, fruiting from June to September probably toward the end of the rainy season (Jan-Apr) and then sporadically with occasional rains during the dry season.

Etymology. The species epithet honours Dr Michael Nee, whose collections from Bolivia have provided the much needed material to complete descriptions of many recently published new species within *Solanum*, including the two described here. His collections and taxonomic work over the past 50 years have contributed to the understanding of morphological diversity of *Solanum*. His taxonomic work in the genus has been fundamental in resolving and typifying the 6,967 published names of *Solanum*.

Conservation status. The preliminary IUCN (IUCN 2014) threat status of *S. michaelis* is Endangered (EN) based on the small known extent of the species occurrence (EOO=2,716 km²) as well as the extremely small observed area of occupancy (AOO=20 km²). Although collection densities in the tropical Andes remain low, the very narrow distribution of the new species suggests conservation concern, because *S. michaelis* is likely to be highly vulnerable to grazing pressure and changes in rainfall patterns due to its ephemeral ecology. The Chaco woodlands in Bolivia and Paraguay are highly threatened by land use change due to agricultural expansion and logging (Huang et al. 2009). Two populations of *S. michaelis* are known to occur within the protected area network in Bolivia, one in the Parque Nacional de Gran Chaco Kaa-lyá along the border with Paraguay, and another in the Parque Nacional de Serranía del Aguara-güe.

Additional specimens examined. **BOLIVIA. SANTA CRUZ: Prov. Cordillera**, Parque Nacional Kaa-Iyá del Gran Chaco, hito 27 de noviembre, 20°05'16"S, 61°55'19"W, 320 m, 17 Jul 1998 (fl,fr), *A. Fuentes 2607* (NY); alrededor del pueblo de la Brecha, 22 May 1999 (fl,fr), *R. Chávez de Michel 2677* (LPB, NY); 4 km de Puerto Guaraní, al N frontera Paraguaya, 20°30'S, 62°15'W, 400 m, 19 Jun 1992 (fl,fr), *B. Mostacedo 380* (MO). **TARIJA: Prov. Gran Chaco**, 10 km S de Palmar Grande, camino Yacuiba-Villa Montes, 10 Sep 1977 (fl,fr), *A. Krapovickas 31088* (MO); 2 km N de Palmar Grande, 38 km S de Villa Montes, 21°27'S, 63°30'W, 400 m, 10 Sep 1977 (fl), *A. Krapovickas 31137* (K, MO); 0.5 km E of Chuvère, 21°32'15"S, 63°48'10"W, 870 m, 23 Mar 2007 (fl,fr), *M. Nee 54876* (MO, NY).

Discussion. *Solanum michaelis* differs from the co-occurring and morphologically similar *S. sarrachoides* and the higher elevation yungas species *S. physalifolium* in having larger anthers (2.5–3.2 mm long), while both *S. sarrachoides* and *S. physalifolium* have anthers < 2.2 mm long. *Solanum physalifolium* has similar shiny green-mottled berries, but occurs at higher elevations (1,400–2,900 m) in yungas or wet forest vegetation and has broadly ovate calyx lobes that partially enclose the fruit at maturity. *Solanum tweedianum* has similar sized anthers but a longer calyx tube (ca. 1.5–2.0 mm in flower and to ca. 5 mm or more in fruit) which fully encloses the berry both during development and at fruit maturity (Barboza et al. 2013). *Solanum michaelis* has similarly long calyx lobes but a shorter calyx tube in both flower (0.8–1.3 mm) and fruit (2.0–2.5 mm) that does not enclose the fruit and appears to sometimes have reflexed calyx lobes at fruit maturity (e.g., *Fuentes & Navarro 2607*).

***Solanum woodii* Särkinen & S.Knapp, sp. nov.**

urn:lsid:ipni.org:names:77158525-1

Fig. 3

Diagnosis. Similar to *Solanum tweedianum* Hook., but differing in having shorter calyx lobes in flower (1.2–2.1 mm) and fruit (2.0–3.5 mm) and broadly ovoid anthers, and to *Solanum physalifolium* Rusby but differing in having long-triangular calyx lobes, shorter filaments 0.1–0.4 mm long, and broadly ovoid anthers.

Type. BOLIVIA. **Santa Cruz:** Prov. Valle Grande, pasando el puente Santa Rosa, a 78 km desde Serrano hacia Valle Grande, 18°42.483'S, 64°17.585'W, 1169 m, 4 Apr 2003 (fl, fr), *J.R.I. Wood 19616* (holotype: LPB).

Description. Decumbent, slender annual (fide labels) herb to 30–40 cm. Stems 1.0–5.0 mm in diameter, terete, much branching, pale yellow or greenish beige, glabrescent; new growth densely pubescent with spreading translucent 5–8-celled simple uniseriate glandular trichomes c. 0.5 mm long, some to 1 mm. Sympodial units difoliate, not geminate. Leaves simple, (2.3–)4.5–8.0 cm long, (1.5–)2.2–4.3 cm wide, elliptic to ovate, thin-membranous; adaxial surface moderately pubescent with spreading hairs as on stem evenly spaced along lamina and veins; abaxial surface more densely pubescent along veins; major veins 5–7 pairs; base attenuate to decurrent; margins entire to shallowly and unevenly toothed, the lobes narrow; apex acute; petiole 0.8–4.5 cm long, sparsely pubescent with simple 5–8-celled uniseriate trichomes like those of the stems. Inflorescences 1.5–3.0 cm long, simple, opposite the leaves, with (2–)3–7 flowers, sparsely pubescent with simple 5–8-celled uniseriate trichomes like those of the stems; peduncle 0.9–1.8 cm long, ca. 0.3 mm in diameter at the apex and ca. 0.5 mm in diameter at the base; pedicels spaced 0–1 mm apart, 0.7–1.1 cm long, ca. 0.2 mm in diameter at the base and ca. 0.3 mm in diameter at the apex, straight and spreading at anthesis, articulated at the base. Buds ovoid, white, the corolla strongly exerted from the calyx before anthesis, exceeding the lobes by up to two times their length. Flowers 5-merous, all perfect. Calyx tube 0.6–0.7 mm long, the lobes 1.2–2.1 mm long, 0.8–1.0 mm wide, ovate to elliptic in outline with acute apices, somewhat spreading at anthesis, sparsely pubescent with simple 5–8-celled uniseriate glandular trichomes like those of the stems. Corolla 1.0–1.5 cm in diameter, white with a greenish-purple central star at the base, stellate, lobed to the middle, the lobes 4.0–6.0 mm long, 2.0–3.0 mm wide, reflexed at anthesis, sparsely pubescent abaxially with very short 1–2-celled simple uniseriate glandular trichomes. Stamens equal; filament tube ca. 0.5 mm long; free portion of the filaments 0.1–0.4 mm long, adaxially pubescent with 4–7-celled uniseriate glandular trichomes; anthers (2.5–)3.0–3.8 mm long, 1.2–1.4 mm wide at base, ca. 0.5 mm at tip, tapering and narrowly triangular to triangular in outline, yellow, poricidal at the tips, the pores lengthening to slits with age. Ovary globose, glabrous; style 4.5–5.0 mm long, exerted 1.5–2.0 mm beyond the anther cone, curved at the very tip, densely pubescent with 2–3-celled simple uniseriate trichomes in the basal 1/3 where included in the anther cone; stigma minutely capitate, the surface papillate. Fruit a globose berry, 5–9 mm in diameter, green (immature), the pericarp thick and shiny;



Figure 3. *Solanum woodii*. **A** Flowering stem **B** Inflorescence with details of buds, calyx and corolla **C** Flower at full anthesis (**A–B** Wood 21787; **C** Nee et al. 51967; photos by Gwen Davis).

fruiting pedicels 0.7–1.0 cm long, ca. 0.5 mm in diameter at the base, ca. 0.6 mm in diameter at the apex, spaced 0–1 mm apart, spreading to recurved; fruiting calyx tube ca. 1 mm long, the lobes 2.0–3.5 mm long, spreading to reflexed. Seeds 15–30 per berry, 1.6–2 mm long, 1–1.5 mm wide, flattened, teardrop-shaped with a subapical hilum, yellow, the surface minutely pitted, the testal cells pentagonal in outline with the lateral cell walls elongate and the seeds from mature fruits appearing hairy. Stone cells absent.

Distribution (Figure 4). Endemic to Bolivia in the Departments of Chuquisaca and Santa Cruz, growing in Chaco and Chaco forests of inter-Andean valleys, in dry Chaco woodlands on sandy and clay soils near water sources, rivers and in moist depressions in partial or full shade; between 300–1,800 m elevation.

Ecology. Flowering and fruiting during the wet season from January–April.

Etymology. The species epithet honours John R.I. Wood who has collected extensively in central and eastern Bolivia and mentored numerous young Bolivian botanists. Material collected by John throughout his career has been the basis for the description of many new species, and here we add yet another to that long list.

Conservation status. The preliminary IUCN (IUCN 2014) threat status of *S. woodii* is Vulnerable (VU, B1) based on the small extent of occurrence (EOO=19,656 km²). The area of occupancy is even smaller (AOO=36 km²) and would merit status as endangered (EN), but knowing that collection densities in this part of south-central

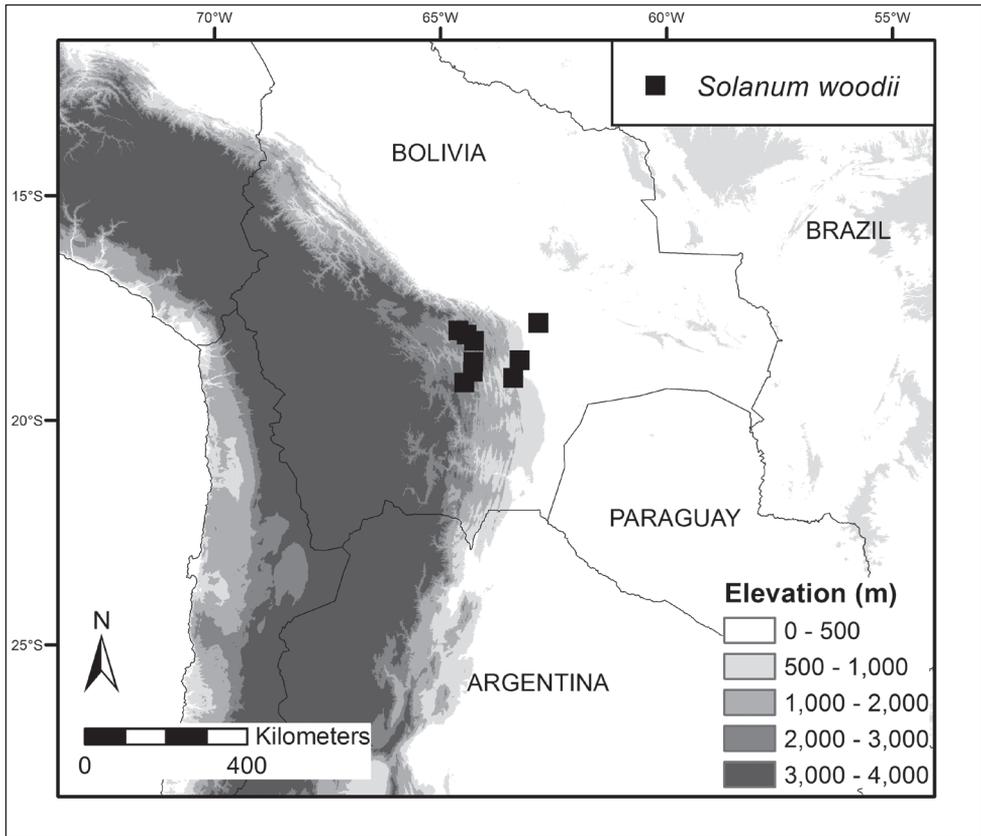


Figure 4. Distribution map of *Solanum woodii*.

Bolivia remain low and that the collections are mainly along the sparse road network, we prefer basing our assessment on the extent rather than area of occurrence. No occurrences are known within protected areas in Bolivia thus far.

Additional specimens examined. BOLIVIA. CHUQUISACA: Prov. Belisario Boeto, bajando de Nuevo Mundo hacia Santa Rosa, en dirección al Río Grande, 18°55'37"S, 64°17'07"W, 1,350 m, 2 Mar 2006 (fl,fr), *J.R.I. Wood 22341* (K). **SANTA CRUZ: Prov. Andrés Ibáñez,** 5–8 km E-SE of Comunidad Don Lorenzo, nr Quebrada Caracoré, on rd to Estancia Caracoré, La Bola area, 17°50'S, 62°50'W, 310 m, 4 Jan 1996 (fl,fr), *M. Nee 46692* (MO, NY). **Prov. Caballero,** El Canal, a 7 km N de Saipina, 18°00'20"S, 64°36'15"W, 1,500 m, 31 Mar 1994 (fl,fr), *J. Balcázar 368* (MO); cerca de Pulquina hacia el Río Mizque, ca. 2 km antes de llegar al primer cruce de río y ca. 1 km de la comunidad Witron, 18°05'57"S, 64°25'52"W, 1,562 m, 20 Feb 2007 (fl,fr), *J.R.I. Wood 22840* (K). **Prov. Cordillera,** along gravel rd eastward, just E of new highway from Santa Cruz to Abapó, the turnoff 3 km N of bridge over Río Seco, 18°63'33"S, 63°23'33"W, 510 m, 19 Apr 1998 (fl), *M. Nee 49056* (MO); floodplain and adjacent upland along the Río Seco, 1.5 km NW of highway at the town of Río Seco along

rd to La Florida, 18°40'S, 63°15'W, 525 m, 24 Mar 2002 (fl), *M. Nee 51967* (MO). **Prov. Vallegrande**, steep slopes of valley of the Río Grande, on rd from Pucará to the new bridge over the Río Grande, 10 km (by winding road) NW of Puente Santa Rosa, 18°70'00"S, 64°28'33"W, 1,500 m, 29 Jan 1994 (fl), *M. Nee 44742* (MO); bajando de Pucará hacia Santa Rosa del Río Grande, 18°14'43"S, 64°16'00"W, 1,787 m, 6 Mar 2005 (fl,fr), *J.R.I. Wood 21787* (K); La Higuera, bajando de Pucará al puente de Santa Rosa, 18°42'06"S, 64°16'23"W, 1,580 m, 18 Feb 2007 (fl,fr), *J.R.I. Wood 22790* (K).

Discussion. *Solanum woodii* is unusual in having tapering, somewhat cone-shaped anthers with a beak-like tip (see Fig. 1C); this character, however, can be difficult to see in older flower with dehisced anthers. Amongst other glandular-viscid herbaceous solanums it could be confused with *S. tweedianum* and *S. physalifolium*. *Solanum woodii* is sympatric with *S. tweedianum* but the latter species has longer calyx lobes in flower (3.5–5(–7) mm) and fruit (>5 mm), and slightly larger ellipsoid anthers (3.0–)4.0–4.5 mm long that are rectangular in outline (equally wide along their entire length) rather than broadest at the base; the calyx of *S. tweedianum* is accrescent and completely covers the berry at maturity, while that of *S. woodii* is spreading and does not become accrescent.

The unusual anther shape in *S. woodii* resembles that of the enigmatic *S. anomalostemon* S.Knapp & M.Nee described from the dry inter-Andean valley of the Rio Apurimac in southern Peru (Knapp and Nee 2009). *Solanum anomalostemon* is morphologically unique within *Solanum* in having cordate anthers, and was thought to belong to the Morelloid clade (Knapp and Nee 2009). Recent molecular phylogenetic evidence, however, showed it belongs to the Mapiriense clade (Särkinen et al. 2015c), along with a small group of species that have similar tapering anthers (see Bohs 2005). Despite the similarity in anther shape, preliminary molecular data suggest *S. woodii* is a member of the Morelloid clade rather than closely related to *S. anomalostemon* and other members of the Mapiriense clade (T. Sarkinen, unpubl. data).

Key to glandular-pubescent herbaceous solanums in Chaco vegetation

- 1 Anthers 0.8–2.1 mm long.....2
- Anthers 2.5–5.0 mm long.....3
- 2 Calyx lobes completely enclosing the corolla in bud; inflorescences with flowers clustered near the tips; leaf base truncate *Solanum sarrachoides*
- Calyx lobes not completely enclosing the corolla in bud; inflorescences with flowers spaced 1–3 mm apart along the rachis; leaf base rounded to cuneate
..... *Solanum nitidibaccatum*
- 3 Anthers 2.5–3.2(–3.8) mm long; calyx (tube and/or lobes) covering 0–20% of the berry in fully mature fruits.....4
- Anthers (3.8–)4.0–5.0 mm long; calyx (tube and/or lobes) covering at least 50% of the berry in fully mature fruits.....5
- 4 Calyx with spreading trichomes 1.5–3.5 mm long; anthers ellipsoid, rectangular in outline; fruiting pedicels spaced (0–)1–2 mm apart.....*Solanum michaelis*

- Calyx with spreading trichomes 0.5–1.0 mm long; anthers conical, triangular in outline; fruiting pedicels spaced 0–1 mm apart..... *Solanum woodii*
- 5 Calyx lobes 2.5–3.0 mm long in flower; fruiting calyx not markedly enlarged and inflated, the calyx tube slightly growing but neither tube nor lobes accrescent; fruit often slightly visible or calyx tube reaching just beyond the top of the berry*Solanum atriplicifolium*
- Calyx lobes 3.5–5(-7) mm long in flower; fruiting calyx markedly enlarged and inflated, both calyx tube and lobes accrescent; fruit fully covered by calyx tube *Solanum tweedianum*

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Supplementary material I

Occurrence records

Authors: Tiina Särkinen, Sandra Knapp

Data type: Excel csv file

Explanation note: Occurrence records of the two new *Solanum* species.

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Taxonomic revision of Neotropical *Murdannia* Royle (Commelinaceae)

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Abstract

This study provides a taxonomic revision for the Neotropical species of the genus *Murdannia*. Six species are recognized as native, including a new species and a new combination, while two Asian species are recognized as invasive. We present an identification key, a table summarizing the morphologic differences among the species, a new synonym, six lectotypifications, a distribution map, and descriptions, comments and photographic plates for each species. We also provide comments on the morphology of the Neotropical species of *Murdannia*, comparing them with the Paleotropical species, and a discussion of inflorescence architecture in the genus as a whole.

Keywords

Aquatic plants, Brazil, Commelinales, Commelineae, dewflower, Neotropical flora, spiderwort

Introduction

Murdannia Royle is one of the largest genera in Commelinaceae, comprising ca. 60 species (Faden 1998; eMonocot 2010; The Plant List 2013; Govaerts and Faden 2016). It was described by Royle (1840), based on *Aneilema scapiflorum* Roxb. [= *M. edulis* (Stokes) Faden], and was named after Murdan Ali, the keeper of the Saharanpur Botanic Garden herbarium at India. Unaware of Royle's name, Brückner (1926) described *Phaeneilema* G.Brückn., and transferred several species from *Aneilema* to his new genus (Brückner 1926, 1927). A few years later, in his treatment for Commelinaceae in Engler's *Natürlichen Pflanzenfamilien*, Brückner (1930) realized that *Phaeneilema* and *Murdannia* were congeneric and made the required combinations. Pichon (1946) pointed out the existence of two names prior to *Murdannia* (i.e. *Dilasia* Raf. and *Streptylis* Raf.), both published by Rafinesque (1838) in his *Flora Telluriana*. Since both names were published in the same work and none had priority over the other, *Dilasia* was adopted by Pichon (1946) as the accepted name. Nevertheless, Brenan (1952), noted that most of the necessary combinations in *Murdannia* had already been made by Brückner (1930). Thus, the author proposed to conserve *Murdannia* against *Dilasia* and *Streptylis*, to avoid the unnecessary creation of about 30 new combinations in the monospecific *Dilasia* (Brückner 1930; Merrill 1937).

Murdannia nom. cons. is currently placed in subfamily Commelinoideae, tribe Commelineae, together with *Aneilema* R.Br., *Buforrestia* C.B.Clarke, *Commelina* L., *Floscopa* Lour., *Pollia* Thunb., and *Stanfieldiella* Brenan, among others (Faden and Hunt 1991; Evans et al. 2003; Burns et al. 2011; Faden 1998). As aforementioned, *Murdannia* species have been historically treated under *Aneilema* by several authors (e.g. Brown 1810; Clarke 1881; Bentham and Hooker 1883; Woodson 1942), and sometimes also under *Commelina*. Nevertheless, *Murdannia* can be easily differentiated from *Aneilema* and *Commelina* by its flowers commonly enantiostylous, petals sessile and equal to subequal, three antesealous stamens (one sometimes staminodial), three antepetalous staminodes, 3-lobed antherodes, capsules always equally 3-locular, and 3-valved (Brenan 1952, 1966; Faden 1998). The genus has a Pantropical and Warm Temperate distribution, being especially diverse in Asia, where most (more than 50%) of the accepted species and morphological diversity are known to occur (Nandikar 2013; Ancy 2014; Ancy and Nampy 2014; Nandikar and Gurav 2015). Most recent studies on *Murdannia* have focused on the Paleotropical species, especially the Asian (e.g. Faden 2001; Nandikar 2013; Ancy 2014; Ancy and Nampy 2014; Nandikar and Gurav 2015) and the African (Faden 2012) members of the genus. Nevertheless, very little is known about the Neotropical species of the genus (Pellegrini et al. 2013). A total of four Neotropical species of *Murdannia* were accepted in the most recent account on the group (Barreto 1997; eMonocot 2010), with the occurrence of *M. schomburgkiana* (Kunth) G.Brückn. in Brazil being considered doubtful. Barreto (1997), in her unpublished Ph.D. thesis and based on the limited material she had available, also considered the *M. gardneri* (Seub.) G.Brückn. species complex to be composed of a sole and widely polymorphic and distributed species. In the most recent checklist

for the Brazilian Flora (BFG 2015), Barreto's taxonomic viewpoints were followed in detail, with the sole addition of *M. nudiflora* (L.) Brenan as an invasive species.

Recent field and herbaria studies have shed some light in this neglected group. As a first attempt to clarify the taxonomy and systematics of Neotropical Commelinaceae, the present study provides a revision of the Neotropical species of *Murdannia*, with the description of a new species (endemic to Central-Western Brazil), and a new combination. We also provide a detailed taxonomic treatment on the group and comments on the morphology and systematics of *Murdannia* as a whole.

Methods

The descriptions and phenology of the species were based on herbaria, spirit, fresh material and literature. Descriptions of *M. engelsii* M.Pell. & Faden, sp. nov., *M. nudiflora* and *M. paraguayensis* (C.B.Clarke ex Chodat) G.Brückn. were complemented, using spirit samples kindly provided by the collectors, and living samples. Specimens from the following herbaria were also analyzed: ALCB, B, BHCB, BHZB, BM, BRIT, C, CEP-EC, CESJ, CNMT, CVRD, ESA, F, FCAB, FLOR, FURB, G, GH, GUA, HAMAB, HAS, HB, HBR, HERBAM, HRB, HSTM, HUEFS, HURB, IAC, ICN, INPA, K, MBM, MBML, MG, MO, MY, NY, P, PORT, R, RB, RFA, RFFP, SP, SPF, TANG, TCD, UEC, UPCB and US (herbaria acronyms according to Thiers, continuously updated). The distribution of the species is based on herbarium materials, field data and literature. The classification of the vegetation patterns follows IBGE (2012). The indumenta and shapes terminology follows Radford et al. (1974); the inflorescence terminology and morphology follows Weberling (1965, 1989) and Panigo et al. (2011); the fruit terminology follows Spjut (1994) and Ancy and Nampy (2014); and seeds terminology follows Faden (1991) and Ancy and Nampy (2014). The conservation statuses were proposed following the recommendations of *IUCN Red List Categories and Criteria, Version 3.1* (IUCN 2001). GeoCAT (Bachman et al., 2011) was used for calculating the Extent of Occurrence (EOO) and the Area of Occurrence (AOO). The generic description of *Murdannia* presented in this work applies only to the Neotropical region, and is not meant to reflect the entire morphological diversity of this widespread and diverse genus.

Results

In the present work, we accept six species native to the Neotropical region, with a new combination and a new species, and recognize two invasive Asian species. We present below descriptions for all native species, detailed diagnosis for the two invasive species, and a table summarizing the morphologic differences between all species found in the Neotropical region (Table 1). We also provide comments on the morphology of the Neotropical species of *Murdannia*, comparing them with the Paleotropical species, and a discussion of inflorescence architecture in the genus as a whole.

Table 1. Morphologic characters differentiating the species of *Mundannia* known for the Neotropical region.

Characters	<i>M. burchellii</i>	<i>M. engelstii</i>	<i>M. gardneri</i>	<i>M. nudiflora</i>	<i>M. paraguayensis</i>	<i>M. schomburgkiana</i>	<i>M. semifoliata</i>	<i>M. aff. triquetra</i>
Phyllotaxy	Spirally-alternate	Distichously-alternate	Spirally-alternate	Distichously-alternate	Spirally-alternate, sometimes becoming distichously-alternate at apex	Spirally-alternate	Spirally-alternate	Spirally-alternate
Inflorescence	Terminal or axillary in the uppermost nodes; pedunculate	Terminal or axillary in the uppermost nodes; pedunculate	Terminal or axillary in the uppermost nodes; pedunculate	Terminal or axillary in the uppermost nodes; pedunculate	Terminal or axillary in the uppermost nodes; pedunculate	Mainly axillary; sessile	Mainly axillary; sessile	Mainly axillary; sessile
Cincinnus bracts	Cup-shaped, apex caudate	Flat, apex acute	Cup-shaped, apex acuminate	Cup-shaped, apex acute	Flat, apex acute	Tubular, apex truncate	Tubular, apex truncate	Not observed
Cincinnati	(1–)2–16, alternate to sub-opposite, 2–9-flowered	1, solitary, 2–7-flowered	16–38, verticillate, 2–11-flowered	1, solitary, 2–12-flowered	9–24, verticillate, 1-flowered	1–2–(3), fascicle-like, 1-flowered	1–2–(3), fascicle-like, 1-flowered	1–2–(3), fascicle-like, 1-flowered
Floral buds	Narrowly ovoid to ovoid	Ovoid	Narrowly ovoid to ovoid	Ellipsoid to oblongoid	Narrowly ovoid	Ellipsoid	Ellipsoid	Ellipsoid
Flower symmetry	Enantiosylous	Enantiosylous	Enantiosylous	Zygomorphic	Enantiosylous	Actinomorphic	Actinomorphic	Actinomorphic?
Petals pubescence	Glabrous	With minute glandular hairs at base on the adaxial surface	Glabrous	Glabrous	With minute glandular hairs at base on the adaxial surface	Densely bearded with moniliform hairs on the adaxial surface	Densely bearded with moniliform hairs on the adaxial surface	Glabrous
Filaments pubescence	Glabrous	With glandular hairs	Glabrous	Bearded with moniliform hairs	With glandular hairs	Bearded with moniliform hairs	Bearded with moniliform hairs	Not observed
Anthers	Narrowly elliptic to narrowly oblong, connective lilac, anthers sacs white	Elliptic, connective white to lilac, anthers sacs white to light-lilac	Elliptic, connective lilac to white, anthers sacs white to lilac	Elliptic to oblong, connective bluish-lilac to white, anthers sacs purple to dark-purple	Elliptic to oblong, connective purple to bluish-purple, anthers sacs lilac to purple	Elliptic to oblong, connective brown, anthers sacs brownish-lilac	Linear-oblong to oblong, connective purple, anthers sacs lilac to purple	Not observed
Antherodes	Sagittate, golden yellow	Subsagittate to subcordate, golden-yellow	Cordate, golden yellow	Hastrate, white to cream	Sagittate, golden yellow	Hastrate, golden yellow	Hastrate, golden yellow	Not observed

Characters	<i>M. burchellii</i>	<i>M. engelii</i>	<i>M. gardneri</i>	<i>M. nudiflora</i>	<i>M. paraguayensis</i>	<i>M. schomburgkiana</i>	<i>M. semifoliata</i>	<i>M. aff. triquetra</i>
Gynoecium pubescence	Glabrous	With glandular hairs	Glabrous	Glabrous	With glandular hairs	Glabrous	Glabrous	Glabrous
Fruiting pedicel	Erect	Deflexed	Erect	Erect	Deflexed	Erect	Erect	Apparently erect
Capsules	Subglobose to globose	Broadly ovoid to broadly ellipsoid	Subglobose to globose	Ovoid to subglobose	Oblongoid to broadly oblongoid	Oblongoid to broadly oblongoid	Oblongoid to broadly oblongoid	Oblongoid to ellipsoid
Seeds	1 per locule, reniform to broadly ellipsoid, ventri-lateral appendage present	1 per locule, reniform to broadly ellipsoid, ventri-lateral appendage present	1 per locule, reniform to broadly ellipsoid, ventri-lateral appendage present	2 per locule, broadly ellipsoid to oblongoid, ventri-lateral appendage absent	2 per locule, reniform to broadly ellipsoid, ventri-lateral appendage present	6 per locule, cuboid to polygonal, ventri-lateral appendage absent	6 per locule, cuboid to polygonal, ventri-lateral appendage absent	3 per locule, transversely ellipsoid, ventri-lateral appendage absent

***Murdannia* Royle, Ill. Bot. Himal. Mts. 1: 403, pl. 95, f. 3. 1839.**

Aphylax Salisb., Trans. Hort. Soc. London 1: 271. 1812, nom. nud. Type species. *Aphylax spiralis* (L.) Salisb. [≡ *Murdannia spirata* (L.) G.Brückn.].

Baoulia A.Chev., Bull. Soc. Bot. France 58 (8): 217. 1912. Type species. *Baoulia tenuissima* A.Chev. [≡ *M. tenuissima* (A.Chev.) Brenan].

Dichaespermum Wight, Icon. Pl. Ind. Orient. 6: 31. 1853. Type species (designated here). *Dichaespermum lanceolatum* Wight [≡ *M. lanceolata* (Wight) Kammathy].

Dilasia Raf., Fl. Tellur. 4: 122. 1838, nom. rej. Type species. *Dilasia vaginata* (L.) Raf. [≡ *M. vaginata* (L.) G.Brückn.].

Ditelesia Raf., Fl. Tellur. 3: 69. 1837 nom. rej. Type species. *Ditelesia nudiflora* (L.) Raf. [≡ *Murdannia nudiflora* (L.) Brenan].

Phaeneilema G.Brückn., Bot. Jahrb. Syst. Beibl. 137: 63. 1926, nom. illeg. Type species. *Phaeneilema sinicum* (Ker Gawl.) G.Brückn. [= *M. simplex* (Vahl) Brenan]

Prionostachys Hassk., Flora 49: 212. 1866. Type species (designated here). *Prionostachys ensifolia* Hassk. ex C.B. Clarke [= *M. gigantea* (Vahl) G.Brückn.].

Streptylis Raf., Fl. Tellur. 4: 122. 1838, nom. rej. Type species. *Streptylis bracteolata* Raf. [= *M. spirata* (L.) G.Brückn.].

Talipulia Raf., Fl. Tellur. 2: 17. 1837, nom. rej. Type species. *Talipulia malabarica* (L.) Raf. [= *Murdannia nudiflora* (L.) Brenan].

Type species. *Murdannia scapiflora* (Roxb.) Royle [= *Murdannia edulis* (Stokes) Faden].

Description. *Herbs*, perennial or annual, rhizomatous or not, with a definite or indefinite base, terrestrial to paludal to rooted emergent aquatics. *Roots* thin and fibrous or tuberous and fusiform. *Rhizomes* short to elongate. *Stems* trailing and ascending at the apex or erect, unbranched to densely branched, rooting in the rhizome and at the basal nodes, rarely at the distal ones when they touch the substrate. *Leaves* sessile; distichously or spirally-alternate, congested at the apex of the stem or evenly distributed along the stem; lamina flat to slightly falcate to falcate and/or conduplicate, base symmetrical, midvein inconspicuous to conspicuous, adaxially impressed or not, abaxially prominent or not, secondary veins conspicuous to inconspicuous. *Synflorescence* composed of a solitary main florescence or with 1–several cöfloreences. *Main florescences (inflorescences)* terminal or axillary in the in the uppermost nodes, not perforating the leaf-sheaths; main florescence a thyrses, composed of 1–many cincinni; basal bract reduced to leaf-like; peduncle bracts (sterile bracts) absent; cincinni bracts persistent; cincinni, sessile to pedunculate, contracted to elongate, bracteoles flat or tubular, persistent or caducous. *Flowers* bisexual or male (the male ones with a reduced gynoeceum), actinomorphic, zygomorphic or enantiostylous, chasmogamous, flat (not tubular); pedicels erect at anthesis and pre-anthesis, erect or deflexed at post-anthesis; sepals 3, equal, free, cucullate, membranous to chartaceous, dorsally not keeled, margins hyaline, accrescent and persistent in fruit; petals 3, sessile, equal to subequal, free, deliquescent, glabrous or with minute glandular hairs at base or medially bearded with moniliform hairs on the adaxial surface; stamens (2–)3, equal, antesepalous,

filaments bent ca. 30° either to the left or to the right, free, glabrous or with minute glandular hairs or medially bearded with moniliform hairs, anthers dorsifixed, rimose, connective narrow, anther sacs parallel, elongate; staminodes 3–(4), antepetalous (if 4 staminodes are present, than 1 antesealous to the lower sepal), filaments free, glabrous, minutely glandular-puberulous basally or medially bearded with moniliform hairs, antherodes dorsifixed, 3-lobed, indehiscent, connective expanded, golden yellow or mauve to purple; ovary sessile, bent ca. 30° on the opposite direction as the stamens, smooth, glabrous or glandular-puberulous, 3-locular, locules equal, locule 1–2–(6)-ovulate, style erect or gently curved at the apex, stigma truncate to capitate, papillate. *Capsules* loculicidal, 3-valved, apiculate due to persistent style base, smooth, glabrous or glandular-puberulous. *Seeds* exarillate, farinose, uniseriate, 1–2–(6) per locule, reniform to broadly ellipsoid or cuboid to polygonal, slightly to strongly cleft towards the embryotega, ventrally flattened or not, testa costate to slightly rugose or shallowly scrobiculate to scrobiculate to foveolate, with ridges radiating from the embryotega, appendaged or not, hilum elliptic or linear, embryotega lateral to semilateral or semidorsal.

Ecology and habitat. As with most aquatic plants, Neotropical *Murdannia* are seldom collected throughout their distribution range. Despite that, they seem to be locally common or uncommon, depending on the species. They all seem to be intimately related to permanent and seasonal water bodies of drier domains and vegetation, such as flooded grasslands in the Cerrado, Chaco and Pantanal domains, or the white sand formations in the Amazon basin.

Morphological relationships among the Neotropical species and within the genus. *Murdannia* is one of the six (i.e. *Aneilema*, *Buforrestia*, *Commelina*, *Floscopa* and *Pollia*) out of 41 genera of Commelinaceae distributed in the Neotropics and Palearctics. (Faden 1998). Although few in number, the Neotropical species of *Murdannia* exhibit all the extremes in inflorescence morphology found in *Murdannia* as a whole. The terminal thyrses consisting of well-spaced whorls of cincinni, present in *M. gardneri* and *M. paraguayensis*, is elsewhere present only in the rare Central African *M. allardii* (De Wild.) Brenan, and in the Asian species *M. divergens* (C.B. Clarke) G.Brückn, and *M. juncooides* (Wight) R.S.Rao & Kammathy (Ancy 2014; Faden & Pellegrini pers. obs.). Glandular-pubescent sepals and pedicels, present in *M. burchellii* (C.B. Clarke) M.Pell., comb. et stat. nov., *M. englesii*, *M. gardneri*, and *M. paraguayensis*, are otherwise known only from the Asian species *M. medica* (Lour.) D.Y.Hong (usually present) and *M. spectabilis* (Kurz) Faden. Moniliform hairs on the upper surface of the petals, present in *M. schomburgkiana* (Kunth) G.Brückn. and *M. semifoliata* (C.B. Clarke) G.Brückn., are recorded only in the Asian and African *M. simplex* (Vahl) Brenan. One-seeded capsule locules, which characterize *M. burchellii*, *M. englesii* and *M. gardneri*, are known only in the Asian/Malaysian *M. vaginata* (L.) G.Brückn., and in the Indian *M. assamica* Nampy & A.Ancy (Ancy and Nampy 2014). Finally, characters present in one or more Neotropical species that are not recorded elsewhere in the genus, include: (1) inflorescences with whorls of 1-flowered cincinni (present in *M. paraguayensis*); (2) the presence of glandular hairs on the inflorescence axis, cincinnus peduncles and axes

(present in *M. burchellii*, *M. englesii*, *M. gardneri*, and *M. paraguayensis*); (3) petals with minute glandular hairs at base on the adaxial surface (present in *M. englesii* and *M. paraguayensis*); (4) the presence of glandular hairs on the filaments, ovaries and capsules (present in *M. englesii* and *M. paraguayensis*); (5) long moniliform hairs on the petals and not confined to the petal bases (present in *M. schomburgkiana* and *M. semifoliata*); and (6) appendages on the seeds (present in *M. burchellii*, *M. englesii*, *M. gardneri* and *M. paraguayensis*).

Inflorescence architecture in *Murdannia*. Brenan (1966) has shown a great diversity of inflorescence architecture in *Murdannia*, with variations in the position of the main florescence, total number of cincinni, number of nodes with cincinni, number of cincinni per node, and degree of development of each cincinnus. According to Panigo et al. (2011), the basic inflorescence pattern for Commelinaceae is a many-branched, pedunculate and terminal thyrse, with verticillate cincinni, each cincinnus multi-flowered. Based on Brenan (1966) and Panigo et al. (2011), we could also infer that the plesiomorphic inflorescence architecture for *Murdannia* would correspond to the basic inflorescence pattern for Commelinaceae. Brenan (1966) indicates that most of the variation in inflorescence architecture could be derived from this basic type, as exemplified by the Asian *M. divergens*, by only three changes. On the other hand, Panigo et al. (2011) states that additional changes would be necessary to express all the known variation in the inflorescence morphology for *Murdannia*, as: (1) the production of cophlorescences, in addition to the main florescence; (2) variation in the length of the peduncle and internodes of the main florescence; (3) variation in the number of cincinni per node; (4) variation in the arrangement of cincinni on each node of the main florescence; (5) variation in the length of the cincinnus peduncle; and (6) variation in the total flower number per cincinnus. These changes can occur separately or in different combinations. In the most extreme cases, the inflorescences are mainly axillary, each being fascicle-like, and composed of a few 1-flowered cincinni.

If we were to consider this stepwise change a possible evolutionary sequence within *Murdannia*, then the South American species with the most plesiomorphic inflorescence type would be *M. gardneri*. By its reduced number of cincinni per node and change in their arrangement, the inflorescence of *M. burchellii* could be morphologically derived from *M. gardneri*. *Murdannia paraguayensis*, shares the numerous verticillate cincinni of *M. gardneri*, but each cincinnus is reduced to a single flower. *Murdannia englesii* has terminal or terminal and axillary inflorescences, that are reduced to single cincinni, but the cincinnus is 2–several-flowered. The most reduced inflorescences, and perhaps the ones that accumulated the greatest number of stepwise changes, can be observed in *M. schomburgkiana* and *M. semifoliata*, in which most inflorescences are fascicle-like, axillary in the distal leaves, and with all cincinni 1-flowered. Species with similarly reduced inflorescences are numerous in Asia [e.g. *M. blumei* (Hassk.) Brenan, *M. crocea* (Griff.) Faden, *M. keisak* (Hassk.) Hand.-Mazz., *M. lanuginosa* (Wall. ex C.B. Clarke) G.Brückn., *M. pauciflora* (Wight) G.Brückn., *M. triquetra* (Wall. ex C.B. Clarke) G.Brückn., and *M. versicolor* (Dalzell) G.Brückn.], and represented in

Africa by *M. axillaris* Brenan (Faden 2012; Ancy 2014). Nonetheless, some of them show characters not present in any of the Neotropical species, such as annual habit, biseriate seeds and yellow to orange flowers. Thus, in the absence of a well sampled molecular phylogeny it would be impossible to state whether the Neotropical species represent one or several distinct lineages in *Murdannia*.

Key to the native and invasive species of *Murdannia* in the Neotropics

- 1 Inflorescences composed of 2–several verticillate or alternate to subopposite cincinni, rarely composed of a solitary cincinnus, bracteoles persistent; flowers enantiostylous, sepals with glandular hairs or with a mixture of glandular and eglandular hairs, androecium glabrous or with minute glandular hairs; seeds with a ventri-lateral appendage..... **2**
- Inflorescences composed of a solitary cincinnus or fascicle-like, bracteoles caducous; flowers non-enantiostylous, sepals glabrous, androecium medially bearded with moniliform hairs; seeds without a ventri-lateral appendage **5**
- 2 Bracteoles cup-shaped; pedicels erect at post-anthesis and in fruit; petals glabrous, filaments, ovaries and capsules glabrous; hilum in a deep depression..... **3**
- Bracteoles flat; pedicels deflexed at post-anthesis and in fruit; petals with minute glandular hairs at base on the adaxial surface, filaments, ovaries and capsules with glandular hairs; hilum in a shallow depression **4**
- 3 Cincinni alternate, rarely subopposite, sinuate; plants generally delicate; stems prostrate, thin, densely branched at the base; leaves chartaceous, linear to linear-oblong; main axis of inflorescence with sparse eglandular and glandular hairs; cincinnus bracts with caudate apex; seeds densely farinose, the testa costate to slightly rugose ... ***M. burchellii* (C.B.Clarke) M.Pell.** (Fig. 1)
- Cincinni verticillate, straight; plants generally robust; stems ascending to erect, succulent, little branched at base to unbranched; leaves succulent, linear-lanceolate to lanceolate; main axis of inflorescence with dense glandular and sparse eglandular hairs; cincinnus bracts with acuminate apex; seeds farinose, the testa scrobiculate to foveolate ***M. gardneri* (C.B.Clarke) G.Brückn.** (Figs 3–4)
- 4 Inflorescence reduced to a solitary cincinnus (but sometimes several clustered in a synflorescence near towards the shoot apex), peduncles with a mixture of eglandular (scabrid) and glandular to densely glandular hairs, cincinni 2–7-flowered; plants without a definite base; leaves distichously-alternate; flowers buds ovoid; capsules broadly ovoid to broadly ellipsoid, locules 1-seeded..... ***M. engelsii* M.Pell. & Faden** (Fig. 2)
- Inflorescence a terminal thyrse composed of several whorls of 1-flowered cincinni, peduncles with glandular to densely glandular hairs, cincinni 1-flowered; plants with a definite base; leaves spirally-alternate; flower buds ellipsoid to narrowly ellipsoid; capsules oblongoid to broadly oblongoid, locules 2-seeded..... ***M. paraguayensis* (C.B.Clarke ex Chodat) G.Brückn.** (Fig. 6)

- 5 Leaves distichously-alternate; inflorescences long-pedunculate, exerted from the leaf-sheaths, cincinni 2–12-flowered, pendent; flowers zygomorphic, stamens 2, staminodes 4 (1 staminode antesealous, sometimes lacking the antherode), antherodes white to cream; capsules ovoid to subglobose.....
.....*M. nudiflora* (L.) Brenan (Fig. 5)
- Leaves spirally-alternate; inflorescences sessile, enclosed by the leaf-sheaths; cincinni 1-flowered, erect; flowers actinomorphic, stamens 3, staminodes 3, antherodes yellow (flowers uncertain in *M. aff. triquetra*); capsules oblongoid to ellipsoid..... **6**
- 6 Annuals without a definite base; roots thin; stems trailing, apex ascending, densely branched; petals glabrous; capsules with 3-seeded locules; seeds transversely ellipsoid ... *M. aff. triquetra* (Wall. ex C.B. Clarke) G.Brückn. (Fig. 9)
- Perennials with a definite base; roots tuberous; stems erect (only the short rhizome prostrate), unbranched; petals medially bearded with moniliform hairs on the adaxial surface; capsules with 6-seeded locules; seeds cuboid to polygonal..... **7**
- 7 Leaf-blades margins glabrous throughout, inflorescences-bearing leaves with expanded blades (2.2–13.6 cm long); anthers brown
.....*M. schomburgkiana* (Kunth) G.Brückn. (Fig. 7)
- Leaf-blades margins ciliate at least at base, inflorescences-bearing leaves reduced to bladeless sheaths or with much reduced blades (0.2–1.8 cm long); anthers purple.....*M. semifoliata* (C.B. Clarke) G.Brückn. (Fig. 8)

1. *Murdannia burchellii* (C.B. Clarke) M. Pell., comb. et stat. nov.

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Figs 1, 10

Aneilema gardneri var. *burchellii* C.B. Clarke, Monogr. Phan. 3: 217. 1881. Lectotype (designated here): BRAZIL. s.loc., fl., fr., s.dat., W.J. Burchell 8165 (K barcode K000363240!; isolectotypes: GH barcode GH00415446!, P barcode P02088020!).

Aneilema gardneri var. *glabrior* C.B. Clarke, Monogr. Phan. 3: 217. 1881. Lectotype (designated here): BRAZIL. Goyaz, fl., fr., 1841, G. Gardner 4020 (P barcode P02088023!; isolectotypes: BM not found, G barcode G00098263!, NY barcode NY00247402!). **Syn. nov.**

Description. *Herbs* ca. 14.0–55.0 cm tall., perennial, rhizomatous with a definite base, terrestrial to paludal to rooted emergent in flooded fields. *Roots* thin, fibrous, brown to dark-brown, densely to sparsely pilose with medium to dark brown hairs, emerging from the rhizome and from the basal most nodes. *Rhizomes* short, light to medium brown, buried in the sand or ground. *Stems* trailing with ascending apex, thin, densely branched or branched only at the base; internodes 1.8–8.4 cm long, green to vinaceous to reddish brown, sparsely pilose to hispid with hyaline hairs, becoming glabrous with



Figure 1. *Murdannia burchellii* (C.B. Clarke) M. Pell. Lectotype of *Aneilema gardneri* var. *burchellii* (K barcode K000363240). Photograph courtesy of Royal Botanic Gardens, Kew, London.

age, with a line of eglandular hyaline hairs opposite the leaf above. *Leaves* spirally-alternate, evenly distributed along the stems, the distal ones gradually smaller than the proximal ones; sheaths 0.3–1.3 cm long, vinaceous to reddish brown, sparsely pilose to hispid with hyaline hairs, becoming glabrous with age, hairs hyaline, margins setose, with a line of eglandular hairs opposite to the leaf above; lamina 2.7–13 × 0.3–0.6 cm, linear to linear oblong, membranous, conduplicate, slightly falcate, light green to greyish green on both sides, drying light brown to olive-green on both sides, sparsely pilose to hispid, becoming glabrous with age, rarely glabrous, base truncate, margins green, ciliate to setose throughout or only at base, apex acuminate to mucronate; midvein conspicuous, impressed adaxially, prominently acute abaxially, secondary veins 2–(3) pairs, adaxially inconspicuous to slightly conspicuous, dark green, abaxially somewhat conspicuous, dark green. *Inflorescences* 1–2–(4) thyrsi, terminal or axillary in the uppermost nodes, thyrses with (1–)2–16, alternate to subopposite cincinni; peduncles 2.3–7.6 cm, with a sparse mixture of eglandular (scabrid) and glandular, hyaline hairs; basal bract reduced or leaf-like, 1.4–5.1 × 0.1–0.3 cm, lanceolate to linear, sparsely pilose to hispid, rarely glabrous, base truncate, margins ciliate to setose, apex acuminate, veins inconspicuous, concolorous or green; cincinni bracts ca. 0.2–1.1 × 0.1–0.4 cm, triangular to broadly triangular, cup-shaped, light green to lilac, glabrous to pilose at base, base amplexicaul, non-perfoliate, margins glabrous to sparsely ciliate, apex caudate; cincinni 2–9-flowered, erect, sinuate, cincinnus peduncle 0.4–2.2 cm, green to vinaceous to purple, with a mixture of sparse eglandular (scabrid) and sparse or more numerous glandular, hyaline hairs, cincinnus internodes 0.2–1.1 cm long, green to vinaceous to purple, with a mixture of sparse eglandular (scabrid) and sparse or more numerous glandular, hyaline hairs; bracteoles ca. 1.8–3.7 × 0.9–1 mm, persistent, triangular to broadly triangular, cup-shaped, light green to lilac, glabrous to sparsely pilose, base amplexicaul, non-perfoliate, margins glabrous or rarely sparsely ciliate, apex acuminate. *Flowers* bisexual or male, enantiostylous, ca. 0.5–1.2 cm diameter; floral buds narrowly ovoid to ovoid, 2.1–4 × 1–2 mm, green to lilac; pedicels 0.3–1 cm long, green to vinaceous to purple, with a mixture of sparse eglandular (scabrid) and sparse or more numerous glandular, hyaline hairs, erect and elongate in fruit; sepals 3.2–5 × 1.5–2 mm, triangular to ovate-triangular, cucullate, green, glandular to densely glandular, hyaline hairs, apex acuminate, margins hyaline light green to hyaline lilac; petals equal, 4–6.3 × 3–4.2 mm, obovate to narrowly obovate, slightly cucullate, pale lilac to lilac to pink, rarely white, glabrous, base cuneate, margins entire, apex obtuse to rounded; stamens 3, equal, filaments glabrous, gently curved at the apex, 3.8–5.2 mm long, pale lilac to lilac or white, anthers narrowly elliptic to narrowly oblong, 0.8–1.0 × 0.3–0.7 mm, connective lilac, anthers sacs white, pollen white; staminodes 3, equal, filaments glabrous, straight, 1.6–2.1 mm long, pale lilac to white, antherodes sagittate, 0.8–0.9 × 0.9–1.0 mm, connective golden yellow, lobes conspicuous, cream-colored to pale yellow; ovary ellipsoid to oblongoid, 0.9–1.8 × 0.6–0.8 mm, 3-locular, white to light green, smooth, glabrous, style gently curved at the apex, ca. 1.8–3.6 mm, pale lilac to lilac or white, stigma truncate, white to lilac. *Capsules* 2.8–4.4 × 3–4.8 mm, subglobose to globose, apiculate due to persistent style, 3-locular, 3-valved, light

brown when mature, glabrous, smooth. *Seeds* 1 per locule, 1.9–2.8 × 1.3–2.1 mm, reniform to broadly ellipsoid, cleft towards the embryotega, ventrally flattened, testa dark brown to greyish brown, densely farinose, costate to slightly rugose, with ridges radiating from the embryotega, with a tan appendage that extends ventri-laterally to the embryotega and basally into the hilum; embryotega semilateral, relatively inconspicuous, generally covered by a cream farina, without a prominent apicule; hilum linear, approximately the same length as the seed, in a deep depression.

Specimens seen. **BOLIVIA. Santa Cruz:** San Ignacio de Velasco, 30 km acia S, 12 Apr 1988, B. Bruderreck 310 (LPB, US). **BRAZIL. Goiás:** Provincia Goyaz, Salinas, May–Jul 1844, M.A. Weddell 2103 (P); loc. cit., May–Jul 1844, M.A. Weddell 2106 (P); s.loc., 1841, G. Gardner 3481 (K); Colinas do Sul, Vila Borba, 15 Jun 1993, G. Hatschbach et al. 59587 (MBM, MO, USU); Formoso, arredores de Formoso, 3 May 2012, R.J.V. Alves 8898 (R); Paraíso, ca. 27 km sul de Paraíso, 23 Mar 1968, H.S. Irwin et al. 21659 (K, NY, UB); loc. cit., 23 Mar 1968, H.S. Irwin et al. 21717 (NY, UB); **Maranhão:** Carolina, 1 Jun 1950, J.M. Pires & G.A. Black 2564 (UFMA, US); **Pará:** Ilha do Marajó, 15 Aug 1901, fl. fr., M. Guedes 2314 (BM); Serra do Cachimbo, Jun 1955, M. Alvarenga s.n. (RB 90541); loc. cit., 12 Dec 1956, J.M. Pires et al. 6104 (NY, UFMA); Itaituba, arredores da base aérea do Cachimbo, 25 Apr 1983, M.N. Silva et al. 90 (INPA, K, MG, NY, US); loc. cit., 26 Apr 1983, M.N. Silva et al. 118 (INPA, MG, NY, US); **Piauí:** Piauíhy, Parnaguá, marshy places, Aug–Sep 1839, fl., fr., G. Gardner 2743 (BM, K); **Tocantins:** Araguaina, 20 km ao Sul, 26 Mar 1976, G. Hatschbach & R. Kummrow 38378 (MBM, US). **VENEZUELA. Apure:** Departamento Muñoz, módulos F. Corrales de la UNELLEZ, entre los caños Guaritico y Caicara, 25 Oct 1980, B. Stergios 2379 (PORT, US); loc. cit., 10 Sep 1981, fr., G. Aymard 466 (PORT); loc. cit., 13 Sep 1981, B. Stergios et al. 9568 (PORT, US); loc. cit., 9 Dec 1986, G. Aymard & R. Schargel 5017 (PORT, US); loc. cit., 12 Dec 1986, G. Aymard & R. Schargel 5071 (PORT, US); **Cojedes:** San Carlos, en extremo Sur del Hato “El Laurel”, mas o menos km. 17 al sur de San Carlos, 21 Aug 1976, fl., fr., B. Trujillo 13843 (MY); **Guárico:** Calabozo, ca. 39 km SSW of Calabozo on Hato Masaguaral, 17 Sep 1983, R. Rondeau 469 (US); **Portuguesa:** Guanare, terrenos de la UNELLEZ, Mesa de Cavacas, 6 Sep 1986, fl., fr., B. Stergios 7151 (PORT).

Distribution and habitat. *Murdannia burchellii* has a very fragmented distribution, probably due to lack of collections, being known to occur in Bolivia, Brazil (in the states of Goiás, Maranhão, Pará, Piauí and Tocantins), and Venezuela (Fig. 10). It grows in shady to open sandy river banks of the Amazon and Cerrado domains.

Phenology. It was found in bloom and fruit from October to July.

Conservation status. *Murdannia burchellii* possesses a wide EOO (ca. 3,513,319.273 km²), but due to the few and scattered collections known for this species, its AOO is considerably smaller (ca. 22,500.000 km²). Thus, following the IUCN recommendations (IUCN 2001), *M. burchellii* should be considered Least Concern. Nonetheless, it is important to highlight the small number of collections and how fragmented the distribution of *M. burchellii* is. Also, the most recent collection was

made in 1993. Which may indicate an ongoing decrease of size of the subpopulations and the loss of habitat for this species.

Nomenclatural notes. When describing *Aneilema gardneri* var. *burchellii*, Clarke (1881) lists two collections (*W.J. Burchell 8165* and *M.A. Weddell 2106*). Since the name of Clarke's new variety honors W.J. Burchell, it seems logical to designate his collection as the lectotype. Aside from that, this collection is well distributed in several herbaria around the world. Furthermore, the specimen from K herbarium matches Clarke's description and has hand annotations made personally by Clarke. Thus, we designate this specimen as the lectotype for *Aneilema gardneri* var. *burchellii*.

When describing *Aneilema gardneri* var. *glabrior*, Clarke (1881) cites three collections by *G. Gardner (2743, 3481, 4020)*. The specimen of at K *Gardner 4020* is mounted on the same sheet as *Gardner 3481*, and both being annotated by Clarke as *A. gardneri* var. *glabrior*. *Gardner 4020* is also the most well distributed of the three collections. Nonetheless, the specimen of at K represents *M. gardneri*, so it cannot be designated as the type of *A. gardneri* var. *glabrior*. Thus, the specimen at K is not considered part of the original material. One of us (RBF) examined and recorded a specimen of *Gardner 4020* at BM in 1993, with the following data on the label: "Moist campos between Natividade and Conceição, Feby 1840, Herb. Gardner." While this would appear to be the most logical choice for a lectotype, the specimen was not photographed when other types were photographed at BM, and it cannot be found today. Therefore, the specimen at P is here designated as the lectotype. This specimen also bears an identification in Clarke's handwriting.

Discussion. *Murdannia burchellii* is morphologically similar to *M. gardneri* due to the general aspect of the plants, indumentum and by the presence of a ventri-lateral appendage in the seeds. It was traditionally treated as part of *M. gardneri* s.l. due to the number of cincinni per inflorescence, the posture of the pedicels at post-anthesis and in fruit, general floral and capsule morphology, and due to the hilum being positioned in a deep depression (Table 1). Nevertheless, both species can be readily differentiated by the stature and robustness of the plants, the insertion of the cincinni in the main axis of the inflorescence and testa ornamentation. Furthermore, the cincinni in *M. burchellii* are conspicuously sinuate, while the cincinni in *M. gardneri* are straight. After analyzing the syntypes for *Aneilema gardneri* var. *glabrior*, it became clear that they were conspecific with *M. burchellii*. All specimens possess the characteristic alternate to subopposite cincinni, being differentiated only from *M. burchellii* by sparser eglandular and glandular hairs in the inflorescence. All the analyzed specimens possessed some type of indumentum in the inflorescence, despite Clarke's description (1881) stating they were completely glabrous.

Some young specimens of *Murdannia burchellii* with inflorescences reduced to a solitary cincinnus, can be confused with specimens of *M. engelsii*. Nevertheless, these can be differentiated by their glabrous stems, leaf-blades with truncate base, sinuate cincinni, cup-shaped bracteoles, and glabrous androecium and gynoecium (vs. stems with glandular hairs, leaf-blades with an amplexicaul base, straight cincinni, flat bracteoles and minutely glandular-pubescent androecium and gynoecium in *M. engelsii*) (Table 1).

2. *Murdannia engelsii* M.Pell. & Faden, sp. nov.

urn:lsid:ipni.org:names:77158529-1

Figs 2, 10

Diagnosis. Similar to *M. paraguayensis* due to its deflexed pedicels at post-anthesis and when fruiting; petals with minute glandular hairs at base on the adaxial surface; filaments, ovaries, styles and capsules with minute glandular hairs, and capitate stigma. It can be differentiated by its trailing stems, distichously-alternate leaves, inflorescence reduced to a solitary cincinnus, peduncles with a mixture of eglandular and glandular hairs, cincinni 2–7-flowered, capsules broadly ovoid to broadly ellipsoid, and 1-seeded locules.

Type. BRAZIL. Mato Grosso: Itaúba, Resgate de Flora da UHE Colíder, lote G de supressão, 260 m, floresta do Planalto dos Parecís, prainha arenosa no rio Teles Pires, fl., fr., 27 May 2015, *M.E. Engels et al.* 3474 (holotype: RB!; isotypes: CNMT!, HERBAM!, MBM!, US!, TANG!).

Description. *Herbs* ca. 10.0–36.0 cm tall, perennial, rhizomatous without a definite base, terrestrial to paludal in river banks. *Roots* thin, fibrous, brown, densely to sparsely pilose with hyaline hairs, emerging from the basalmost nodes and rhizome. *Rhizomes* long, trailing, light brown to light green, shallowly buried in the sand. *Stems* ascending to erect, thin, herbaceous to slightly succulent, usually densely branched or branched only at the base, sometimes branching from the upper nodes; internodes 1.3–3.5 cm long, green, with a mixture of eglandular (scabrid) and glandular hairs, becoming glabrous with age, with a line of eglandular hairs opposite the leaf above, hairs hyaline. *Leaves* distichously-alternate, evenly distributed along the stems, rarely somewhat congested at the apex of the stems, the distal ones gradually smaller than the proximal ones; sheaths 2–2.5 mm long, green, with glandular hairs, becoming glabrous with age, hairs hyaline, margins sparsely ciliate, with a line of eglandular hairs opposite the leaf above, hairs hyaline; lamina (0.5–)1.6–6 × 0.3–1 cm, membranous, generally conduplicate, rarely flat, slightly falcate to falcate, green on both sides, drying olive-green on both sides, narrowly elliptic to narrowly lanceolate or narrowly ovate, glabrous on both sides or the uppermost usually with glandular hairs at least basally, base amplexicaul, margins green, ciliate to setose at base or the uppermost sometimes with glandular hairs, apex acuminate; midvein slightly conspicuous, slightly impressed adaxially, prominently acute abaxially, secondary veins 2(–3) pairs, inconspicuous to slightly conspicuous on both sides, dark green. *Inflorescences* 1–2(–5), terminal or axillary from the uppermost nodes, consisting of a solitary cincinnus; peduncles 1–1.4 cm, with a mixture of eglandular (scabrid) and glandular to densely glandular hyaline hairs; basal bract reduced, 5–5.5 × 4–4.5 mm, lanceolate to ovate, adaxially glabrous, abaxially glabrous or with glandular hairs, base amplexicaul, margins ciliate at base, apex acute, veins inconspicuous on both sides, dark green; cincinni 2–7-flowered, erect, straight, peduncle 3.5–8 mm long, green, with glandular to densely glandular, hyaline hairs, cincinnus internodes 4.5–8 mm long, green, with glandular to densely glandular hyaline hairs; cincinnus bract and bracteoles ca. 1–1.5 × 0.9–1 mm, persistent, ovate, flat, light green, with a sparse mixture of eglandular (scabrid) and glandular hairs near

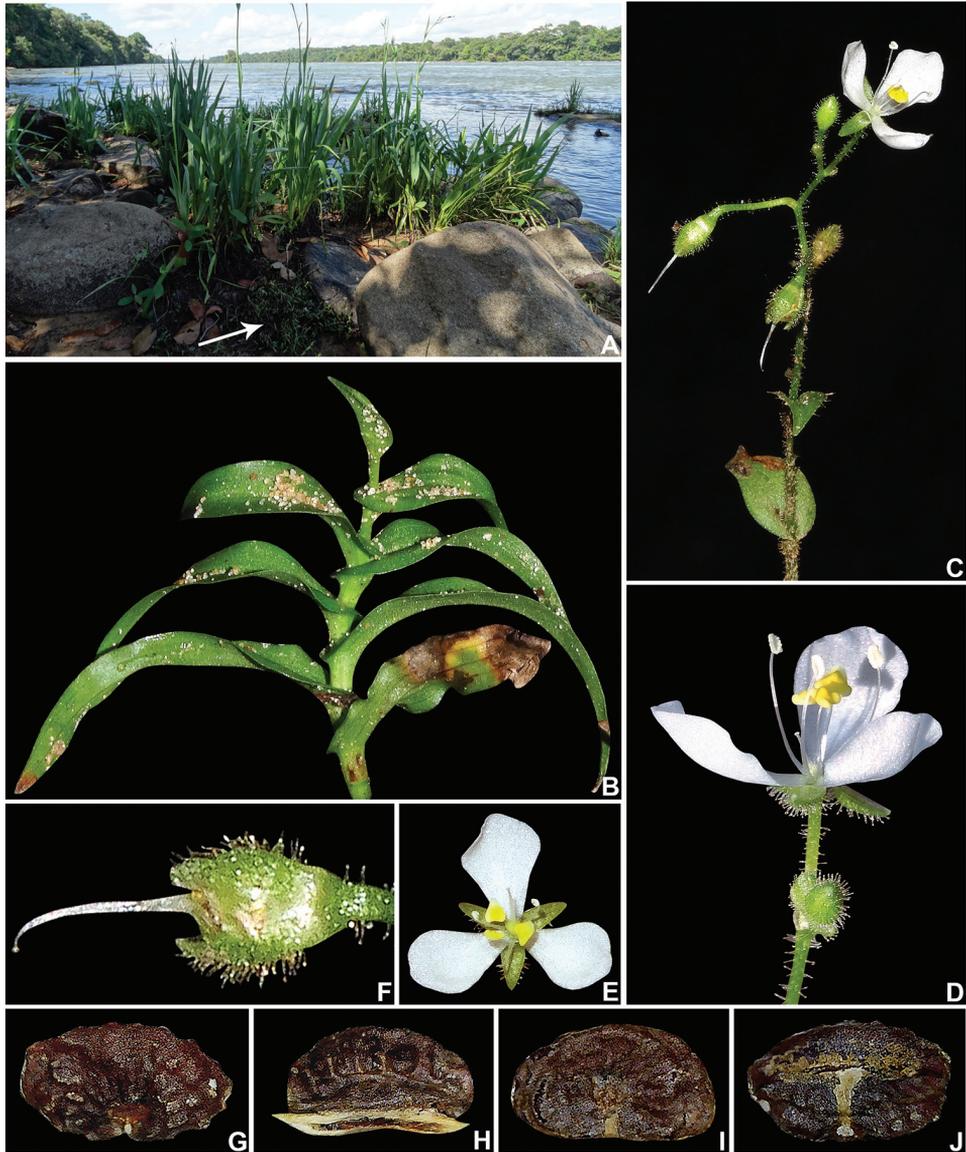


Figure 2. *Murdannia engelsii* M.Pell. & Faden. **A** Sandy banks of rio Teles Pires, white arrow showing a subpopulation of *M. engelsii* **B** detail of the stem, showing the conduplicate and falcate leaves, with amplexicaul bases **C** detail of the inflorescence, showing the deflexed pedicels at post-anthesis **D** side view of a male flower, showing the short and bent style. **E** front view of a bisexual flower, showing the long curved style **F** detail of a young fruit, showing the pedicel and sepals with glandular hairs, gently curved style and capitate stigma **G–J** seeds: **G** dorsal view of a seed, showing the scrobiculate and cleft testa, and the semilateral embryotega **H** ventral view of the same seed, showing the ventral furrows and tan appendage surrounding the hilum **I** dorsal view of another seed, showing the shallowly scrobiculate and slightly cleft testa, and the semidorsal embryotega **J** ventral view of the same seed, with the appendage removed, showing the linear hilum in a shallow depression. K, dorsal view of a seed, showing the smooth testa. Photographs **A–F** by M.E. Engels, **G–J** by R.F. Almeida.

the base, base amplexicaul, non-perfoliate, margins glabrous, apex acute. *Flowers* bisexual or male, enantiostylous, 1–1.4 cm diam.; floral buds ovoid, 2.8–3.1 × 2.5–3 mm, green; pedicels 1–6 mm long, green, with glandular to densely glandular, hyaline hairs, deflexed and slightly elongate in fruit; sepals 3–3.5 × 0.5–0.8 mm, triangular to ovate-triangular, cucullate, green, with glandular to densely glandular, hyaline hairs, apex acute, margins hyaline light green; petals equal, 4.5–7.3 × 2.5–4.5 mm, obtrullate, rarely obovate, slightly cucullate, pale lilac to lilac, mauve or pink, rarely white, with minute glandular hairs at the base on the adaxial surface, base cuneate, margins entire, apex obtuse to rounded; stamens 3, equal, filaments basally with minute glandular hyaline hairs, gently curved in the middle, 4.1–5.9 mm long, pale lilac to lilac or white, anthers elliptic, 0.6–0.7 × 0.3–0.7 mm, connective white to lilac, anthers sacs white to pale lilac, pollen white; staminodes 3, equal, filaments with minute glandular hyaline hairs, straight, 1.3–1.7 mm long, white to pale lilac, antherodes subsagittate to subcordate, 0.9–1.0 × 0.9–1.0 mm, connective golden yellow, lobes conspicuous, cream-colored to pale yellow; ovary ovoid to ellipsoid, 0.9 × 0.7–0.8 mm, 3-locular, white to light green, smooth, with minute glandular hyaline hairs, style curved at the apex, ca. 3.6–8 mm, white to pale lilac or lilac, stigma capitate, white to lilac. *Capsules* 3-locular, 3-valved, 3.2–4.5 × 2–2.5 mm, broadly ovoid to broadly ellipsoid, apiculate due to persistent style, light brown when mature, with minute glandular hyaline hairs, sometimes glabrescent with age, smooth. *Seeds* 1 per locule, 1.8–2.0 × 1–1.2 mm, reniform to broadly ellipsoid, cleft towards the embryotega, ventrally flattened, testa medium to dark brown, sparsely farinose, scrobiculate to shallowly scrobiculate, with ridges radiating from the embryotega, sometimes with 4–7 ventral furrows, with a tan appendage that extends ventri-laterally to the embryotega and basally into the hilum; embryotega semilateral to semidorsal, relatively inconspicuous, generally covered by a cream farina, without a prominent apicule; hilum linear, approximately the same length as the seed, in a shallow depression.

Specimens seen (paratypes). **BRAZIL. Mato Grosso:** Itaúba, resgate de Flora da UHE Colíder, Lote G de supressão, floresta do Planalto dos Parecís, região de ecótono entre a Floresta Amazônica e Cerrado, 3 Jun 2016, M.E. Engels & A.S. Bezerra 4510 (HERBAM, MBM, RB); Poconé, rodovia Transpantaneira, 17 May 1983, J. Barcia et al. 1560 (R); loc. cit., Fazenda Nova Berlim, Transpantaneira highway, km 85, 3 May 1992, M. Schessl 2602b (CH, UFMT, ULM, US); loc. cit., highway Poconé-Porto Cercado, 30 May 1992, M. Schessl 2631g (CH, CPAP, UFMT, ULM, US); loc. cit., estrada para Porto Cercado, km 18, 22 Apr 1993, A.L. Prado 2017 (UEC, UFMT); loc. cit., Fazenda Ipiranga, 8 May 1993, A.L. Prado & R. Ribeiro 2045 (HURB, UEC, UFMT); loc. cit., Fazenda Ipiranga, Pousada Piuvial, vazante da sede, km 11 da rodovia Transpantaneira, 20 May 1996, V.J. Pott et al. 3186 (CPAP, US); Vila Bela da Santíssima Trindade, Parque Estadual Serra de Ricardo Franco, margem do rio Guaporé, 23 May 1978, P.G. Windisch 1863 (RB); **Mato Grosso do Sul:** Corumbá, Fazenda Caceres, próximo da sede de Nhecolândia, 12 Aug 1988, V.J. Pott et al. 595 (CPAP, MBM, US); loc. cit., Fazenda Alegria, Nhecolândia, 30 Jul 1989, A. Pott et al. 4912 (CPAP, MBM, US); loc. cit., próximo ao mata burro na divisa com Retiro

Mandovi, Nhecolândia, 3 Aug 1999, V.J. Pott & A. Rodrigues 3993 (CPAP, US); **Tocantins:** Pium, Ilha do Bananal, Parque Nacional do Araguaia, base física do rio Javaés, antigo acampamento do Projeto Quelônios do Amazônia, 27 Mar 1999, M. Aparecida da Silva et al. 4167 (IBGE, RB).

Etymology. The epithet honors the collector of the holotype, the Brazilian botanist Mathias Erich Engels, Orchidaceae taxonomist and dear friend of the authors.

Distribution and habitat. *Murdannia engelsii* is endemic to Brazil, being known from the states of Tocantins, Mato Grosso and Mato Grosso do Sul (Fig. 10). It grows in shady to open sandy river banks of the Amazon, Cerrado and Pantanal domains. Its prostrate stems produce dense mats, generally near rocks and grasses.

Phenology. It was found in bloom and fruit from March to August.

Conservation status. *Murdannia engelsii* possesses both a wide EOO (ca. 514,893.048 km²) and a wide AOO (ca. 15,000.000 km²). Following the IUCN recommendations (IUCN 2001), *M. engelsii* should be considered Least Concern. Nevertheless, most of the known populations of *M. engelsii* are in areas currently being deforested and turned into pasture sites for cattle. We believe that this species is highly affected by human activity and should be considered Vulnerable [VU, A2cd+ B2ab(ii, iii,v)+D2].

Discussion. *Murdannia engelsii* is morphologically similar to *M. burchellii*, *M. gardneri* and *M. paraguayensis* due to indumentum and flower morphology, and also similar to *M. paraguayensis* due to the deflexed pedicels in fruit. However, *M. engelsii* can be easily differentiated by its inflorescence reduced to a solitary cincinnus (*vs.* thyrsi with several, verticillate or alternate to subopposite cincinni). It can be easily differentiated from *M. burchellii* and *M. gardneri* by inflorescence morphology, position of the pedicels at post-anthesis and in fruit, by the indumentum of the filaments, gynoeceum and capsules, and seed morphology. *Murdannia engelsii* is much more similar to *M. paraguayensis*, due to several key characters. These are the only species in the genus to have petals with minute glandular hairs at the base on the adaxial surface, androeceum and gynoeceum with glandular hairs, and the only Neotropical species to have pedicels deflexed post-anthesis and in fruit. Nevertheless, *M. engelsii* can be differentiated by its trailing habit (*vs.* erect in *M. paraguayensis*), leaves distichously-alternate (*vs.* spirally-alternate), inflorescence reduced to a solitary cincinnus (*vs.* inflorescence with several verticillate cincinni), cincinni 2–7-flowered (*vs.* 1-flowered), capsules broadly ovoid to broadly ellipsoid (*vs.* oblongoid to broadly oblongoid), and locules 1-seeded (*vs.* 2-seeded). *Murdannia engelsii* can also be confused with *M. nudiflora*, due to their small stature, phyllotaxy and inflorescence morphology. However, they can be easily differentiated by its erect cincinni (*vs.* pendulous), persistent bracteoles (*vs.* caducous), corolla actinomorphic (*vs.* zygomorphic), three stamens and three staminodes (*vs.* two stamens and four staminodes), filaments with minute glandular hairs (*vs.* bearded with moniliform hairs), and locules 1-seeded (*vs.* locules 2-seeded) (Table 1). One of the most striking features of *M. engelsii* would be occasional production of several inflorescences clustered towards the apex of a shoot, forming a synflorescence. This synflorescence resembles a single inflorescence with several alternate cincinni.

3. *Murdannia gardneri* (Seub.) G.Brückn., Nat. Pflanzenfam. (ed. 2)15a: 173. 1930.
Figs 3–4, 10

Phaeneilema gardneri (Seub.) G.Brückn., Notizbl. Bot. Gart. Berlin–Dahlem 10 (91): 56. 1927.

Aneilema gardneri Seub., in Martius, Fl. Bras. 3 (1): 259. 1855. Lectotype (designated here): BRAZIL. Goyaz, moist places near Villa de Arrayal, fl., fr., April 1841, G. Gardner 4021 (K barcode K000363236!; isolectotypes: B barcode B100367834!, BM barcodes BM001172132!, BM001172133!, G barcodes G00098261!, G00098262!, G00165012!, K barcode K000363237!, NY barcodes NY00247400!, NY00247401!, P barcode P02088022!, US barcode US00091574!).

Description. *Herbs* ca. 30.0–150.0 cm tall, perennial, rhizomatous with a definite base, terrestrial to paludal to rooted emergent in flooded fields. *Roots* thin, fibrous, medium to dark brown, densely to sparsely pilose with medium to dark brown hairs, emerging from the short rhizome and from the basalmost nodes. *Rhizomes* short, light to medium brown, buried in the sand or ground. *Stems* prostrate, with erect to ascending apex, succulent, unbranched to little-branched at the base; internodes 1.9–10.7 cm long, green to vinaceous, glabrous to sparsely pilose or hispid, becoming glabrous with age, with a line of eglandular hairs opposite the leaf above, hairs hyaline. *Leaves* spirally-alternate, evenly distributed along the stems, sessile, the distal ones gradually reduced; sheaths 0.5–3.2 cm long, green to vinaceous, sparsely pilose to hispid, becoming glabrous with age, hairs hyaline, margins ciliate to hispid, with a line of eglandular hairs opposite the leaf above, hairs hyaline; lamina 4.2–17.4 × 0.7–1.3 cm, chartaceous, conduplicate, slightly falcate to falcate, green on both sides, drying light brown to olive-green on both sides, linear-lanceolate to lanceolate, sparsely pilose to hispid, becoming glabrous with age, rarely glabrous, base truncate to rounded, margins light green, ciliate to setose only at base, apex acuminate; midvein inconspicuous, slightly impressed adaxially, slightly obtuse abaxially, secondary veins 3–4(–5) pairs, adaxially inconspicuous to slightly conspicuous, light green, abaxially somewhat conspicuous. *Inflorescences* 1–(3) thyrsi, terminal or axillary from the uppermost nodes, thyrses with 16–38 verticillate cincinni, arranged in 2–9 whorls; peduncles 2.7–8.4 cm, with a mixture of eglandular (scabrid) and glandular, hyaline hairs; basal bract leaf-like, 2.4–7.2 × 0.3–0.9 cm, linear-lanceolate to lanceolate, sparsely pilose to hispid, rarely glabrous, base rounded, margins ciliate to setose only at base, apex acuminate, veins inconspicuous, concolorous to light green; cincinni bracts ca. 0.4–0.8 × 0.1–0.3 cm, ovate to broadly ovate, cup-shaped, light green to lilac, glabrous to pilose, base truncate, margins glabrous to sparsely ciliate, apex acuminate; cincinni 2–11-flowered, ascending, straight, peduncle 0.5–1.3 cm, light green to vinaceous to purple, with a mixture of eglandular (scabrid) and glandular or all glandular hyaline hairs, internodes 0.9–5.2 mm long, light green to vinaceous to purple, with a mixture of eglandular (scabrid) and glandular or all glandular, hyaline hairs; bracteoles ca. 1.8–4.1 × 2.8–4.2 mm, persistent, broadly ovate to depressed ovate, cup-shaped, light green to lilac or pink, sparsely pilose, base amplexicaul,

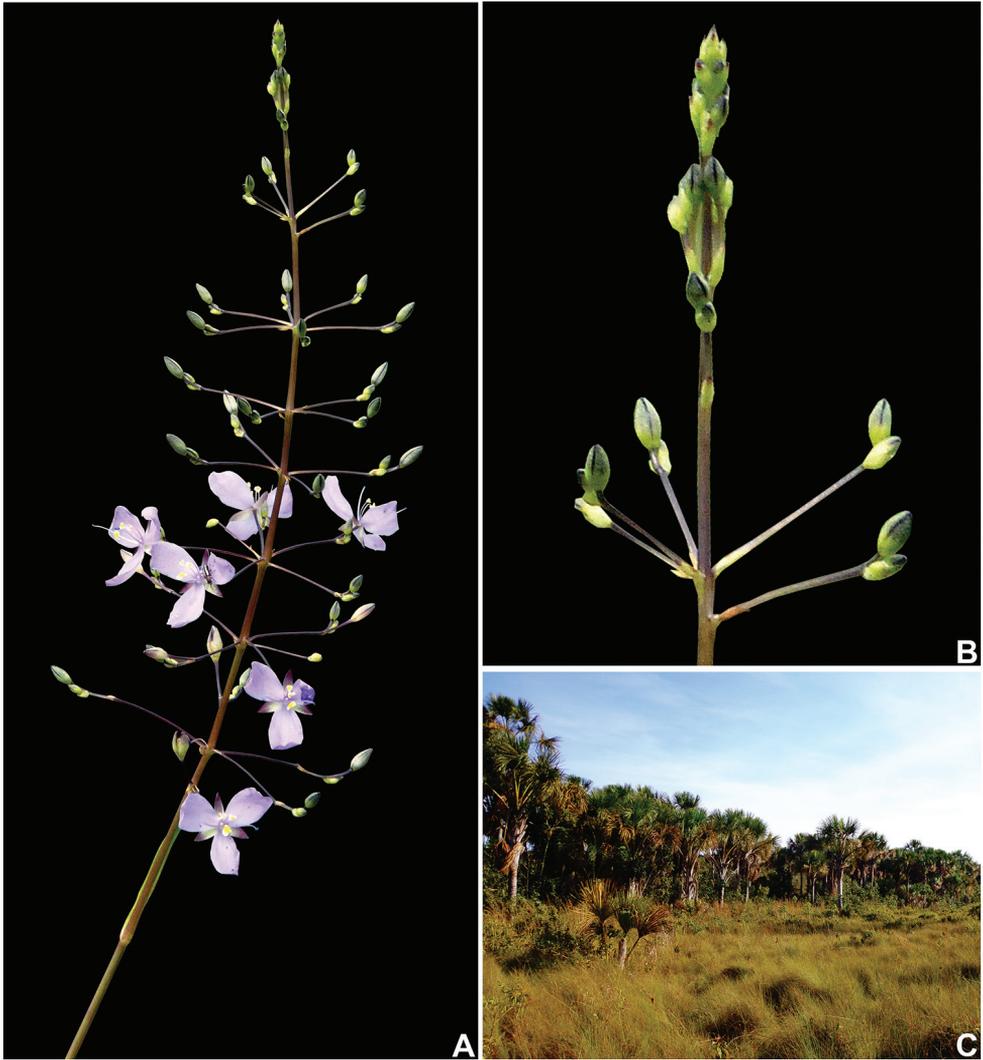


Figure 3. *Murdannia gardneri* (Seub.) G.Brückn. **A** Inflorescence, showing the verticillate cincinni and open lilac flowers **B** detail of the inflorescence, showing the ascending and straight cincinni **C** flooded grassland in the state of Minas Gerais. Photographs **A–B** by W. Milliken, **C** by I.L.M. Resende.

non-perfoliate, margins glabrous to ciliate, apex acuminate. *Flowers* bisexual or male, enantiostylous, ca. 1.4–2.3 cm diam.; floral buds narrowly ovoid to ovoid, 2.6–5.3 × 1.2–2.4 mm, light green to pink to vinaceous; pedicels 2.2–7.3 mm long, light green to vinaceous to purple, with a mixture of eglandular (scabrid) and glandular or all glandular, hyaline hairs, erect and elongate in fruit; sepals 3.6–6.1 × 3.2–4.8 mm, triangular to ovate-triangular, cucullate, green to lilac to vinaceous to purple, with glandular to densely glandular, hyaline hairs, apex acuminate, margins hyaline light green to hyaline pink; petals equal, 0.7–1.2 × 0.6–0.8 cm, obovate to elliptic-obovate, slightly cucullate,



Figure 4. *Murdannia gardneri* (Seub.) G.Brückn. Isolectotype of *Aneilema gardneri* (P barcode P02088022). Photograph courtesy of the Muséum National d'Histoire Naturelle, Paris.

pale lilac to lilac, purple or pink, rarely white, glabrous, base cuneate, margins entire, apex acute to obtuse; stamens 3, equal, filaments glabrous, gently curved at the apex, 6.2–9.4 mm long, pale lilac to lilac or white, anthers elliptic, 0.7–0.9 × 0.3–0.4 mm, connective lilac to white, anthers sacs white to lilac, pollen white; staminodes 3, equal, filaments glabrous, straight, 3.1–5.3 mm long, pale lilac to white, antherodes cordate, 0.7–0.9 × 0.8–0.9 mm, connective golden yellow, lobes conspicuous, cream-colored to pale yellow; ovary ellipsoid to broadly ellipsoid, 0.6–0.8 × 0.4–0.6 mm, 3-locular, white to light green, smooth, glabrous, style gently curved at the apex, ca. 4.8–6.2 mm, pale lilac to lilac or white, stigma truncate, white to lilac. *Capsules* 3.6–4.5 × 3.4–4.2 mm, 3-locular, 3-valved, subglobose to globose, apiculate due to persistent style, light brown when mature, glabrous, smooth. *Seeds* 1 per locule, 1.9–2.6 × 1.2–1.8 mm, reniform to broadly ellipsoid, strongly cleft towards the embryotega, ventrally flattened, testa dark brown to greyish brown, sparsely farinose, scrobiculate to foveolate, with ridges radiating from the embryotega, with a tan appendage that extends ventri-laterally to the embryotega and basally into the hilum; embryotega semilateral, relatively inconspicuous, without a prominent apicule; hilum linear, approximately the same length as the seed, in a deep depression.

Specimens seen. BRAZIL. Bahia: Correntina, Chapadão Ocidental da Bahia, Islets and banks of the rio Corrente, 23 Apr 1980, R.M. Harley et al. 21668 (CEPEC, HRB, K, MBM, US); loc. cit., 21 Jan 1997, G. Hatschbach et al. 66044 (MBM); **Goiás:** Cavalcante, estrada rio Trairas/rio Custódio, km 2, 28 Nov 2006, G. Pereira-Silva & G.A. Moreira 11159 (CEN, RB); Colinas do Sul, fazenda Saracura, estrada de manutenção das novas linhas de transmissão Minacu/Niquelândia, 8 Sep 1995, B.M.T. Walter et al. 2604 (CEN, RB); Goyaz, 1841, G. Gardner 4020 (K barcode K000363238, US barcode US00160560); Itumbiara, rodovia Itumbiara–Rio Verde, a 31 km de Itumbiara, 18 Apr 1978, G.J. Shepherd et al. 7415 (F ex UEC); Niquelândia, 27 km de Colinas em direção a Niquelândia, próximo ao rio Tocantinzinho, 6 May 1998, M.A. Silva et al. 3772 (IBGE, RB, US); Teresina de Goiás, km 12 da estrada GO-118, sentido Nova Roma, 29 April 1996, B.A.S. Pereira & D. Alvarenga 3027 (IBGE, RB); **Mato Grosso:** Novo Mundo, Parque Estadual do Cristalino, entrada para Fazenda J.J., 26 January 2008, D. Sasaki et al. 1934 (HERBAM, HURB, SPF); **Minas Gerais:** Ituiutaba, 26 May 1946, A. Macedo 760 (US); **Tocantins:** Conceição do Tocantins, rodovia TO-050, km 375, fazenda São José, próximo do rio Santa Isabel, 11 May 2000, G. Hatschbach et al. 70903 (MBM); Gurupi, próximo à Gurupi, 20 Apr 1978, R.P. Orlandi 73 (HRB, RB).

Distribution and habitat. *Murdannia gardneri* is endemic to Brazil, being known from the states of Bahia, Goiás, Mato Grosso, Minas Gerais and Tocantins (Fig. 10). It grows in open sandy river banks or flooded grass fields, of the Cerrado domain.

Phenology. It was found in bloom and fruit throughout the year.

Conservation status. *Murdannia gardneri* possesses a EOO of ca. 497,658.992 km² and a AOO of ca. 20,000.000 km². Most of the known collections are concentrated in central Brazil, where the native vegetation is commonly removed to give place to livestock. This is especially common in the Cerrado domain, due to its savanna

vegetation being easier to remove than the dense rainforests of the Amazon and Atlantic Forest domains. Thus, we believe that *M. gardneri* should be considered Nearly Threatened.

Nomenclatural notes. When describing *Aneilema gardneri*, Seubert (1855) lists two collections from G. Gardner (4020 and 4021). As aforementioned, *Gardner 4020* consists of a mixture of *M. burchellii* and *M. gardneri*. Fortunately, the same is not true for *Gardner 4021*. Furthermore, the *Gardner 4020* specimen at P was designated by us as the lectotype for *A. gardneri* var. *glabrior*. Thus, we designate a specimen at K as the lectotype for *A. gardneri*.

Discussion. *Murdannia gardneri* is morphologically similar to *M. burchellii* and *M. paraguayensis* due to their phyllotaxy and by the number of cincinni per inflorescence. It is morphologically more similar to *M. burchellii* due to the posture of the pedicels at post-anthesis and when fruiting, general floral and capsule morphology, and due to the hilum being positioned in a deep depression. Nevertheless, both species can be easily differentiated based on the insertion of the cincinni in the main axis of the inflorescence (alternate to subopposite in *M. burchellii* vs. verticillate in *M. gardneri*), the ornamentation of the testa (costate to slightly rugose vs. scrobiculate to foveolate), robustness of the plants (delicate vs. robust, branching pattern (densely branched at base vs. unbranched to little-branched), leaf-blade consistency (chartaceous vs. succulent), and some indumentum differences. On the other hand, *M. paraguayensis* can be readily differentiated from *M. gardneri* by its 1-flowered cincinni (vs. many-flowered in *M. gardneri*), deflexed pedicels post-anthesis and when fruiting (vs. erect), filaments with minute glandular hairs (vs. glabrous), gynoeceium and capsules with glandular hairs (vs. glabrous), capsule oblongoid to broadly oblongoid (vs. subglobose to globose), locules 2-seeded (vs. 1-seeded), and hilum in a shallow depression (vs. in a deep depression) (Table 1).

4. *Murdannia nudiflora* (L.) Brenan, Kew Bull. 7(2): 189. 1952.

Fig. 5

Phaeneilema nudiflorum (L.) G.Brückn., Notizbl. Bot. Gart. Berlin–Dahlem 10 (91): 56. 1927.

Ditelesia nudiflora (L.) Raf., Fl. Tellur. 3: 69. 1837.

Aneilema nudiflorum (L.) R.Br., Prodrumus Florae Novae Hollandiae: 271. 1810.

Commelina nudiflora L., Sp. Pl. 1: 41. 1753. Lectotype (designated by Merrill 1937): INDIA. s.loc., fl., fr., s.dat., P. Osbeck s.n. (LINN barcode LINN-HL65-12!).

Diagnosis. *Herbs* annual, with a definite base, terrestrial to paludal to rooted emergent in flooded fields. *Roots* thin, fibrous, brown, densely to sparsely pilose, emerging from the basal most nodes. *Rhizomes* absent. *Stems* prostrate, erect to ascending apex, unbranched or branched at the base, glabrous. *Leaves* distichously-alternate, distributed along the stems, rarely 1–2 congested at base, the distal ones gradually smaller than the basal ones;

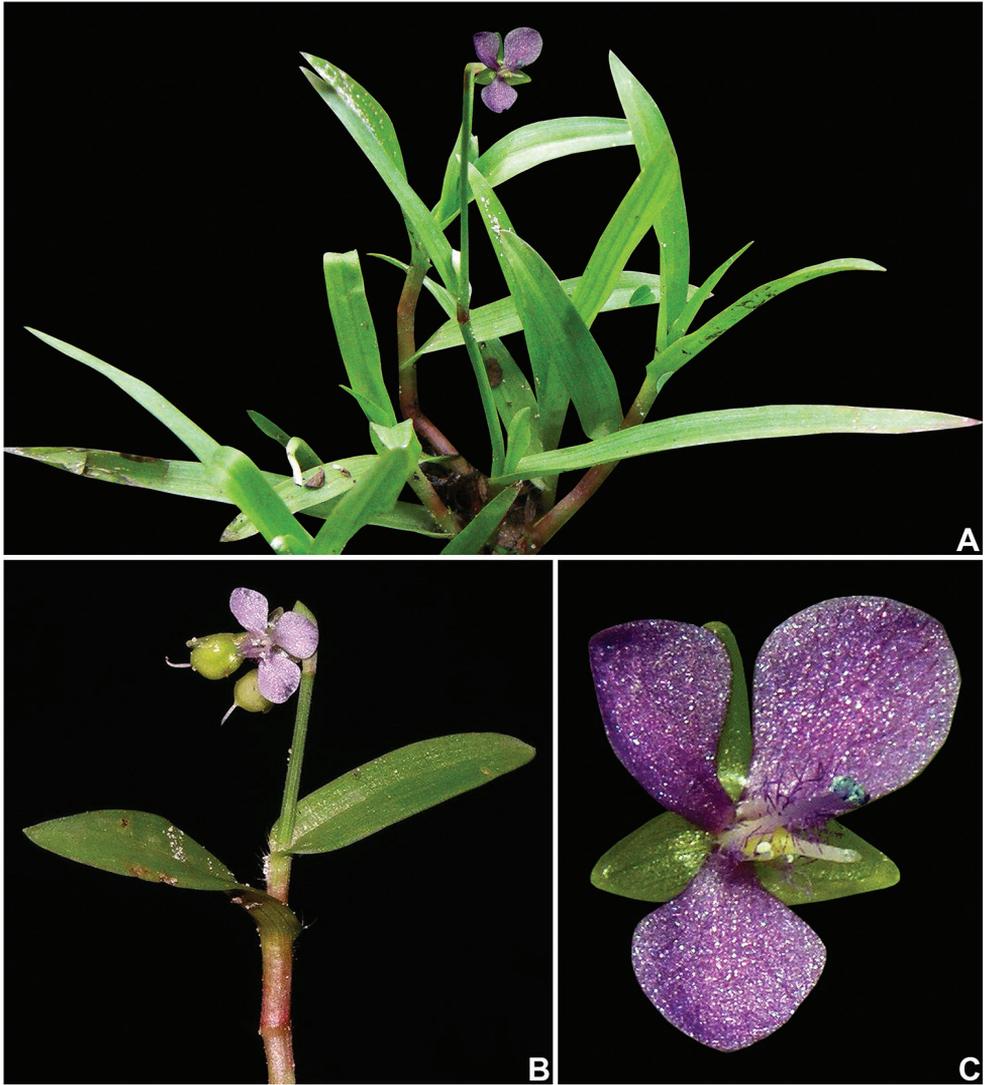


Figure 5. *Murdannia nudiflora* (L.) Brenan. **A** Habit **B** detail of a stem, showing the apical and long-pedunculate inflorescence **C** front view of a bisexual flower. Photograph **A**, **C** by W. Vargas and **B** by M.E. Engels.

lamina membranous, conduplicate, linear to linear-lanceolate or lanceolate-oblong, glabrous or with eglandular hairs. *Inflorescences* 1–(2), terminal or axillary from the uppermost node, long-pedunculate, exerted from the leaf-sheaths, consisting of a solitary cincinnus; basal bract inconspicuous; cincinni bracts cup-shaped; cincinni 2–12-flowered, pendent, bracteoles cup-shaped, caducous. *Flowers* bisexual or male, zygomorphic due to the position of the lateral petals; pedicels erect and elongate in fruit; sepals ovate-elliptic to ovate-triangular, cucullate, glabrous; petals subequal, obovate to spatulate to obtrullate, slightly cucullate, pale lilac to purple or mauve, glabrous; stamens 2 (opposite

to the lower petals), equal, filaments gently sigmoid, closely parallel to each other, white at the base, lilac at the middle, purple at the apex, densely bearded with moniliform, purple hairs, anthers elliptic to oblong, connective bluish lilac to white, anthers sacs purple to dark purple, pollen white; staminodes 4, 1 staminode antesealous, opposite to the lower sepal, filament white to lilac, medially bearded with moniliform, purple hairs, antherode small, white, sometimes lacking, 3 antepetalous, filaments straight, pale lilac to white, glabrous or sparsely medially bearded with moniliform, purple hairs, antherodes hastate, white to cream; ovary ellipsoid to oblongoid, 3-locular, light green smooth, glabrous, style strongly curved at the apex, white to pale lilac, glabrous, stigma capitate, lilac. *Capsules* 3-locular, 3-valved, ovoid to subglobose, apiculate due to persistent style, light brown when mature, smooth, glabrous. *Seeds* 2 per locule, broadly ellipsoid to oblongoid, not cleft towards the embryotega, ventrally ridged, testa yellowish brown to brown, foveolate-reticulate, with pale warts around depressions, farinose, appendage absent; embryotega semilateral, relatively inconspicuous, without a prominent apicule; hilum elliptic, approximately $\frac{1}{2}$ the length of the seed, on a weak ridge.

Distribution and habitat. Native to Tropical Asia to Malaysia and naturalized in West Africa, North America, Central America, the West Indies and South America; in the New World ranging from the southeastern United States to Argentina. In Brazil it is known to occur in the states of Acre, Alagoas, Amazonas, Bahia, Ceará, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraíba, Paraná, Rio Grande do Sul, Santa Catarina, São Paulo and Tocantins, in disturbed vegetation, roadsides and near rice crops.

Phenology. It was found in bloom and fruit throughout the year.

Discussion. *Murdannia nudiflora* can be easily recognized by its caduceus bracteoles, single terminal cincinni, two fertile stamens and four staminodes, and capsules with 2-seeded locules (Table 1).

5. *Murdannia paraguayensis* (C.B. Clarke ex Chodat) G.Brückn., Nat. Pflanzenfam. (ed. 2)15a: 173. 1930.

Figs 6, 10

Phaeneilema paraguayensis (C.B. Clarke ex Chodat) G.Brückn., Notizbl. Bot. Gart. Berlin–Dahlem 10 (91): 56. 1927.

Aneilema paraguayense C.B. Clarke ex Chodat, Bull. Herb. Boissier, sér. 2, 1: 437. 1901. Lectotype (designated here): PARAGUAY. Departamento de Canindeyú: Sierra de Maracayú, fl., fr., Oct 1898–1899, E. Hassler 5083 (G barcode G00195432!; isolectotypes: BM barcode BM000526690!; G barcode G00009034!, NY barcode NY00247403!).

Description. *Herbs* ca. 20.0–150.0 cm tall, perennial, rhizomatous with a definite base, terrestrial to paludal to rooted emergent in flooded fields. *Roots* thin, rarely thick, fibrous, medium to dark brown, densely to sparsely pilose with medium to dark brown

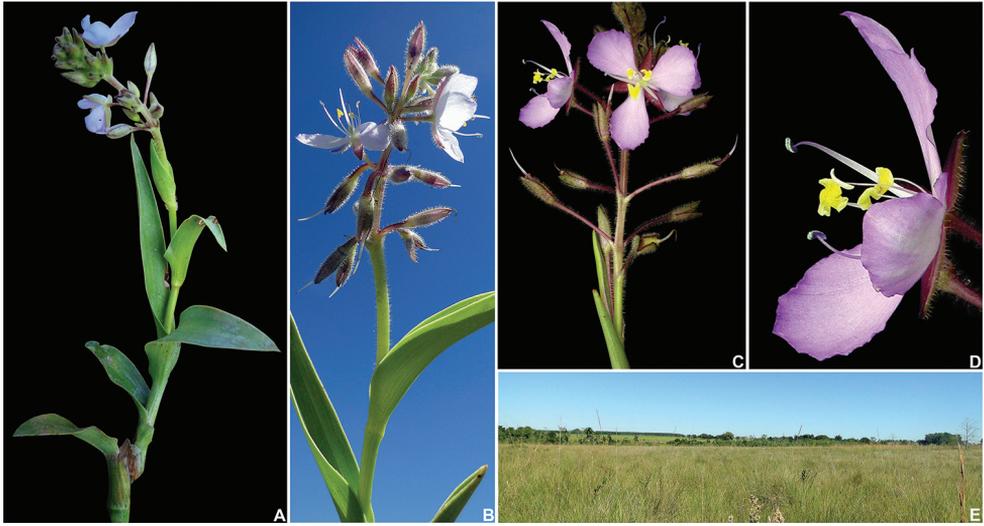


Figure 6. *Murdannia paraguayensis* (C.B.Clarke) G.Brückn. **A** Detail of a flowering shoot, showing the succulent stem, succulent, canaliculate and falcate leaves, and an inflorescence with lilac flowers **B** Detail of the apex of a flowering shoot, showing a terminal inflorescence with white flowers, and pedicels deflexed post-anthesis **C** Inflorescence showing the 1-flowered verticillate cincinni and open mauve flowers **D** Side view of a male flower, showing the sepals with glandular hairs **E** flooded grassland in Sidrolândia, Mato Grosso do Sul. Photograph **A** by I.L.M. Resende, **B, E** by S.N. Moreira and **C–D** by V.C. Souza.

hairs, emerging from the short rhizome and from the basalmost nodes. *Rhizomes* short, light to medium brown, buried in the sand or ground. *Stems* prostrate, with erect to ascending apex, succulent, unbranched or only branched at the base; internodes 3.4–13.0 cm long, green to vinaceous, glabrous to sparsely pilose, becoming glabrous with age, with a line of eglandular hyaline hairs opposite the leaf above. *Leaves* spirally-alternate, sometimes becoming distichously-alternate at apex, evenly distributed along the stems, the distal ones gradually smaller than the basal ones; sheaths 1.2–3.3 cm long, green to vinaceous, glabrous to pilose along the fused edge, sometimes with a few scattered long, glandular hairs, margins ciliate to sparsely setose at base, hairs hyaline; lamina 2.5–23.6 × 0.4–1.2 cm, succulent, canaliculate, slightly falcate to falcate, green on both sides, drying light brown to olive-green or light green on both sides, linear-lanceolate to linear-elliptic or linear-oblong, glabrous, base truncate to rounded, margins light green to pink or vinaceous, ciliate to sparsely setose only at base, apex acute to acuminate; midvein conspicuous or inconspicuous, slightly impressed adaxially, slightly obtuse abaxially, secondary veins 2–3(–4) pairs, adaxially inconspicuous or slightly conspicuous, light green, abaxially slightly conspicuous. *Inflorescences* 1–(2), thyrsi, terminal or axillary from the uppermost node, thyrses with 9–24 verticillate cincinni, arranged in 3–9 whorls; peduncles 1.2–7.5 cm, with glandular to densely glandular, hyaline hairs; basal bract leaf-like, 2.1–3.2 × 0.9–1.2 cm, lanceolate, glabrous, base rounded, margins ciliate to setose only at base, apex acute to acuminate, veins inconspicuous or slightly conspicuous, concolorous to light green; cincinni bracts ca.

1.4–5.1–(10.0) × 1.0–1.6 mm, lanceolate to ovate, light green to pink or vinaceous, glandular-pubescent to glabrous, base truncate, margins glabrous, sometimes with a tooth at the base in each side, apex acute; cincinni 1-flowered, patent to erect, straight, peduncle inconspicuous, internodes absent; bracteoles ca. 0.8–1.2 × 0.3–0.6 mm, persistent, triangular, flat, light green to pink, glabrous, base truncate, margins glabrous, apex acute. *Flowers* bisexual or male, enantiostylous, ca. 1.3–2.5 cm diam.; floral buds narrowly ovoid, 5.3–6.2 × 2.6–3.2 mm, light green to pink; pedicels 1.0–5.2 mm long, light green to pink or vinaceous, with glandular to densely glandular, hyaline hairs, deflexed and elongate in fruit; sepals 5.3–8.0 × 1.8–4.7 mm, triangular to ovate-triangular, cucullate, light green to pink to vinaceous, with glandular to densely glandular, hyaline hairs, apex acuminate, margins hyaline light green to hyaline pink or vinaceous; petals equal, 0.8–1.3 × 0.5–0.7 cm, obovate to narrowly obovate, slightly cucullate, white to lilac to purple or mauve, with minute glandular hairs at base on the adaxial surface, base cuneate, margins entire to erose at the apex, apex acute to obtuse; stamens 3, equal, filaments gently curved at the apex, 6.0–9.6 mm long, pale lilac to lilac or purple, with minute glandular, hyaline hairs, anthers elliptic to oblong, 0.9–2.0 × 0.4–0.7 mm, connective purple to bluish purple, anthers sacs lilac to purple, pollen white; staminodes 3, equal, filaments straight, 3.1–5.3 mm long, pale lilac to white, with minute glandular, hyaline hairs, antherodes sagittate, 0.8–2.3 × 0.8–1.1 mm, connective golden yellow, lobes conspicuous, cream-colored to pale yellow; ovary ellipsoid to oblongoid, 1.5–3.5 × 0.7–1.3 mm, 3-locular, light green to green, smooth, with densely glandular, hyaline hairs, style gently curved at the apex, ca. 3.5–8.0 mm, pale lilac to lilac, with minute glandular, hyaline hairs, stigma capitate, lilac to purple. *Capsules* 5.1–9.8 × 3.2–5.0 mm, 3-locular, 3-valved; oblongoid to broadly oblongoid, apiculate due to persistent style, light brown when mature, smooth, with sparse glandular, hyaline hairs, sometimes becoming glabrous with age. *Seeds* 2 per locule, 3.4–4.2 × 1.7–2.1 mm, reniform to broadly ellipsoid, strongly cleft towards the embryotega, ventrally flattened, testa dark brown to greyish brown, sparsely farinose, scrobiculate, with ridges radiating from the embryotega, with a tan appendage that extends ventri-laterally to the embryotega and basally into the hilum; embryotega semilateral, relatively inconspicuous, without a prominent apicule; hilum linear, approximately the same length as the seed, in a shallow depression.

Specimens seen. **BRAZIL. Distrito Federal:** Brasília, immediately N of Brasília, rio Torto, 18 Sep 1965, H.S. Irwin et al. 8425 (NY, RB, US); **Mato Grosso:** Santa Cruz Do Xingu, Parque Estadual do Xingu, limite norte do parque, 6 Mar 2011, D.C. Zappi et al. 3166 (K, RB, UNEMAT); São Félix do Araguaia, estrada entre a vila Pontinópolis e a Serra dos Magalhães, 21 Mar 1997, V.C. Souza et al. 14814 (ESA, RB); Sinop, estrada para Porto dos Gaúchos, ca. 500 km leste do rio Teles Pires, 22 Oct 2004, V.C. Souza 30056 (ESA); Xavantina, Camp B of Base Camp, 10 Jan 1968, D. Philcox & A. Ferreira 3958 (K); loc. cit., 10 km E from base, ca. 270 km from Xavantina, 6 Mar 1968, fl, D.R. Gifford RG76 (K); loc. cit., s.dat., fl., fr., G.R.D. Smith 43 (K); loc. cit., Oct–Nov 1967, fl., J. Ramos & R. Sousa R7 S30 (K); loc. cit., 1 km S of base camp, 14 Mar 1968, D. Philcox & A. Ferreira 4539 (K, NY, P, UB);

loc. cit., Xavantina-Cachimbo road, 1 km E of km 244, 15 Mar 1968, D. Philcox & A. Ferreira 4550 (K, NY, P, RB, UB); loc. cit., close to the Xavantina-São Félix do Araguaia road, 11 Apr 1968, J.A. Ratter et al. 992 (K, NY, P, UB); loc. cit., córrego do Porco, 240 km N of Xavantina, 7 May 1968, J.A. Ratter et al. 1339 (K, NY, P, RB, UB); loc. cit., 5 Oct 1968, R.M. Harley 10489 (K, NY, P, RB, UB); loc. cit., 10 Oct 1968, R.M. Harley et al. 10591 (K, NY, P, RB); loc. cit., arredores do acampamento da expedição inglesa até o córrego do Surucucu, 10 Oct 1968, Sidney & Onishi 1356 (RB, UB); **Mato Grosso do Sul:** Indaiá do Sul/Chapéu Azul, cachoeira aos fundos da cidade, 18 Feb 1996, M.R. Pietrobon da Silva et al. 2923 (MBM); Sidrolândia, fazenda Olho D'água, km 392 da Estrada Campo Grande-Sidrolândia, 19 Apr 2013, S.N. Moreira et al. 1451 (BHCB); **Minas Gerais:** Araxá, próximo a Araxá, vale do rio Araguaí, 1 Nov 1970, A.P. Duarte 13912 (HB, MBM). **PARAGUAY. Amambay:** Sierra de Amambay, April 1912–1913, E. Hassler 11347 (BM, K, P).

Distribution and habitat. *Murdannia paraguayensis* occurs in Paraguay and central Brazil, being known from the states of Distrito Federal, Goiás, Mato Grosso, Mato Grosso do Sul and Minas Gerais (Fig. 10). It grows in open flooded grass fields, of the Amazon, Cerrado, Chaco and Pantanal domains.

Phenology. It was found in bloom and fruit throughout the year.

Conservation status. *Murdannia paraguayensis* possesses one of the widest distribution ranges among Neotropical *Murdannia*, with a EOO of ca. 886,876.606 km² and a AOO of ca. 22,500.000 km². Thus, following the IUCN recommendations (IUCN 2001), *M. paraguayensis* should be considered Least Concern.

Nomenclatural notes. When describing *Aneilema paraguayensis*, Chodat (1901) only mentions “Ipé-hu, Oct., 5083”, at the end of his brief diagnosis. According to Stafleu & Cowan (1979), Hassler’s Paraguayan collections are generally housed at G. After consulting several herbaria, we found a specimen at NY herbarium, two specimens at G, and one at BM that matched the protologue. Thus, we selected as the lectotype the specimen at G which shows the typical deflexed pedicel characteristic of this species.

Discussion. *Murdannia paraguayensis* has been historically confused with *M. gardneri* s.l., due to the verticillate cincinni in the inflorescence. For differences between *M. burchellii*, *M. gardneri* and *M. paraguayensis*, see the comments on those species above and Table 1. Despite this historic confusion, *M. paraguayensis* is morphologically very similar to *M. engelsii*, due to its petals, androecium and gynoecium with glandular hairs, pedicels deflexed postanthesis and in fruit, and capitate stigma. Nevertheless, *M. paraguayensis* can be differentiated by its erect habit (*vs.* trailing in *M. engelsii*), leaves spirally-alternate (*vs.* distichously-alternate), much larger inflorescences with several whorls of cincinni (*vs.* consisting of a solitary cincinnus), peduncle solely with glandular hairs (*vs.* with a mixture of eglandular and glandular hairs), cincinni 1-flowered (*vs.* 2–7-flowered), capsules oblongoid to broadly oblongoid (*vs.* broadly ovoid to broadly ellipsoid), and locules 2-seeded (*vs.* locules 1-seeded).

The specimen *H.S. Irwin et al.* 8425 looks very distinctive from the other analyzed specimens due to its: apparently creeping habit, leaves distichously-alternate at

apex, sheaths with a few scattered long glandular hairs, blades with strongly undulate margins, short congested inflorescence, and very short pedicels. Nevertheless, it possesses the same inflorescence architecture, capsules with glandular hairs, and 2-seeded locules. We believe that the blades with strongly undulate margins may be a result of the drying process. Thus, we consider that these collections don't merit any taxonomic recognition.

6. *Murdannia schomburgkiana* (Kunth) G.Brückn., Nat. Pflanzenfam. (ed. 2)15a: 173. 1930.

Figs 7, 10

Phaenilema schomburgkiana (Kunth) G.Brückn., Notizbl. Bot. Gart. Berlin–Dahlem 10 (91): 56. 1927.

Ancilema schomburgkianum Kunth, Enum. Pl. 4: 661. 1843. Lectotype (designated here): GUYANA. s.loc., fl., fr., Oct 1841, R.H. Schomburgk 842 (B barcode B100367820!; isolectotypes: 2 ex BM not found, G barcodes G00176335!, G00176336!, G00176337!, P barcodes P02088026!, P02088027!, TCD barcode TCD0008088!).

Description. *Herbs* ca. 30.0–65.0 cm tall, perennial, rhizomatous with a definite base, terrestrial to paludal to rooted emergent in open flooded savannas. *Roots* tuberous, thick and fusiform, medium to dark brown, densely to sparsely pilose with medium to dark brown hairs, emerging from the short rhizome and from the basal nodes. *Rhizomes* short, brown, buried in the sand or soil. *Stems* erect, succulent, unbranched; internodes 1.0–11.5 cm long, green to vinaceous, glabrous, sometimes with a line of hyaline eglandular hairs opposite the leaf above. *Leaves* spirally-alternate, evenly distributed along the stems, sessile, the distal ones gradually smaller than the basal ones; sheaths 0.8–2.2 cm long, green to vinaceous, glabrous, with a line of hyaline, eglandular hairs opposite the leaf above; lamina 2.2–14 × 0.4–1.0 cm, membranous to succulent, canaliculate, slightly falcate, green on both sides, glaucous, drying olive-green to light green on both sides, linear-elliptic to linear-lanceolate, glabrous, base truncate to rounded, margins light green, glabrous, apex acuminate; midvein slightly conspicuous to inconspicuous, slightly impressed adaxially, slightly obtuse abaxially, secondary veins 2–3–(4) pairs, adaxially inconspicuous to slightly conspicuous, light green, abaxially slightly conspicuous. *Inflorescences* 1–4, terminal or axillary in the uppermost nodes, fascicle-like, composed of 1–2–(3) verticillate cincinni; peduncles absent; basal bract inconspicuous; cincinni bracts 1.6–1.8 × 0.3–0.4 cm, tubular, amplexicaul; cincinni 1-flowered, erect, straight, peduncle 1.0–1.9 cm long, light green to pink or vinaceous, glabrous; bracteoles inconspicuous, generally caducous. *Flowers* bisexual or male, actinomorphic, ca. 1.3–2.3 cm diam.; floral buds ellipsoid, 5.0–5.8 × 1.5–1.8 mm, light green to pink; pedicels 0.6–1.1 cm long, light green to pink to vinaceous, glabrous, erect and elongate in fruit; sepals 6.5–10.0 × 3.2–4.1



Figure 7. *Murdannia schomburgkiana* (Kunth) G.Brückn. Isolectotype of *Aneilema schomburgkianum* (P barcode P02088026). Photograph courtesy of the Muséum National d'Histoire Naturelle, Paris.

mm, triangular to ovate-triangular, cucullate, pink to pinkish brown, glabrous, apex acute, margins hyaline pink to hyaline vinaceous; petals equal, 0.8–1.3 × 0.8–1.0 cm, obovate to broadly obovate, slightly cucullate, lilac to purple, medially bearded with lilac to purple, moniliform hairs on the adaxial surface, base cuneate, margins entire, apex acute to obtuse; stamens 3, equal, filaments gently curved at the apex, 4.4–5.2 mm long, lilac to purple, densely bearded with moniliform, lilac to purple hairs, hairs slightly shorter than the filaments, anthers elliptic to oblong, 1.7–2.4 × 0.6–1.0 mm, connective brown, anthers sacs brownish lilac, pollen brownish lilac; staminodes 3, equal, filaments straight, 4.1–5.0 mm long, pale lilac to lilac, densely bearded with moniliform, lilac to purple hairs, hairs slightly shorter than the filaments, antherodes hastate, 0.9–1.7 × 1.3–1.7 mm, connective golden yellow, lobes conspicuous, cream-colored to pale yellow; ovary ellipsoid to oblongoid, 1.9–3.1 × 0.7–1.3 mm, 3-locular, light green to green, smooth, glabrous, style gently curved at the apex, ca. 4.1–5.4 mm, lilac to purple, stigma capitate, lilac to purple. *Capsules* 5.9–8.5 × 2.8–4.6 mm, 3-locular, 3-valved, oblongoid to broadly oblongoid, apiculate due to persistent style, light brown when mature, smooth, glabrous. *Seeds* (immature) 6 per locule, 2.7–3.3 × 2.6–3.1 mm, cuboid to polygonal, slightly cleft towards the embryotega, testa dark brown to greyish brown, densely farinose, scrobiculate, with ridges radiating from the embryotega; embryotega semilateral, relatively inconspicuous, without a prominent apicule, generally covered by a cream farina; hilum linear, ½ the length of the seed or smaller, on a weak ridge.

Specimens seen. **BRAZIL. Amazonas:** Provincia do Rio Negro, Rio Madeira, fl., s.dat., s.leg. s.n. (P barcode P03653202); s.loc., fl., Oct 1894, A.R. Ferreira 755 (K). **GUYANA. Rupununi District:** foot of Mount Shiriri, fl., 19 Jun 1995, M.J. Jansen-Jacobs et al. 4175 (P, U, US); loc. cit., Manari, Takatu river, fl., 5 Aug 1995, M.J. Jansen-Jacobs et al. 4764 (U, US); loc. cit., upper Rupununi river, fl., *Appun 2361* (K).

Distribution and habitat. *Murdannia schomburgkiana* is known from only four collections from Guyana (including the type) and perhaps only one collection from Brazil (in the state of Amazonas) (Fig. 10). It grows in open flooded grass fields and savannas in the Amazon domain. The distance between the Rio Madeira specimen and the other specimens collected in Guyana, make clear how poorly collected this species is. It is widely possible that field trips focusing on the group or in the white sand formations in the state of Amazonas will fill this distribution gap.

It is interesting to highlight that both specimens from Brazil might represent different sheets of the same collection. Firstly, it is known that Dr. Alexandre Ferreira collected exclusively in Brazilian territory. Thus, despite the locality not being clearly stated in the label of the specimen at Kew, this is the only possible option. Secondly, the specimen at Paris was collected in Brazil, Provincia Rio Negro, at the margins of Rio Madeira (currently state of Amazonas). This was one of the most important areas collected by Ferreira, during his philosophical travels, and probably the longest part of this fieldtrip. Also, it is widely known that many specimens collected by Friar Vellozo, Dr. Vellozo de Miranda and Dr. Alexandre Ferreira, were taken from Lisbon to Paris, during the Napoleonic Wars. Finally, the labels of both specimens possess comple-

mentary information, where the locality in the label of the Paris' specimen is one of locations where Ferreira collected, and the date is congruent with this specific fieldtrip. Moreover, the specimens on both sheets are very similar in appearance.

Phenology. It was found in bloom from June to October, and in fruit in October.

Conservation status. *Murdannia schomburgkiana* is only known from five (or at most six) collections, including the type species. Furthermore, the last known collections for this species are 11 years old, and the AOO of *M. schomburgkiana* is of only ca. 12.000 km². Following the IUCN recommendations (IUCN 2001), *M. schomburgkiana* should be considered Endangered [EN, B1a+C2a(ii)+D1].

Nomenclatural notes. When describing *Aneilema schomburgkiana*, Kunth (1843) mentions “Rob. Schomburgk misit sub. no. 842”. According to Stafleu and Cowan (1985), Robert Schomburgk's collections are generally housed at BM or K. Despite having found two specimens at BM, the specimen at B (B100367820) possesses the annotation “Ex. herb. Kunth misit. 1841.”, made in Kunth's handwriting and matching the protologue, and it is widely known that Kunth's herbarium was part of B (Stafleu and Cowan 1979). Thus, it was the obvious choice for a lectotype. The two sheets at BM were observed and described in detail by one of us (RBF) in 1993. However, they were not photographed when other types at BM were photographed, and the specimens cannot currently be located. If found they should be treated as isolectotypes.

Discussion. *Murdannia schomburgkiana* can be easily confused with *M. semifoliata* (C.B. Clarke) G.Brückn., due to their tuberous roots, reduced inflorescences enclosed by the leaf-sheaths, cincinni bracts tubular, petals medially bearded with moniliform hairs on the adaxial surface, filaments densely bearded with moniliform hairs, the number of seeds per locule of the capsule, and seed morphology. Their petals medially bearded with moniliform hairs on the adaxial surface, are quite unique within *Murdannia*. As aforementioned, this character is otherwise only known in Commelinaceae in *M. simplex* (in which the hairs are tiny and only present at the petal, being fundamentally different), and in the distantly related genera *Cochliostema* Lem. and *Geogenanthus* Ule (Tribe Tradescantieae, subtribe Dichorisandrinae; Hardy and Faden 2004; Pellegrini in press). Nevertheless, the distribution of both species does not overlap and they grow in different environments (white sand formations *vs.* flooded grass fields). *Murdannia schomburgkiana* can be differentiated by its 2.2–13.6 cm long blades of the leaves bearing inflorescences (*vs.* 0.2–1.8 cm long), leaf-blades margins glabrous (*vs.* ciliate), cincinni bracts 1.6–1.8 cm long (*vs.* 0.4–1.3 cm long), and brown anthers (*vs.* purple) (Table 1).

Despite the few collections known for this species, it is the authors' opinion that the morphological, geographical and environmental factors are enough to differentiate both species. *Murdannia schomburgkiana* and *M. semifoliata* are very similar to each other, and quite distinct from the remaining Neotropical species of the genus. They are morphologically similar to some Asian and African species with fascicle-like, mainly axillary inflorescences, and 1-flowered cincinni, such as *M. axillaris* and *M. triquetra*.

7. *Murdannia semifoliata* (C.B. Clarke) G.Brückn., Nat. Pflanzenfam. (ed. 2)15a: 173. 1930.

Figs 8, 10

Phaeneilema semifoliata (C.B. Clarke) G.Brückn., Notizbl. Bot. Gart. Berlin–Dahlem 10 (91): 56. 1927.

Aneilema semifoliatum C.B. Clarke, C.B. Clarke in Moore, Trans. Linn. Soc. London, Bot. 4: 498. 1895. Lectotype (designated here): BRAZIL. Mato Grosso: Santa Cruz [do Xingú], fl., Oct 1891–1892, S.M. Moore 541 (BM barcode BM000938202!; isolectotypes: B barcode B100367821!, NY barcode NY00247404!).

Description. *Herbs* ca. 20.0–70.0 cm tall, perennial, rhizomatous with a definite base, terrestrial to paludal to rooted emergent in open flooded fields. *Roots* tuberous, thick and fusiform, medium to dark brown, densely to sparsely pilose with medium to dark brown hairs, emerging from the short rhizome and from the basal nodes. *Rhizomes* short, brown, buried in the sand or soil. *Stems* erect, succulent, unbranched; internodes 1.2–13.3 cm long, green to vinaceous, glabrous, with a line of hyaline, eglandular hairs opposite to the leaf above. *Leaves* spirally-alternate, evenly distributed along the stems, the distal ones much smaller than the basal ones (which are generally bladeless sheaths with lamina no longer than 1.8 cm); sheaths 0.5–2.3 cm long, green to vinaceous, glabrous, with a line of hyaline, eglandular hairs opposite to the leaf above, margins setose to ciliate; lamina 0.2–8.9 × 0.2–0.7 cm, succulent, canaliculate, slightly falcate, green on both sides, glaucous, drying olive-green on both sides, linear-triangular to triangular, glabrous, base truncate, margins light green, setose at the base, ciliate at the middle, glabrous at the apex, apex acuminate; midvein inconspicuous on both sides, rarely slightly obtuse abaxially, secondary veins inconspicuous. *Inflorescences* (1–)2–6, terminal and axillary from the uppermost nodes, fascicle-like, composed of 1–2–(3) verticillate cincinni; peduncles absent; basal bract inconspicuous; cincinni bracts 0.4–1.3 × 0.1–0.3 cm, tubular, amplexicaul; cincinni 1-flowered, erect, straight, peduncle 0.8–4.2 mm long, light green to pink to vinaceous, glabrous, internodes inconspicuous; bracteoles inconspicuous, generally caducous. *Flowers* bisexual or male, actinomorphic, ca. 0.6–2.3 cm diam.; floral buds ellipsoid, 4.9–7.2 × 1.7–2.2 mm, light green to pink; pedicels 1.4–1.1 mm long, light green to pink to vinaceous, glabrous, erect and elongate in fruit; sepals 4.8–8.0 × 1.8–3.3 mm, triangular to ovate-triangular, cucullate, pink to pinkish brown, glabrous, apex acute, margins hyaline pink to hyaline vinaceous; petals equal, 0.5–1.2 × 0.3–0.8 cm, obovate, slightly cucullate, lilac to purple or mauve, rarely white, medially bearded with moniliform hairs on the adaxial surface, hairs lilac to purple, base cuneate, margins entire, apex acute to obtuse; stamens 3, equal, filaments gently curved at the apex, 3.2–5.0 mm long, lilac to purple, densely bearded with moniliform, lilac to purple hairs, hairs slightly shorter than the filaments, anthers linear-oblong to oblong, 2.0–3.5 × 0.4–0.7 mm, connective purple, anthers sacs lilac to purple, pollen lilac; staminodes 3, equal, filaments straight, 3.1–4.3 mm long, pale lilac to lilac, densely bearded with moniliform, lilac to purple hairs, hairs

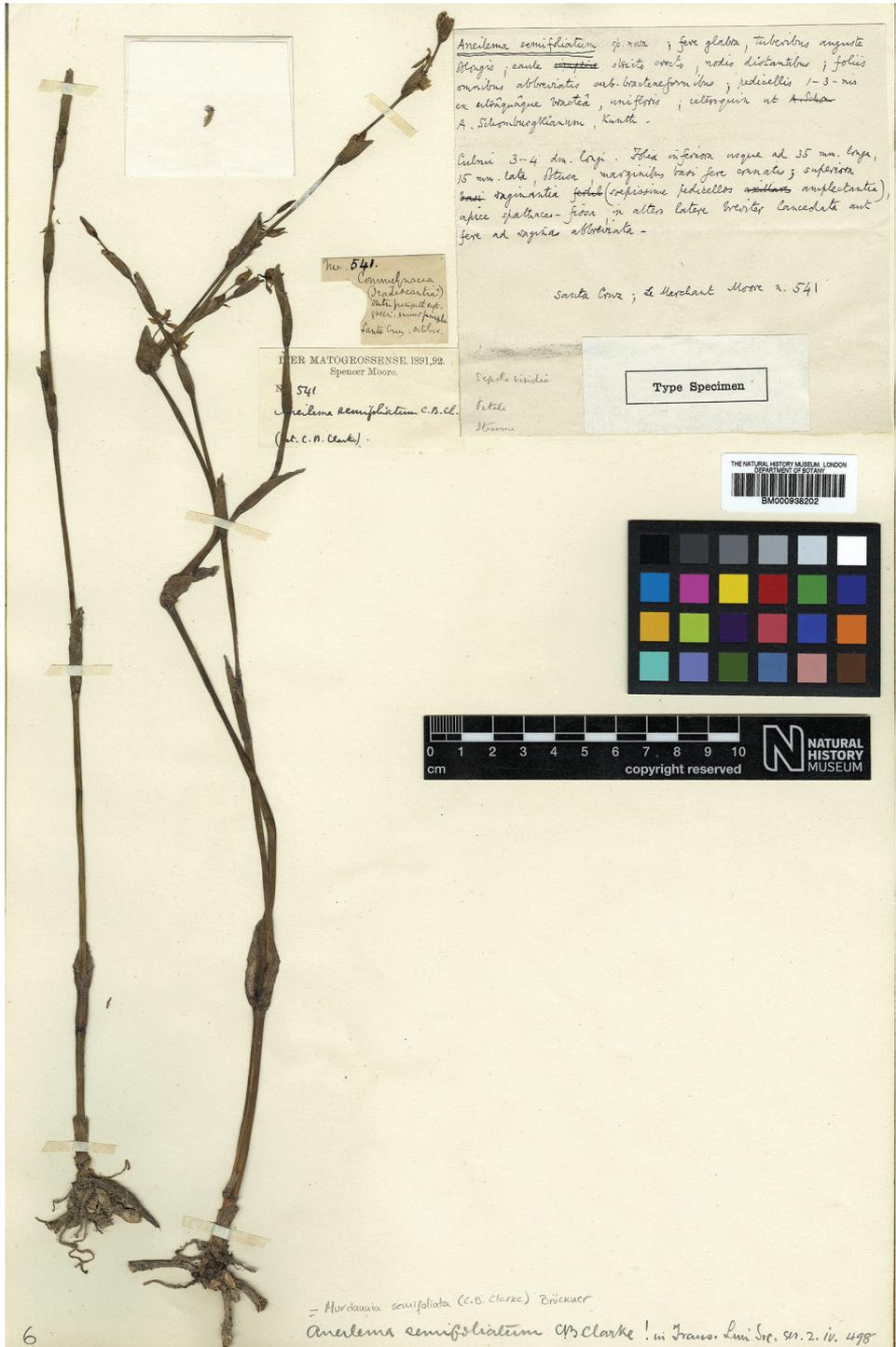


Figure 8. *Murdannia semifoliata* (C.B. Clarke) G.Brückn. Lectotype of *Aneilema semifoliatum* (BM barcode BM000938202). Photograph courtesy of The Natural History Museum of London.

slightly shorter than the filaments, antherodes hastate, 0.7–2.0 × 0.5–1.2 mm, connective golden yellow, lobes conspicuous, cream-colored to pale yellow; ovary ellipsoid to oblongoid, 1.5–3.3 × 0.5–1.0 mm, 3-locular, light green to green, smooth, glabrous, style gently curved at the apex, ca. 3.2–4.5 mm, lilac to purple, stigma capitate, lilac to purple. *Capsules* 5.8–1.2 × 3.3–5.6 mm, 3-locular, 3-valved; oblongoid to broadly oblongoid, apiculate due to persistent style, light brown when mature, smooth, glabrous. *Seeds* 6 per locule, 2.2–3.1 × 2.0–2.8 mm, cuboid to polygonal, slightly cleft towards the embryotege, testa dark brown to greyish brown, densely farinose, scrobiculate, with ridges radiating from the embryotege; embryotege semilateral, relatively inconspicuous, without a prominent apicule, generally covered by a cream farina; hilum linear, less than ½ the length of the seed, on a weak ridge.

Specimens seen. **BOLIVIA. Santa Cruz:** San Ignacio de Velasco, Oct 1958, M. Cardenas 5629 (BOLV, US). **BRAZIL. Mato Grosso:** Bananalzinho, Nov 1914, J.G. Kuhlmann 89 (R, SP); Braco, rio Arinos, 26 Sep 1943, J.T. Baldwin Jr. 3097 (US); Cuiabá, entre Cuiabá e Goyaz, Nov–Dec 1844, M.A. Weddell 3018 (P); loc. cit., rodovia MT-364, 35 km S de Cuiabá, 13 Nov 1975, G. Hatschbach 37491 (K, MBM); Nova Olímpia, Chapada dos Guimarães, 10 Oct 1995, J.H.A. Dutilh 199 (UEC); Poconé, 50 km S of Poconé on Transpantaneira highway to Porto Jofre, 27 Oct 1985, W. Thomas et al. 4641 (INPA, NY, US); loc. cit., highway Poconé-Porto Cercado, ca. km 21, 17 Feb 1992, M. Schessl 100/1-10 (UFMT, US); loc. cit., about 21 km S of Poconé, 7 Oct 1992, M. Schessl 071092-1-1 (UFMT, US); loc. cit., fazenda Ronco Bugiu, ca. 6–8 km à esquerda da rodovia Transpantaneira Poconé-P. Jofre, km 36, 31 Oct 1992, A.L. Prado et al. 3218 (HURB, UEC, UFMT); loc. cit., 22 Nov 1992, A.L. Prado et al. 2736 (HURB, UEC, UFMT); Rosário Oeste, ca. 2 km de Marzagão em direção à Planalto da Serra, 7 Oct 1997, V.C. Souza et al. 20255 (ESA, UFMT, UEC); Santo Antônio de Leverger, Barão do Melaço, km 30 of Leverger highway, 5 Nov 1991, M. Schessl 2421 (CH, UFMT, US); **Mato Grosso do Sul:** Aquidauana, entre as fazendas São Salvador e Costa Rica, 19 Nov 1995, A. Pott et al. 7628 (CGMS, CPAP, US); loc. cit., rodovia Taunay, fazenda Santa Cruz, próximo da aldeia indígena Ipegue, 20 Nov 2002, G. Hatschbach et al. 74377 (MBM).

Distribution and habitat. *Murdannia semifoliata* occurs mainly in Brazil (in the states of Mato Grosso and Mato Grosso do Sul) and in Bolivia (Fig. 10). It grows in open flooded grass fields in the Amazon, Cerrado and Chaco domains.

Phenology. It was found in bloom and fruit from September to February.

Conservation status. *Murdannia semifoliata* possesses a EOO of ca. 298,091.226 km² and a AOO of ca. 22,500.000 km². Despite the relatively great number of collections, most of them are in the state of Mato Grosso, with only one known collection on the state of Mato Grosso do Sul and another one from Bolivia. This whole region is under great threat due to the constant deforestation for cattle ranching. Thus, we believe that following the IUCN recommendations (IUCN 2001), *M. semifoliata* should be considered Nearly Threatened.

Nomenclatural notes. When describing *Aneilema semifoliatum*, Clarke (1895) mentions “Crescit ad Santa Cruz, ubi mens. Oct. floret. (N. 541)”. The specimen at BM

matched the protologue perfectly. Furthermore, it possesses a detailed description and was identified by Clark himself. Thus, it is here designated as the lectotype of *A. semifoliatum*.

Discussion. *Murdannia semifoliata*, as aforementioned, is morphologically similar to *M. schomburgkiana*. They share a peculiar vegetative morphology, inflorescence architecture, and petals medially bearded with moniliform hairs on the adaxial surface, not similar to any other Neotropical species. *Murdannia semifoliata* is especially distinctive due to its extremely reduced blades of the leaves bearing inflorescences, produced during the flowering period (Table 1). In most individuals, the blades are so reduced that the whole plant seems to be aphyllous. Furthermore, *M. semifoliata* and *M. schomburgkiana* are the only Neotropical species to possess more than two seeds per locule, which gives the seeds a peculiar cuboid to polygonal shape.

8. *Murdannia* aff. *triquetra* (Wall. ex C.B. Clarke) G.Brückn., Nat. Pfl.-Syst. (ed. 2) 15a: 173. 1930.

Fig. 9

Phaenilema triquetrum (Wall. ex C.B. Clarke) G.Brückn., Notizbl. Bot. Gart. Berlin-Dahlem 10: 56. 1927.

Aneilema triquetra Wall. ex C.B. Clarke, Monogr. Phan. 3: 208. 1881. Lectotype (designated by Ancy et al. 2015): BANGLADESH. India Orientalis, in Prov. Sylhet, fl., fr., s.dat., N. Wallich 5220 (B barcode B100367814!; isolectotypes: E barcode E00393352!, GDC barcode GDC00489348!; K n.v.).

Diagnosis. *Herbs* ca. 10.0–20.0 cm tall, annual, without a definite base, rooted emergent in flooded fields. *Roots* thin, fibrous, medium to dark brown, densely to sparsely pilose with medium to dark brown hairs, emerging from the basalmost nodes. *Rhizomes* absent. *Stems* trailing, floating on water with ascending apex, succulent, densely branched at the base, glabrous or with minute eglandular hairs. *Leaves* spirally-alternate, evenly distributed along the stems; sheaths 0.7–1.0 cm long, glabrous; lamina 2.0–4.5 × 0.6 cm, narrowly lanceolate to lanceolate-oblong, glabrous membranous, slightly canaliculate, green on both sides, base rounded to amplexicaul, margins glabrous, sometimes undulate, apex acute to acuminate. *Inflorescences* 1–3, terminal or axillary in the distalmost (up to 4) nodes, fascicle-like, sessile, enclosed by the leaf-sheaths, composed of 1–2–(3) verticillate cincinni; peduncle absent; basal bract inconspicuous; cincinni bracts absent; cincinni 1-flowered, erect, straight, peduncle ca. 3.0 mm long, glabrous, internodes inconspicuous; bracteoles absent. *Flowers* male or bisexual, actinomorphic, barely exerted from the sheath; floral buds ellipsoid, light green; pedicels ca. 3 mm long, erect and elongate in fruit; sepals 4.0–5.5 mm long, linear-elliptic, cucullate, light green to pale pink, glabrous; petals equal, elliptic, slightly cucullate, white to pale lilac or pale pink, glabrous; androecium not determinable; ovary ellipsoid, tapering into the style, 3-locular, light green, smooth, glabrous, style straight, 1.7 mm long, glabrous, stigma capitate. *Capsules* 4.5–5.5 × 2.0–2.5 mm, ob-



Figure 9. *Murdannia* aff. *triquetrum* (Wall. ex C.B. Clarke) G. Brückn., from Esteros de Arauca, Colombia. **A** Detail of a stem, showing an apical fruit **B** detail of an internode, showing a side view of a male flower. Photographs by M. Fernández.

longoid to ellipsoid, 3-locular, 3-valved, apiculate due to persistent style, light brown when mature, smooth, glabrous, locules 3-seeded (only 1 counted). *Seeds* (only 1 mature seed seen) transversely ellipsoid, ca. 1.5×0.9 mm, testa brown, with deep dorsal pits and longitudinal furrows, farinose only around the embryotega, appendage absent; embryotega lateral, inconspicuous, without a prominent apicule; hilum linear, less than $\frac{1}{2}$ the length of the seed, borne on a ridge.

Specimen seen. VENEZUELA. Tachira. Distr. Libertador: 10 km S of El Piñal, $71^{\circ}55'W$, $7^{\circ}27'N$, alt. 250 m, 7 Nov. 1982, G. Davidse & A. C. González 21663 (US).

Distribution and habitat. Known for certain only from this collection. The general habitat was recorded as “partially inundated forest remnant with slow stream and pools of standing water” and for this collection as “stems floating in pool of creek.” A photograph of a plant from Colombia, which may or may not be the same species, was sent to the first author, but without a corroborating specimen, so it has not been considered for this description. However, we have illustrated it in Fig. 9 to encourage collectors to look for it.

The *M. keisak* complex is widespread in Asia, ranging from India to China and Japan, growing in flooded grasslands and disturbed areas. In South America, it is known from only two collections, one from Venezuela and one from Colombia. Unfortunately, it seems that the specimen from Colombia went astray during shipping, since it was never received by the first author.

Phenology. It was found in bloom and fruit in November.

Conservation status. Following the IUCN recommendations (IUCN 2001), this species should be considered Data Deficient. Correspondence by the second author

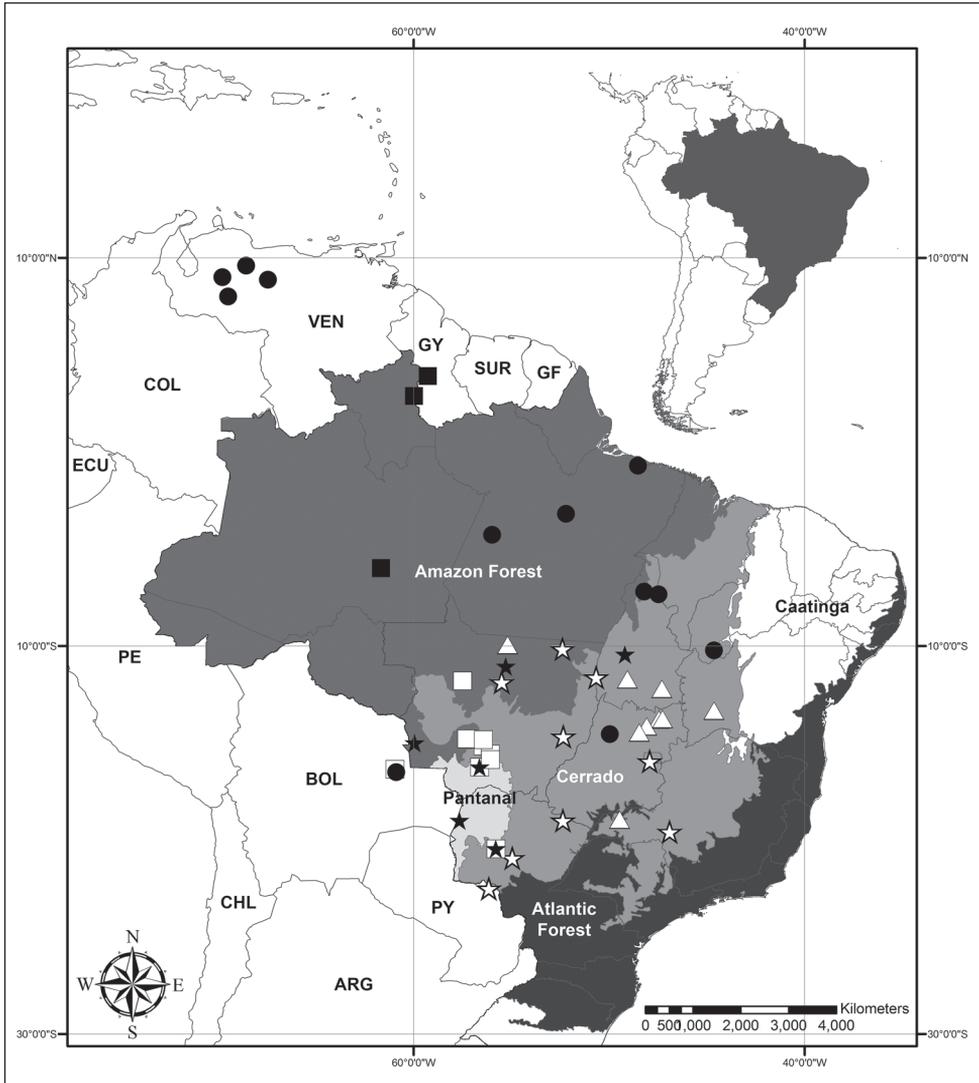


Figure 10. Distribution map of Neotropical *Murdannia* Royle. Full circles *M. burchellii* Full stars *M. engelsii* Triangles *M. gardneri* Stars *M. paraguayensis* Full squares *M. schomburgkiana* Squares *M. semifoliata*.

with the collector Gerrit Davidse, indicated that this was not a disturbed habitat in which one would expect to find introduced weeds. However, the habitat was under great pressure and possibly no longer exists.

Nomenclatural notes. Nandikar and Gurav (2015) designated the specimen at CAL (CAL0000025807) as the lectotype for *A. triquetrum*. Nevertheless, after analyzing the specimen, comparing it to the protologue and to the remaining specimens, it became clear that the specimen at CAL is not conspecific to the specimens at B, E and

GDC. Ancy et al. (2015), unaware of the article published just few months earlier by Nandikar and Gurav (2015), designate the specimen at B (B100367814) as the lectotype for *A. triquetrum*. Their choice matches perfectly the protologue, and thus should be followed instead of the lectotypification made by Nandikar and Gurav (2015). Nonetheless, if ever found, the specimen at K would make a much better choice of a lectotype. At the time of the description of *A. triquetrum* and the completion of his monograph (i.e. 1881), Clarke was working at K, and would had access to a possible specimen in the Wallich Herbarium, housed at Kew.

Discussion. This is a widely distributed species complex, being very common and well collected in Asia. Nevertheless, the morphologic limits between *M. keisak* and *M. triquetra*, as well as the application of these names, varies greatly according to each author. In Flora of China (Hong and DeFilipps 2000), both species are accepted, although somewhat tentatively, and are separated by the length of the sepals, shape and size of the capsule, and number and shape of the seeds. The authors also state that the morphologic differences seem to be associated with the geographic distribution of the taxa. Nevertheless, both descriptions overlap with the description presented by Faden (2000) for *M. keisak*, in North America. Ancy (2014), in her unpublished Ph.D. thesis, presents a thorough taxonomic account on *Murdannia* from India. Her description of *M. triquetra* matches very closely the two specimens known for South America, in sepal, petal and fruit morphology. Nonetheless, Ancy (2014) describes the filaments as being glabrous, contrary to the bearded filaments known for the South American specimens. The author also omits the description of the antherodes, which in the South American specimens are yellow and cordate. Nevertheless, some young flower buds dissected by the second author lacked hairs on the filaments of the stamens and completely lacked staminodes, but that might have been a developmental stage and thus may not be a discrepancy. This could be related to the extremely immature state of the dissected buds, and could explain the discrepancy of our description and the description presented by Ancy (2014). Nandikar and Gurav (2015) published a second account on the Indian species of *Murdannia*. In their treatment, *M. triquetra* differs greatly from the South American specimens. However, it matches very closely the description presented by Hong and DeFilipps (2000), Faden (2000) and Chowdhury et al. (2015) for *M. keisak*. In these descriptions, the antherodes are described as sagittate and ranging from lilac to purple, and clearly do not match the South American specimens.

It is the authors opinion that a study focusing on the specific boundaries between these taxa is necessary. Nevertheless, since this species complex is only invasive in the New World, we also believe that the required investigation should be carried out in the plants native range. It is also possible that these Neotropical collections represent a distinct taxon, not closely related to the other native South American species. But a much better South American sampling for comparison and a much more detailed would be required. Field work, better sampling of herbaria specimens, detailed study of reproductive morphology, analysis of the protologues, and population studies might shed a light on the issue.

Conclusions

Neotropical *Murdannia* is represented by six native species confined to South America, mostly in Brazil. The species can be distinguished from one another by growth habit, branching pattern of the stems, phyllotaxy, indumentum type, inflorescence morphology, indumentum on the petals, androecium and gynoecium, capsule morphology, seed shape, and by the ornamentation of the testa. Two invasive species, native to Asia, are found in the Neotropics. *Murdannia* aff. *triquetra* is recorded for the first time in South America. Despite being rarely collected, the known South American populations seem to be well-established and should be monitored to avoid the dispersal of yet another invasive species of Commelinaceae. It may be mentioned, for the sake of completeness, that the only other *Murdannia* species recorded from the Western Hemisphere is the Asian taxon *M. spirata* (L.) G.Brückn., which is naturalized in southern Florida, United States (Faden 2000).

Despite being seldom collected, Neotropical *Murdannia* are generally described in labels as forming large populations. It is possible that the lack of collections for the group is connected to: (1) the difficulty to access the areas where they occur (e.g. Amazonian river banks); (2) general neglect of aquatic flora, due to logistic difficulties in field work; (3) the difficulty to preserve Commelinaceae flowers in dried specimens, discouraging botanists to collect them; (4) and lack of field work focusing on herbaceous plants. The authors hope that the present work will encourage field workers to collect Commelinaceae specimens in the Amazon, Cerrado, Chaco and Pantanal domains. Furthermore, the increase of collections will enable researchers to monitor these species' populations in order to update and provide more precise conservation assessments for them, and monitor the need for biological control of the known invasive species.

Although several studies focusing on morphology, anatomy and cytology of *Murdannia* are available in the literature, no comprehensive phylogenetic study has been presented up to date. Burns et al. (2011) were the first to sample more than one species of *Murdannia* in a phylogenetic analysis. However, all of the five sampled species were Asian and none represented the type-species. Thus, the monophyly of *Murdannia* is still to be tested in future studies. Ancy (2014) presented a morphological phylogeny, sampling exclusively the species native to India. In her analysis, the clades are supported by characters like inflorescence architecture, androecium, capsule and seed morphology. As aforementioned, the Neotropical species of *Murdannia* are extremely peculiar in a considerable number of morphological characters, and nothing is known regarding their phylogenetic relationships, anatomy or even their cytology. Thus, three important questions about the Neotropical species are: (1) how are they related to one another; (2) what is the relationship between the Neotropical species and the rest of the genus; and (3) how many dispersal events the Neotropical lineages of *Murdannia* would represent. In a more general sense, it would also be important to understand the evolution of morphological characters in the genus on a phylogenetic framework, such as the inflorescence and androecium morphology.

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Phylogenetic analyses and morphological characteristics support the description of a second species of *Tridimeris* (Annonaceae)

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Abstract

Based on phylogenetic and morphological evidence, *Tridimeris chiapensis* Escobar-Castellanos & Ortiz-Rodr., **sp. n.** (Annonaceae), a new species from the karst forest of southern Mexico, is described and illustrated. The new species differs from *Tridimeris habniana*, the only described species in the genus, in that the latter has flowers with sepals densely tomentose outside, one (rarely two) carpel(s) per flower and fruits densely covered with golden-brown hairs, while *Tridimeris chiapensis* has flowers with glabrous sepals outside, two to five carpels per flower and glabrous fruits. Furthermore, a shallow triangular white patch at the base of the inner petals is found in *T. chiapensis*, a morphological character shared with the sister genus *Sapranthus* but absent in *T. habniana*. Geographically, both species occur allopatrically. With just one known locality and seven individuals of *Tridimeris chiapensis* recorded in one sampling hectare, and based on application of the criteria established by the IUCN, we conclude tentatively that the species is critically endangered.

Keywords

Dimery, Neotropical, Miliuseae, tropical rainforest

Introduction

Annonaceae is a plant family composed of about 110 genera and 2,500 species of trees and lianas (Couvreur et al. 2012, Erkens et al. 2012). Most genera of Annonaceae (except *Asimina*, endemic to the USA) are exclusively tropical and many are important floristic elements in several lowland forests. Within continents, the endemism at generic level is very high and only the genus *Xylopia* is pantropical (Doyle and Le Thomas 1997). Recent phylogenetic analyses (Richardson et al. 2004, Chatrou et al. 2012) show that Annonaceae is composed of four major lineages, and on that basis, the family is now classified into four subfamilies: Anaxagoreoideae, Ambavioideae, Annonoideae and Malmeoideae. Of these, Annonoideae (50 genera and 1600 species) and Malmeoideae (50 genera and 700 species) are the most species-rich lineages in Annonaceae (Pirie and Doyle 2012). In Mexico the family is represented by eleven genera, *Anaxagorea*, *Annona*, *Cymbopetalum*, *Desmopsis*, *Guatteria*, *Mosannonna*, *Sapranthus*, *Stenanonna*, *Tridimeris*, *Unonopsis* and *Xylopia*, of which *Tridimeris* is endemic.

Tridimeris is a monotypic and poorly studied genus. Baillon (1869) described its only species, *Tridimeris habniana* Baill., based on exemplars from Veracruz, Mexico (Turner 2013). The species, restricted to eastern Mexico in the states of San Luis Potosí, Puebla and Veracruz (Figure 1), is easily recognizable by its greenish and dimerous flowers (two sepals and four petals) and its large and fleshy fruits densely covered with golden-brown hairs (Schatz 1987). Dimery is uncharacteristic in Neotropical Annonaceae and it has been recorded only in *Anaxagorea silvatica* R. E. Fr., *Ephedranthus dimerus* J. C. Lopes, Chatrou & Mello-Silva and, *Malmea dimera* Chatrou (Lopes et al. 2014). Phylogenetic analyses based on molecular characters (Saunders et al. 2011, Chaowasku et al. 2012, 2014, Xue et al. 2011, 2014, Ortiz-Rodríguez et al. 2016) show that *Tridimeris habniana* belongs to the Malmeoideae tribe Miliuseae, where along with *Desmopsis*, *Sapranthus* and *Stenanonna* it forms the subtribe Sapranthinae (Ortiz-Rodríguez et al. 2016). *Sapranthus* and *Tridimeris* are closely related and together form the sister group of the remaining members of Sapranthinae. Although *Sapranthus* and *Tridimeris* have contrasting floral characteristics, with *Tridimeris* showing axillary, dimerous and greenish flowers whilst *Sapranthus* shows leaf-opposed, trimerous and usually brown to purple colored flowers, both genera are characterized by large and fleshy fruits, these last characteristics being their most obvious synapomorphy (Schatz 1987).

During a floristic study in southern Mexico, several individuals of an unusual species of Annonaceae were collected. The general characteristics of its flowers, notably dimery, suggested that it probably was a species related to the genus *Tridimeris*; however, its fruit characteristics did not fit with those of *Tridimeris habniana*. To elucidate this, we performed molecular phylogenetic analyses including one sample of the putative new species and studied its morphological characteristics in detail to corroborate its identity at the genus level and to determine whether the collections from Chiapas represent a second species of *Tridimeris* for the Mexican flora.

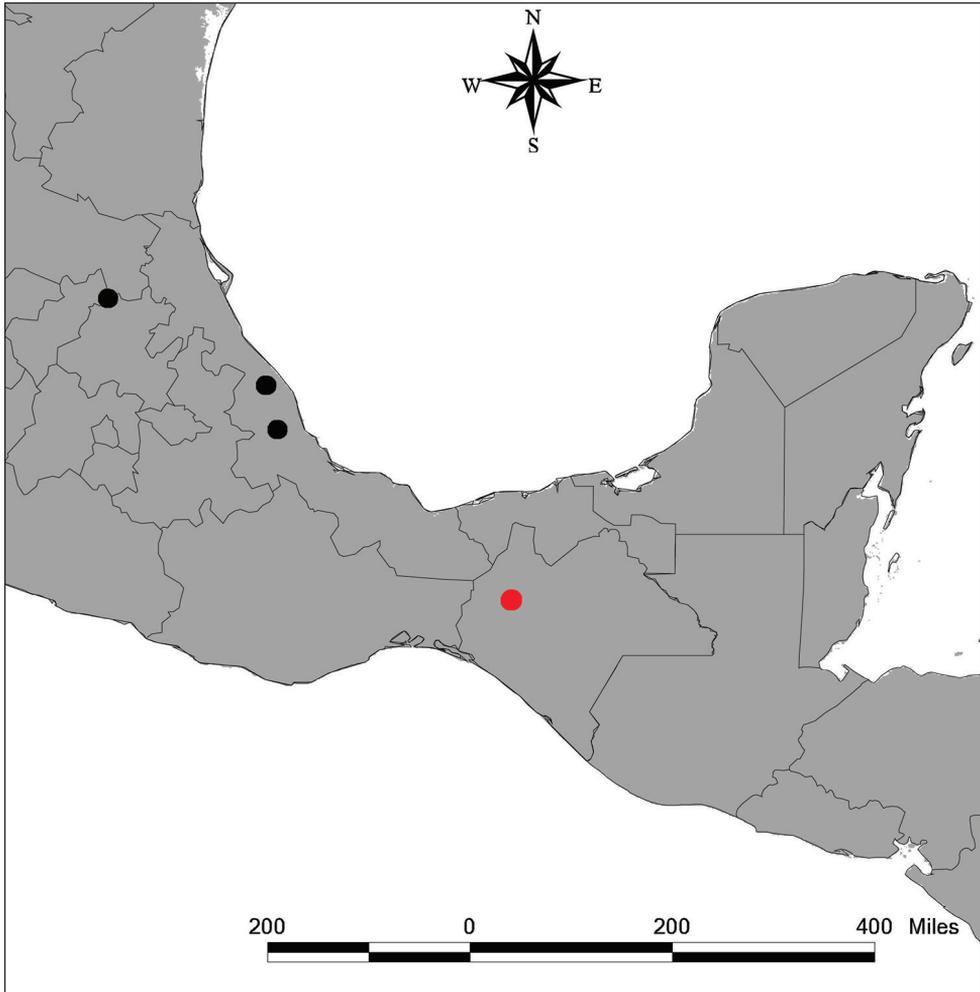


Figure 1. Distribution range of *Tridimeris chiapensis* Escobar-Castellanos & Ortiz-Rodr. (red dot) and *Tridimeris habniana* Baill (black dots).

Material and methods

Molecular data

DNA extraction was performed using a CTAB (acetyl trimethyl ammonium bromide) method (Doyle and Doyle 1987). Four plastid markers, *matK*, *rbcL* and *ycf1* coding regions and *trnL-F* spacer, were amplified and sequenced using the following primers: matK-13F/515R, matK-424F/788F and matK-449F/824R (Su et al. 2008); 1F/724R (Olmstead et al. 1992) and 636F/1460R (Fay et al. 1997; Fay et al. 1998); 72F/1674R and 914F/2323R (Chaowasku et al. 2012); trnL(UUA)/trnF(GGA) (Taberlet et al. 1991). For amplification each 14 μ L PCR contained 2.02 μ L of 5' buffer (Promega, Madison, WI, USA), 2.02 mL $MgCl_2$ (25 mM), 1.02 μ L dNTPs mix (8 mM), 0.22 μ L of each

primer (10 μ M), 0.10 μ L Taq polymerase (5U/ μ L) (Promega), 0.56 μ L of BSA (Promega), 2 μ L of template DNA, and finally dH₂O added to bring to volume. The PCR program used comprised 35 cycles of 94°C for 45 s, 53 °C–65 °C for 30 s (annealing temperatures depending on each primer pair), 72°C for 2 min, with the initial denaturation for 3 min at 94°C and a final extension for 7 min. at 72°C. PCR products were purified with the QIAquick PCR Purification kit (Qiagen) and sequenced using the BigDye Terminator Cycle Sequencing kit (Applied Biosystems, Foster City, California, USA). The products were analyzed on a 310 automated DNA sequencer (Applied Biosystems) at the University of Washington High Throughput Genomics Unit, Seattle, Washington. The sequences obtained were first edited and assembled in Sequencher ver. 4.1 (Gene Codes Corp., Ann Arbor, MI, USA), and subsequently aligned using PhyDE-1 ver. 0.9971 (Müller et al. 2010). Additionally, sequences of the coding region *matK*, *ndhF*, *rbcL* and *ycf1* and *psbA-trnH* and *trnL-F* spacers of other Neotropical genera of Miliuseae (*Desmopsis*, *Sapranthus*, *Stenanona* and *Tridimeris hahniana*) and a few representatives of Asian Miliuseae were obtained from GenBank and included in the molecular matrix. [The samples, localities and GenBank accession numbers are listed in Appendix 1].

Phylogenetic analyses

Phylogenetic relationships among taxa were estimated using Bayesian inference (BI), maximum likelihood (ML), and parsimony methods. Analyses of six cpDNA regions were conducted separately (for regions with information available for the new species) and in combination.

For BI, three partitioning strategies were used: (1) data matrix divided into six partitions based on DNA region identity, (2) six plastid markers concatenated and analyzed without partitioning, and (3) 2-partitioned, distinguishing coding (*matK*, *ndhF*, *rbcL* and *ycf1*) and non-coding (*psbA-trnH* and *trnL-F*) regions. jModelTest ver. 3.06 (Posada 2008) was used to determine the appropriate DNA substitution model and gamma rate heterogeneity for each partition using the Akaike Information Criterion (AIC). The BI analysis was performed using MrBayes ver. 3.2.1 (Ronquist and Huelsenbeck 2003) with two independent runs of four chains and ten million generations with trees sampled every 1000 generations. Convergence was assessed using the standard deviation of split frequencies as a convergence index, with values <0.01 interpreted as indicating good convergence. Tracer ver. 1.5 (Rambaut and Drummond 2007) was used to determine whether the parameter samples were drawn from stationary, unimodal distribution, and whether adequate effective sample sizes (ESS) for each parameter (ESS>200) were reached. The initial 25% of samples of each MCMC run were discarded as burn-in, and the remaining trees were summarized as posterior probabilities; PP values ≥ 0.95 were considered to represent strong support. Analysis performance of each partitioning strategy was assessed using Bayes factor. Bayes factors were calculated from the estimated harmonic means of likelihood using the *sump* command in MrBayes. Decisions were taken based on the 2ln Bayes factor criterion (Kass and Raftery, 1995), for which

the Bayes factor scale of strength of evidence in favor of one hypothesis is: 0–2 (not worthy of mention), >2–6 (positive), >6–10 (strong), >10 (very strong).

For the ML analysis, the dataset was divided based on Bayes factor results (see above and results). Phylogenetic reconstruction was performed using RAxML ver. 8.2.4 (Stamatakis 2014) under the general time-reversible (GTR) nucleotide substitution model and 1000 non-parametric bootstraps using the CIPRES Science Gateway (Miller et al. 2010). Bootstrap support values were interpreted as weak (50–70%), moderate (71–80%) and strong support (81–100%).

The most parsimonious trees were obtained using the ratchet strategy (Nixon 1999) in Winclada ver. 1.0000 (Nixon, K. C. 1999–2002), running NONA ver. 2.0 (Goloboff 1993) on a combined dataset of six plastid regions, with nucleotide characters treated as unordered and equally weighted, 1000 iterations, holding 10 trees per iteration with 10% of nodes constrained, and all other parameters set to default. Branch support was assessed using bootstrap resampling, 1000 bootstrap-resampled pseudoreplicate matrices were each analyzed using 100 random addition sequences (multi*100). Ten trees were retained during TBR swapping after each search initiation (hold/10) using NONA ver. 2.0 and performed in WinClada, with the same interpretations of support level as in the ML analyses.

Morphological differentiation

We examined the specimens of *Tridimeris habniana* deposited at XAL herbarium (Thiers 2016). Also, we consulted the digitized type specimens available at JSTOR Global Plants (<http://plants.jstor.org/>). The putative new species was recognized using the unique combination of features criteria (Donoghue 1985) through comparisons with morphologically similar species and literature review (Schatz 1987). Finally, we elaborated the species description following terminology presented in Hickey (1973).

Conservation status

We assessed the conservation status by calculating the extent of occurrence (EOO) and the area of occupancy (AOO) using the GeoCAT tool (Bachman et al. 2011) and applying the IUCN Red List Categories and criteria (IUCN 2001).

Results

Analysis of individual cpDNA regions

Each individual cpDNA region provided a relatively good resolution within Sapranthinae clade, with most branches resolved in the four separate trees (Suppl. material

1–4). Analyses of the *matK*, *rbcL* and *ycf1* coding regions showed that Sapranthinae is composed of two main subclades, the *Desmopsis-Stenanona* clade and the *Sapranthus-Tridimeris* clade, while the analysis of *trnL-F* spacer showed very low resolution recovering only the *Sapranthus-Tridimeris* clade (Suppl. material 1–4). Each phylogenetic hypothesis unequivocally placed the new species within the *Sapranthus-Tridimeris* clade.

Analysis of combined data

The concatenated 32-accession dataset contained 6419 aligned positions, of which 746 were variable and 208 were parsimony informative. For the Bayesian analyses, the substitution model was GTR+G for *matK*, *trnL-F*, *psbA-trnH* and unpartitioned datasets, GTR+G+I for *rbcL*, *ndhF* and coding datasets and HKY+G for non-coding dataset.

The six partitioned strategy considerably improved the mean $-\ln L$ values in the Bayesian analyses (mean $-\ln L$ non-partitioned = -15754.57 ; mean $-\ln L$ 2-partitioned = -15725.73 ; mean $-\ln L$ 6-partitioned = -15722.11). Bayes factor comparison indicated that the analyses using six partitions provided a better explanation of the data than unpartitioned and 2-partitioned analyses. For the ML analyses the likelihood score of the optimal ML tree, was $\ln L = -15572.87$. The parsimony analysis of the combined regions resulted in 20 most parsimonious trees of 1030 steps with a Consistency Index of 0.79 and a Retention Index of 0.60. The subsequent presentation of the results is restricted to the 50% majority rule consensus tree derived from Bayesian analyses using six partitions.

The partitioned BI, ML and parsimony analyses resulted in similar tree topologies. The 50% majority-rule consensus BI tree resulting is shown in Fig. 2. All phylogenetic analyses indicate that the Neotropical Miliuseae (Sapranthinae subtribe) forms two strongly supported clades: the *Desmopsis-Stenanona* clade (1.0 PP, 100% bootstrap support (MLBS), 98% MP bootstrap support (MPBS)) and the *Sapranthus-Tridimeris* clade (1.0 PP, 98% MLBS, 92% MPBS). The first clade includes the genera *Desmopsis* and *Stenanona*, however, they appear to be not monophyletic and species of both genera appear intermingled. The second clade is composed of *Sapranthus* and *Tridimeris*, with each resolved as monophyletic group (*Sapranthus*, 1.0 PP, 98% MLBS, 97% MPBS; *Tridimeris*, 1.0 PP, 100% MLBS, 90% MPBS). The phylogenetic hypothesis indicates that effectively the new species, *Tridimeris chiapensis*, is part of the genus *Tridimeris*.

Morphological differentiation

Morphologically, *Tridimeris chiapensis* has a set of morphological characters that clearly distinguish it from *T. habniana* (Fig. 3, Table 1). In addition, both species occur in disjunct locations and therefore distributed allopatrically (Fig. 1).

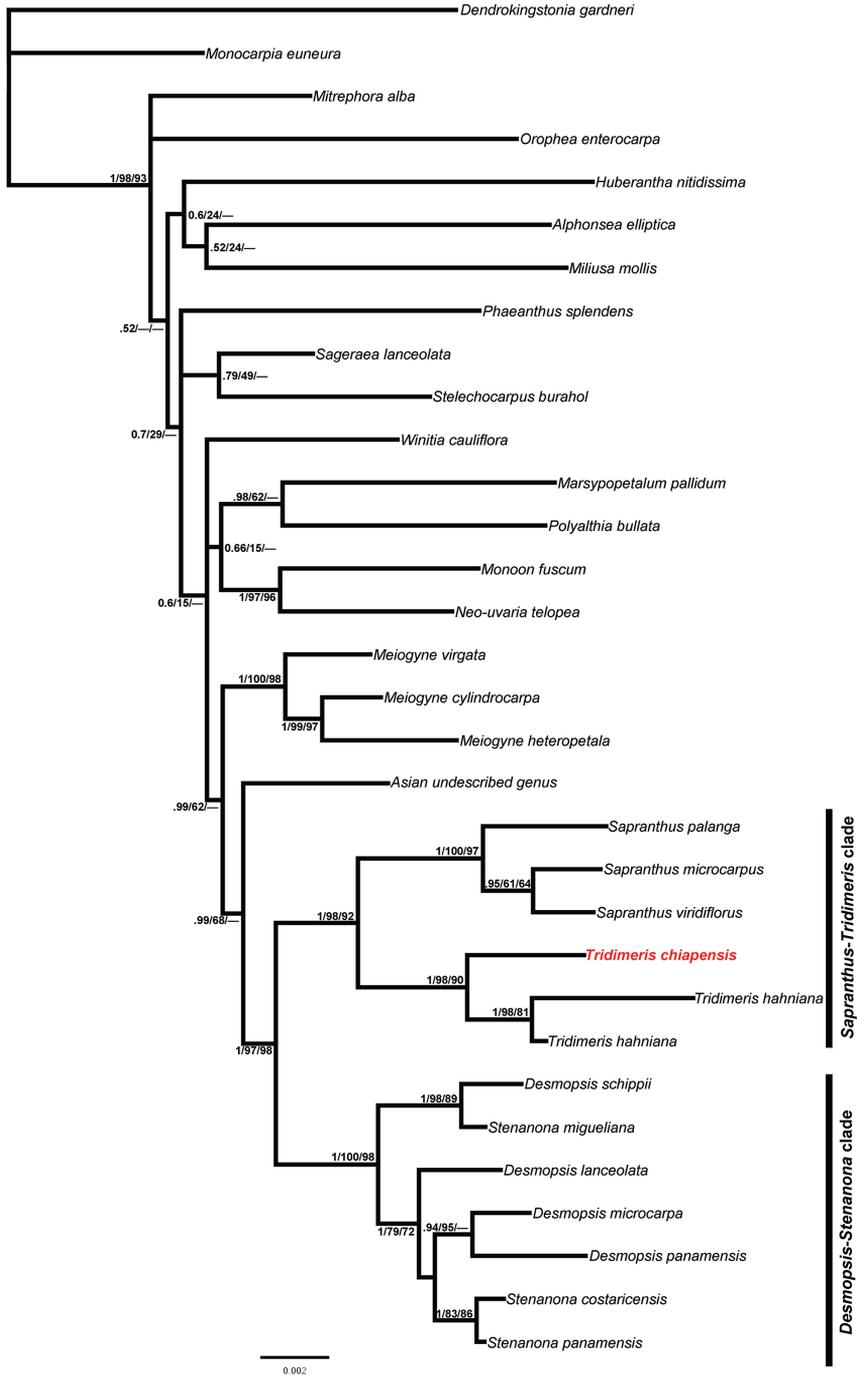


Figure 2. The 50% majority-rule consensus tree from the Bayesian analysis of six cpDNA markers. Numbers on branches of the major clades indicate Bayesian posterior probabilities (PP), maximum likelihood (MLBS) and parsimony (MPBS) bootstrap values in that order. In red, the position of *Tridimeris chiapensis* Escobar-Castellanos & Ortiz-Rodr.

Table 1. Comparison of diagnostic morphological characters of *Tridimeris chiapensis* and *Tridimeris habniana*.

Characters	<i>Tridimeris chiapensis</i>	<i>Tridimeris habniana</i>
Pedicelel	Glabrous	Golden tomentose
Sepals	Glabrous outside	Densely tomentose outside
Inner petals	Thick and fleshy	Flat and thin
Carpels	2–5	1 (occasionally 2)
Monocarps	Glabrous	Golden brown tomentellous
Distribution	Mexico (Chiapas)	Mexico (Puebla, San Luís Potosí and Veracruz)

Discussion

The phylogenetic analyses showed that *Tridimeris chiapensis* and *T. habniana* form a strongly supported monophyletic group (Fig. 2). The two species of *Tridimeris* share axillary inflorescences, dimery flowers (two sepals and four petals), greenish petals, and large and fleshy fruits. Furthermore, both species have pocket domatia in the axils of secondary veins. As in previous studies, *Tridimeris* and *Sapranthus* appear to be closely related (Saunders et al. 2011, Chaowasku et al. 2012, 2014, Xue et al. 2011, 2014, Ortiz-Rodríguez et al. 2016) and together form the *Sapranthus-Tridimeris* clade.

Tridimeris chiapensis clearly differs from *T. habniana* by its number of carpels per flowers, fruit surface, glabrous pedicels and sepals, and by the presence of a triangular white patch near the base of inner petals (Fig. 3). A similar white patch is found in the inner petals of *Sapranthus viridiflorus* G.E. Schatz, which have been considered by Schatz (1998) as a vestigial food body since food bodies are morphological modifications of a specific area of inner petals as food reward for floral visitors (Schatz 1987). However, a more detailed study of these structures is needed, as well as the compounds present in this structure and its anatomical characteristics in order to determine its function.

Ecologically *T. chiapensis* inhabits wet forests on karstic topography around 1000 m elevation, while *T. habniana* occurs in lowland wet forests (200–900 m) or even in cloud forests in the northern portion of its distribution (Schatz 1987). The type locality of *T. chiapensis*, the protected natural area La Pera in Chiapas, is a karstic zone covered mostly by tropical rain forest. This area among other similar regions of southern Mexico, are considered centers of plant endemism (Wendt 1987).

Taxonomic treatment

Tridimeris chiapensis Escobar-Castellanos & Ortiz-Rodr., sp n.

urn:lsid:ipni.org:names:77158527-1

Figs 1–3

Type. Mexico. Chiapas, Municipio de Berriozábal, Zona Sujeta a Protección Ecológica “La Pera”, Campamento “Trepatroncos” carretera Berriozábal-Joaquín Miguel Gutiérrez,

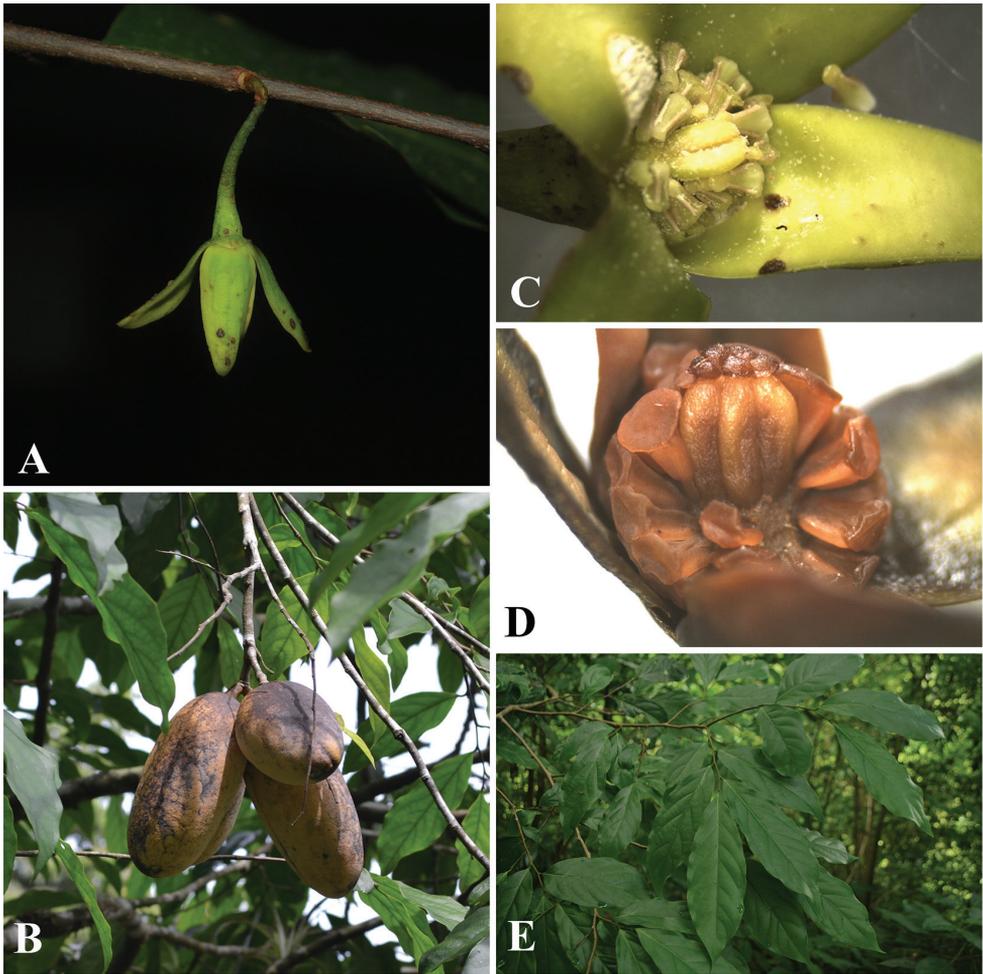


Figure 3. *Tridimeris chiapensis* Escobar-Castellanos & Ortiz-Rodr. **A** Dimerous flower **B** Large and fleshy fruits **C** Flower showing the pollen release and a triangular white patch at the base of the inner petals **D** Five carpels surrounded by numerous stamens **E** Leafy branches. Photographs by Marcos Escobar-Castellanos.

km. 12 desvío a Montebello, 1081 m, 16°52'20.3"N, 93°19'32.5"W, 11 August 2016 (fl) Escobar-Castellanos M. A. 0689 (holotype HEM; isotypes: XAL, MO).

Diagnosis. *Tridimeris chiapensis* is phylogenetically related to *Tridimeris hahniana* with which it shares axillary and dimerous flowers and large and fleshy fruits. However, *Tridimeris chiapensis* differs in having flowers with glabrous sepals, a triangular white patch near the base of inner petals and 2-5 carpels per flower and glabrous fruits (Fig. 3), while *T. hahniana* has flowers with sepals densely tomentose outside, 1 or 2 carpels per flower and fruits densely covered with golden-brown hairs.

Tree 3–9 m tall and 3–14 cm DBH; young branches slightly pubescent, trichomes appressed and golden-brown in color, glabrescent with age. **Leaves** membranaceous to chartaceous, alternate, phyllotaxy distichous, 11–20 cm long to 3.5–8

wide, narrowly elliptic to obovate, the apex acute to acuminate, the base acute to obtuse, sometimes asymmetrical; upper surface glabrous, the lower side glabrescent; venation brochidodromous, 6–9 veins per side, pocket domatia in the axils of the main veins; the midrib impressed above and slightly canaliculate toward the base (sometimes with erect to appressed light-brown hairs), lateral veins barely elevated above; the midrib and lateral veins prominently elevated below and with sparsely light-brown hairs, lateral veins decurrent at midrib insertion; petiole swollen, 0.5–1 cm long, canaliculate, with sparsely light-brown hairs. **Inflorescences** always one-flowered, axillary, sometimes arising on leafless part of branches (ramiflory), the pedicel glabrous, 1–1.7 cm long, bearing 2–3 minute, densely golden tomentose and broadly ovate basal bracts. **Sepals** 2, connate, to 2 mm long \times 4–5 mm wide, decurrent along the pedicel, broadly ovate, rounded at apex, glabrous inside and outside, the margins ciliate. **Petals** 4, in two subequal whorls, 8–14 mm long \times 3–5 mm wide, lanceolate to triangular, green to yellowish green, glabrous inside and outside, the margins ciliate, acute at apex, the base truncate and cusped around the stamens; the outer petals, more or less thin, with faint venation, reflexed at anthesis; the inner petals thicker and fleshier and not reflexed with a shallow, more or less triangular white patch near the base. **Stamens**, c.a. 40, 1–1.5 mm long, extrorse, filament very short, apical part of connective expanded over the thecae, shield-shaped, ellipsoid to angulate, glabrous. **Carpels**, 2–5 per flower, to 2.5 mm long; the stigma more or less globose and essentially glabrous; style absent; the ovaries ellipsoid and more or less curved, like a small banana with sparsely light-brown hairs; the ovules, 12–18, lateral, in two rows. **Monocarps**, 1–4 per fruit, large and fleshy, 8–11 cm long \times 3–5 cm wide, ellipsoid, the apex and base rounded, glabrous, shortly stipitate, stipes to 7 mm long; young monocarps green, yellow to light brown when ripe with a peach-like sweet odor; seeds lunate to wedge-shaped, 1.3–2.2 cm long with lamellate ruminations.

Habitat and ecology. The type locality of *Tridimeris chiapensis* is locally named as “La Pera” and “Pozo Turipache” or “El Pozo” and it lies within the ecological state reserve La Pera, which is mostly covered by tropical rainforest. Thin soils, rough limestone outcrops, caves, crevices, sinkholes and almost no surface water that form a typical karst landscape can be observed around El Pozo (Wake and Johnson 1989). Also, fogs forming cloudbanks are common throughout the year, though absent during the dry season (Wake and Johnson 1989).

Tridimeris chiapensis forms part of the understory vegetation and it is associated with *Mortoniendron ocotense* Ishiki & T. Wendt, *M. vestitum* Lundell, *Trichilia moschata* Sw., *Neea tenuis* Standl., *Pseudolmedia glabrata* (Liebm.) C.C. Berg, *Quararibea funebris* (La Llave) Vischer, *Quercus lancifolia* Schltld. & Cham. and *Heliocarpus appendiculatus* Turcz. (Escobar-Castellanos 2016).

Phenology. The species was found in full bloom in August and bearing fruits in March and May.

Etymology. The specific epithet is in honor of the Mexican state of Chiapas where the species was found.

Conservation status. *Tridimeris chiapensis* is known only from the type locality at the ecological state reserve La Pera. According to the criteria established by the IUCN, it is possible to tentatively determine that the species is Critically Endangered [CR B1ab (iii)]. The Area of occupancy (AOO) of *T. chiapensis* is 0.314 km² and the Extent of occurrence (EOO) is 1.519 km², suggesting a very restricted overall distribution. Although the only known population of the species is located within a protected natural area, only 7 individuals of *Tridimeris chiapensis* in one hectare of sampling were recorded (Escobar-Castellanos 2016). The 3000 ha of La Pera's rainforest estimated by Espinosa (2014) and its species are threatened by non-sustainable activities (logging, fires, illegal settlements) and forests in this region are fragmented and only some remnants persist which are surrounded by roads, croplands and cattle pastures (Medina et al. 2006, Luna-Reyes et al. 2015).

Additional specimens examined. MEXICO. Chiapas, Municipio de Berriozábal: Zona Sujeta a Protección Ecológica "La Pera", Campamento "Trepatroncos" carretera Berriozábal-Joaquín Miguel Gutiérrez, km. 12 desvío a Montebello, 1081 m, 16°52'20.3"N, 93°19'32.5"W, May 2014 (fr) *Escobar-Castellanos M. A. 0599* (HEM), May 2015 (fr) *Ortiz-Rodríguez A. E. 801* (XAL); Zona Sujeta a Protección Ecológica "La Pera", Predio "La Selva", desvío hacia San Joaquín, carretera Berriozábal-Joaquín Miguel Gutiérrez, Sistema kárstico, 14 km al NO de Berriozábal. Plot X, Tree No. 27, 1049 m, 19°52'50.45"N, 93°19'07.92"W, 11 August 2016 (fr) *Escobar-Castellanos M. A. 0690* (HEM); Zona Sujeta a Protección Ecológica "La Pera", Predio "La Selva", desvío hacia San Joaquín, carretera Berriozábal-Joaquín Miguel Gutiérrez, Sistema kárstico, 14 km al NO de Berriozábal, 1050 m, 19°52'54.62"N, 93°19'09.77"W, 31 March 2014 (fr) *Escobar-Castellanos M. A. 0556* (HEM).

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Appendix

Appendix 1. Voucher specimens for the accessions cited in this study. The information is presented in the following order: Taxon; GenBank accessions: *rbcL*; *matK*; *ndhF*; *trnLF*; *psbA-trnH*; *ycf1*; Voucher information (herbaria in parentheses). Long dash (—) = sequence not available.

Alphonsea elliptica Hook.f. & Thomson; AY318966; AY518807; JQ690401; AY319078; JQ690402; KJ418378; Van Balgooy 5141 (L); Gardner & Sidisunthorn ST 2214, Indonesia. **Asian undescribed GenusA**; —; KC857607; KC857608; KC857606; —; JX544757; Chaowasku 108(L) Thailand. *Dendrokingstonia gardneri* Chaowasku; KJ418381; KJ418391; KJ418385; KJ418406; KJ418399; KJ418378; Gardner & Sidisunthorn ST 2214 (L) Thailand. *Desmopsis lanceolata* Lundell; KU727378; KU727296; —; KU727414; KU727337; KY026102; Rubén Martínez Camilo 2370, (XAL) Mexico. *Desmopsis microcarpa* R.E. Fr.; AY319059;

AY518804; JX544771; AY319173; AY841461; JX544758; Chatrou et al. 85 (U) Costa Rica. *Desmopsis panamensis* (B.L. Rob.) Saff.; GQ981723; GQ981981; —; —; GQ982207; —; R. Perez STRI: BCI 158574, no collection data, Panama. *Desmopsis schippii* Standl.; AY319060; AY518805; JQ723786; AY319174; —; —; Chatrou et al. 94 (U) Costa Rica, Alfaro 4572 (U) Costa Rica. *Huberantha nitidissima* (Dunal) Chaowasku; KF682103; JQ889989; KF682116; KF682105; KF709056; JQ889976; Ford & Metcalfe 4708 (HKU) Australia, Ford AF 4967, no collection data, Australia. *Marsypopetalum pallidum* (Blume) Kurz; AY318980; AY518834; —; AY319092; —; —; Kessler PK 3192 (L) Thailand. *Meiogyne cylindrocarpa* (Burck) Heusden; KF301029; AY518796; KF611914; KF573500; KJ418402; JQ723931; L. Raulerson & M. Mesngon 18331 (L) Guam, Ridsdale DV-M1-1930 (L) no locality data, Marler s.n. Tinian Island. *Meiogyne heteropetala* (F. Muell.) D.C. Thomas, Chaowasku & R.M.K. Saunders; JQ723853; AY773280; JQ723790; JQ723906; KC857559; JQ723927; Sankowsky 4140 (BRI) Australia, Kemp TH 7267 (L) Australia. *Meiogyne virgata* (Blume) Miq.; AY318982; AY518798; JQ723805; AY319094; JX544784; JQ723945; Kessler PK 2751 (L) Indonesia. *Miliusa mollis* Pierre; AY318990; AY518851; JQ690503; AY319101; JQ690504; JQ690505; Kessler PK 3207 (L) Thailand. *Mitrephora alba* Ridl.; AY318994; AY518855; JQ723807; AY319106; JQ889978; JQ723947; Chalermglin 530706 (HKU) Thailand. *Monocarpia euneura* Miq.; AY318998; AY518865; AY841412; AY319111; AY841477; —; Slik 2931 (L) Borneo. *Monoon fuscum* (King) B. Xue & R.M.K. Saunders; AY318973; AY518787; JX544779; AY319085; KM924989; JX544767; Kessler PK 3222 (L) Thailand. *Neouvaria telopea* Chaowasku; JX544755; JX544751; JX544778; JX544783; JX544791; JX544766; Chaowasku 77 (L) Thailand. *Orophea enterocarpa* Maingay ex Hook. f. & Thomson; AY319006; AY518815; JQ690416; AY319119; JQ690417; JQ690418; Chalermglin 440403 (TISTR) Thailand. *Phaeanthus splendens* Miq.; JX227921; AY518864; JX544777; AY319126; JX544790; JX544765; Kessler B 1564 (L) Indonesia. *Polyalthia bullata* King; JX227908; JX544825; JX544839; JX227859; JX544809; JX544818; P. Chalermglin 521115 (HKU) Thailand, Chaowasku 34 (L) Thailand. *Sageraea lanceolata* Miq.; AY319050; AY518799; JX544774; AY319164; JX544787; JX544762; Ridsdale DV-M2-1692 (L) Malaysia. *Sapranthus microcarpus* (Donn. Sm.) R.E. Fr.; AY319052; AY518806; —; AY319166; —; —; Maas et al. 8457 (U) Honduras. *Sapranthus palanga* R.E. Fr.; JQ590193; JQ586518; —; —; HG963548; —; Adrian Guadamuz BioBot00012, no collection data, Costa Rica. *Sapranthus viridiflorus* G.E. Schatz; AY319051; AY743493; AY841422; AY319165; AY841515; JQ723955; Chatrou et al. 55 (U) Costa Rica. *Stelechocarpus burahol* (Blume) Hook. f. & Thomson; AY319053; AY518803; JQ723814; AY319167; JX544788; JQ723956; Mols 13 (L) Indonesia, Karim s.n. (HKU), Singapore. *Stenanona costaricensis* R.E. Fr.; AY319069; AY518801; JX544772; AY319183; AY841516; JX544759; Chatrou et al. 67 (U) Costa Rica. *Stenanona migueliana* Ortiz-Rodr. & G.E. Schatz; KU727397; KU727316; —; KU727435; KU727358; KY026103; Andres E. Ortiz-Rodriguez 796 (XAL) Mexico. *Stenanona panamensis* Standl.; AY319070; AY518802; —; AY319184; —; —; Chatrou et al. 100 (U) Costa

Rica. *Tridimeris habniana* Baill.; AY319055; —; —; AY319169; —; —; Schatz 1198 (K), Mexico; JX544753; JX544750; JX544773; JX544782; JX544786; JX544761—; Maas 8646 (U) Mexico. *Tridimeris chiapensis* Escobar-Castellanos & Ortiz-Rodr.; KY026100; KU727329; —; KY026101; —; KY026104; Andres E. Ortiz-Rodriguez 801 (XAL) Mexico. *Winitia cauliflora* (Scheff.) Chaowasku; AY319054; AY518800; JX544776; AY319168; JX544789; JX544764; no collection data, Hort. Bot. Bog. XV-A-196 (L).

Supplementary material 1

Figure S1. The 50% majority-rule consensus tree from the Bayesian analysis of *rbcL* coding region

Authors: Andres Ernesto Ortiz-Rodriguez, Marcos Alberto Escobar-Castellanos, Miguel Angel Pérez-Farrera

Data type: JPEG image

Explanation note: Numbers on branches of the major clades indicate Bayesian posterior probabilities (PP), maximum likelihood (MLBS) and parsimony (MPBS) bootstrap values in that order.

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Supplementary material 2

Figure S2. The 50% majority-rule consensus tree from the Bayesian analysis of *matK* coding region

Authors: Andres Ernesto Ortiz-Rodriguez, Marcos Alberto Escobar-Castellanos, Miguel Angel Pérez-Farrera

Data type: JPEG image

Explanation note: Numbers on branches of the major clades indicate Bayesian posterior probabilities (PP), maximum likelihood (MLBS) and parsimony (MPBS) bootstrap values in that order.

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Supplementary material 3

Figure S3. The 50% majority-rule consensus tree from the Bayesian analysis of *ycf1* coding region

Authors: Andres Ernesto Ortiz-Rodriguez, Marcos Alberto Escobar-Castellanos, Miguel Angel Pérez-Farrera

Data type: JPEG image

Explanation note: Numbers on branches of the major clades indicate Bayesian posterior probabilities (PP), maximum likelihood (MLBS) and parsimony (MPBS) bootstrap values in that order.

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Supplementary material 4

Figure S4. The 50% majority-rule consensus tree from the Bayesian analysis of *trnLF* spacer

Authors: Andres Ernesto Ortiz-Rodriguez, Marcos Alberto Escobar-Castellanos, Miguel Angel Pérez-Farrera

Data type: JPEG image

Explanation note: Numbers on branches of the major clades indicate Bayesian posterior probabilities (PP), maximum likelihood (MLBS) and parsimony (MPBS) bootstrap values in that order.

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Isoetes mississippiensis: A new quillwort from Mississippi, USA

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Abstract

Isoetes mississippiensis S.W. Leonard, W.C. Taylor, L.J. Musselman and R.D. Bray (Isoetaceae, Lycopodiophyta) is a new species known from two sites along tributaries of the Pearl River in southern Mississippi. This species is distinguished from other species in the southeastern United States by a combination of character states including a basic diploid ($2n=22$) chromosome count, laevigate megaspores, and a narrow velum covering less than one-third of the adaxial sporangium wall.

Keywords

Isoetes, Isoëtaceae, lycophyte, quillwort, Mississippi

Introduction

Isoetes (Isoetaceae) is a cosmopolitan genus of heterosporous lycophytes containing 200–300 species (Hickey et al. 2003; Troia et al. 2016). Lycophytes have an extensive fossil record dating from the Devonian and a morphology so conserved that members of the genus *Isoetes* are recognized in the Triassic (Pigg 2001). Extant species are widely distributed from the tropics to the sub-arctic (Troia et al. 2016). They range in habitat

from evergreen aquatics to seasonal terrestrials. Resembling a tuft of chives or grass, they are easily overlooked in the field.

In spite of their antiquity, widespread distribution, and diverse ecological adaptations, *Isoetes* species are remarkably uniform in their morphology. Plants appear simple in form with a lobed subterranean rootstock producing a tuft of linear sporophylls above and below roots along a groove between the lobes. This apparent morphological simplicity makes it easy to recognize a member of the genus, but difficult to distinguish species. Earlier taxonomists relied primarily on habitat, megaspore texture, and megaspore size to separate taxa (Engelmann 1882; Pfeiffer 1922; Reed 1965; Boom 1982). More recently, chromosome counts and molecular markers have been used to further define taxa and infer their phylogeny (Taylor et al. 1993, Hoot et al. 2004; Heafner and Bray 2005; Rosenthal et al. 2014).

Ornamentation and size of megaspores and microspores are important morphological features used to identify species of *Isoetes*. Pfeiffer (1922) erected four sections based on the megaspore ornamentation types cristate, echinate, reticulate, and tuberculate. While these sections are no longer recognized as having phylogenetic value in the genus, the emphasis on macro-ornamentation for identification remains (Brunton 2015). Several categories for megaspores (cristate, echinate, laevigate, psilate, reticulate, rugulate, and tuberculate) and microspores (aculeate, cristate, echinate, laevigate, and psilate) are accepted, though there can be gradation between categories (Taylor et al. 1993; Musselman 2002). Micro-ornamentation of megaspores and microspores is sometimes recognized, but has not been included in any recent taxonomic treatments of the genus (Reed 1965; Boom 1982; Taylor et al. 1993; Brunton 2015). Generally, megaspore size increases with ploidy level (Pereira et al. 2015; Brunton 2015).

The habitat of species of *Isoetes* can be fairly specific and is often used in taxonomic treatments (Engelmann 1882; Reed 1965; Taylor et al. 1993; Brunton 2015). Species are generally segregated as aquatic, amphibious, or terrestrial, based on the proportion of their growing season spent in water (Engelmann 1882; Taylor et al. 1993). Some species occur only in certain habitats, such as rock pools, calcareous glades, oligotrophic lakes, and swamp forests. Widespread species such as *I. melanopoda* Gay and Durieu (*s.s.*) and *I. engelmannii* Braun have more varied habitat preference (Taylor et al. 1993; Brunton 2015).

Characteristics of sporophylls and rootstocks of *Isoetes* may also provide taxonomic information, though the utility of some of these features is questionable. Velum coverage of the sporangium, sporangium shape, sporangium wall coloration, and sporophyll length, number, color, and shape are sometimes used for species identification, but these character states can be subtle and it is unclear how they may be influenced by environmental conditions (Engelmann 1882, Pfeiffer 1922; Reed 1965, Boom 1982, Taylor et al. 1993, Brunton 2015). Cultivated plants often appear different than those *in situ*, and spore development, photosynthetic pathways, and gene expression are significantly altered by water conditions (Brunton 2015; Yang and Liu 2015; Yang and Liu 2016). However, the *gestalt* formed from the combination of these characters usually leads experts to accurate field identification.

While searching for populations of *Isoetes louisianensis* in southwestern Pearl River Co., MS, in the spring of 1996, one of us (Leonard) discovered a population of *Isoetes* that did not appear to be *I. louisianensis* or any other known species. These plants had very long and numerous sporophylls bearing megaspores with a smooth surface rather than an irregularly reticulate texture that is typical of *I. louisianensis* megaspores. In addition, the megaspores of this plant were noticeably smaller than those of *I. louisianensis*. Further investigation turned up a second population downstream in Lotts Creek. Both of these waterways are tributaries of the Pearl River, converging near Picayune, MS.

Methods

Field work was performed in 1996, 1998, and 2013 to obtain specimens for further study. Specimens were deposited in the Old Dominion University herbarium (ODU). Length and width of the rootstock, sporophylls, and sporangia were measured for 10 individuals. Megaspores and microspores were removed from sporangia, cleaned by sonication in distilled water for 90 seconds, and dried on a slide warmer at maximum temperature (approximately 60°C). Light images were captured using a Nikon SMZ800 stereomicroscope with attached Digital Sight camera, and measurements made within the Digital Sight control panel. Spores were prepared for scanning electron microscopy by coating with 25 nm of gold-palladium using a Cressington high resolution sputter coater (Cressington Scientific Instruments Ltd.). Imaging was performed on a Zeiss EVO MA 15 scanning electron microscope. Chromosome counts were determined by root tip squashing as described in Heafner and Bray (2005). Site descriptions were prepared and lists of associated species were made.

Results

Analysis of morphological characters, chromosome counts, and ecological evaluation leads us to conclude our collections represent an undescribed species of *Isoetes*.

***Isoetes mississippiensis* S.W. Leonard, W.C. Taylor, L.J. Musselman & R.D. Bray, sp. nov.**

urn:lsid:ipni.org:names:77158528-1

Type. USA. Mississippi: Lotts Creek (30.57396°N, 89.76196°W, elevation 14 m), 18 June 2013, *P. Schafran MS-08 L. Musselman, S. Leonard, W. Taylor, M. Alford, and D. McNair* (holotype: US; isotypes: MO, NY, ODU, USMS).

Description. Plants amphibious in and along persistent streams. Rootstock subglobose, bilobed, brown, 0.5–1.0 cm long, 1.0–1.5 cm wide. Roots dichotomously branched. Sporophylls (leaves) linear, bright green, darkening with age, pale toward

base, spirally arranged, erect to spreading, up to 40 cm long and 2.0 mm wide at mid-length, in tufts of ca. 20, semi-terete with adaxial surface flattened, becoming more terete distally, with translucent alae ca. 1 mm wide extending along lateral edges from base to ca. one-quarter leaf length, tapering gradually toward apex, abruptly dilated and spatulate toward base where streaks of brown pigmented cells are often evident on pale outer surface of leaf base. Ligule triangular, ca. 1 mm long. Sporangium ovate, most 4–10 mm long, most 4–5 mm wide, adaxial wall spotted to streaked with scattered clusters of brown pigmented cells. Velum incomplete, covering less than one third of sporangium wall. Megaspores globose, white, trilete, macro-ornamentation laevigate with echinate micro-ornamentation, ca. 280–380 μm in diameter, averaging ca. 340 μm . Microspores broadly fusiform, macro-ornamentation echinate with bacillate micro-ornamentation, pale brown in mass, monolete, 25–30 μm long.

Morphology. Rootstocks of all specimens examined vary in length from 0.5–1.0 cm and in width from 1.0–1.5 cm. All rootstocks are subglobose in shape and bilobed. Sporophylls reach a maximum length of 40 cm and maximum width of 2.0 mm at mid-length. Sporangia are 4–10 mm long and 4–5 mm wide. Megaspores are laevigate with echinate micro-ornamentation (Figures 1, 2, 3). Diameter of megaspores varies from 280–380 μm , with an average of 340 μm . Microspores are echinate with bacillate micro-ornamentation, and are 25–30 μm long (Figure 1).

Cytology. Chromosome counts show individuals of *Isoetes mississippiensis* to be diploid ($2n=22$).

Ecology. *Isoetes mississippiensis* occurs in sluggish, persistent streams in southern Mississippi (Figure 4). At the Moody Branch locality, the maintained right-of-way of Mississippi Highway 43 allows abundant sunshine to reach the stream and adjacent wetlands. Small bushes and saplings of titi (*Cyrilla racemiflora*) and red maple (*Acer rubrum*) are periodically cut down and allowed to fall in the stream. Sediment and detritus provide anchors for herbaceous growth of sedges, rushes, and coarse grasses (*Rhynchospora inexpansa*, *Juncus* spp., *Erianthus giganteus*, *Panicum* spp.). In the shallow water stream margin is *Iris virginica*. The woodland edge is suitable habitat for crossvine (*Bignonia capreolata*) and rattan vine (*Berchemia scandens*). Upstream where a defined channel is present the overstory consists of swamp black gum (*Nyssa biflora*), laurel oak (*Quercus laurifolia*), red maple, and encroaching loblolly pines (*Pinus taeda*). Shrubs in the understory are Elliott's blueberry (*Vaccinium elliotii*), yaupon (*Ilex vomitoria*), and titi. In the upper reaches of Moody Branch, the channel is braided and the water sluggish, more typical of a swamp black gum forest with Rankin's jessamine (*Gelsemium rankinii*), Virginia willow (*Itea virginica*), and dog hobble (*Viburnum nudum*).

After flowing west for several kilometers, Moody Branch turns sharply south just west of Mississippi Highway 43 and eventually merges with Lotts Creek. The forested wetland adds pond cypress (*Taxodium ascendens*) and a dense shrub understory with *Smilax laurifolia*. At the Walkiah Bluff Road crossing of Lotts Creek disturbance has been severe, yet *I. mississippiensis* has revegetated new habitat in the roadside ditch north of the road and on sandbars.

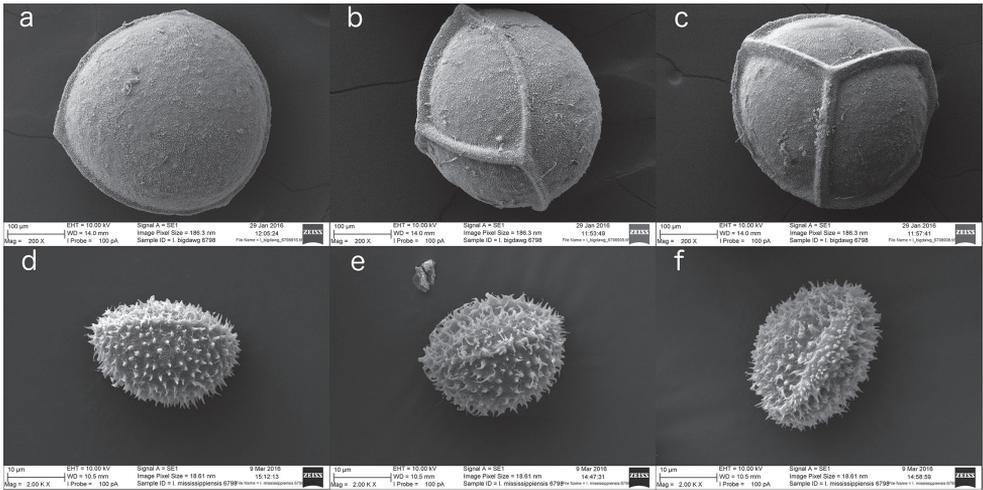


Figure 1. SEMs of megaspores (a, b, c) and microspores (d, e, f) of *I. mississippiensis* displaying distal (a, d), equatorial (b, e), and proximal (c, f) views. Megaspores from Schafran MS-08, microspores from Taylor 6798. Megaspore magnification 200×; microspore magnification 2000×.

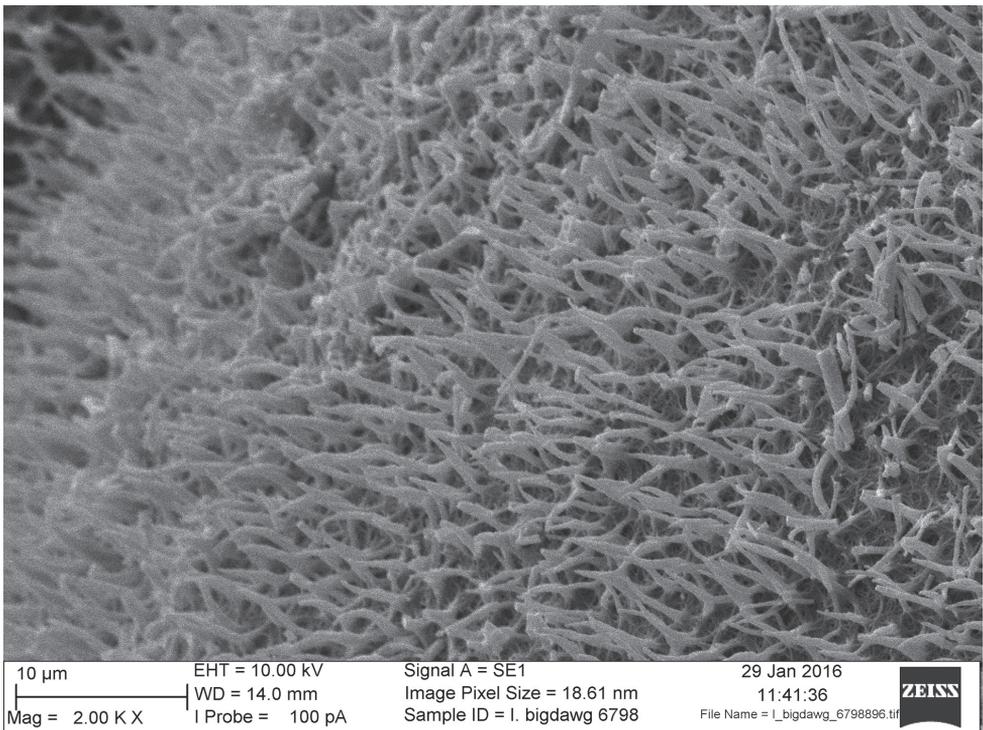


Figure 2. SEM detail of megaspore micro-ornamentation. Magnification 2000×.

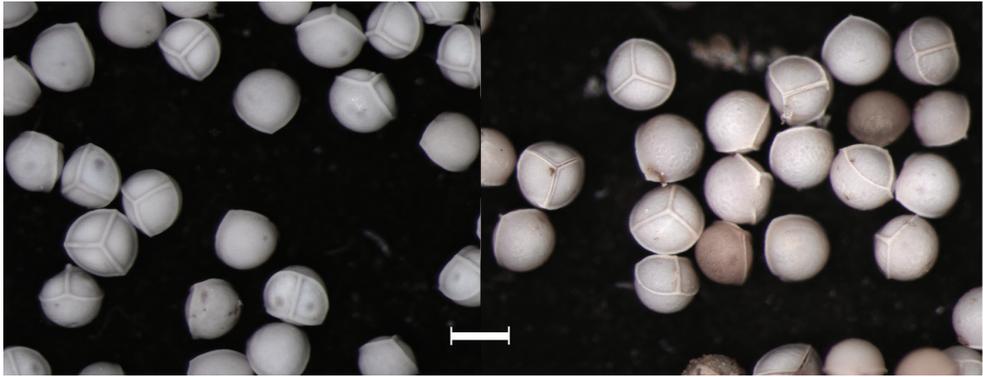


Figure 3. Light microscope image of megaspores of *I. mississippiensis* from Schafran MS-07 (left) and MS-08 (right). Magnification 63 \times . Scale bar = 0.3 mm.



Figure 4. Map showing two localities of *I. mississippiensis*. Inset: Map of Mississippi with detail area highlighted. Map created using ArcGIS software (Esri).

Etymology. This species is named for the state of Mississippi, its only known locality.

Specimens examined. Leonard 9393, 9 March 1996 (MMNS); Leonard 9395, 22 March 1996 (MMNS); Leonard 9831, 2 June 1997 (MMNS); Leonard 12405, 12 May 2011 (ODU); Leonard 12406, 12 May 2011 (ODU); Musselman with Taylor, 98908, 17 October 1998 (ODU); Bolin JB-MS-01, 9 January 2009 (ODU); Schafran

MS-07, 18 June 2013 with Musselman, Leonard, Taylor, and Alford (MO; NY; ODU; USMS); Schafran MS-08, 18 June 2013 with Musselman, Leonard, Taylor, and Alford (US; ODU); Taylor 6798, 18 June 2013 with Musselman, Leonard, Schafran, and Alford(US).

Discussion

Evaluation of the morphological and cytological features of *I. mississippiensis* shows it to be distinct from all other taxa in the southeastern US. In the coastal plain of the Gulf Coast states, nine other species are known: *I. appalachiana*, *I. boomii*, *I. flaccida s.l.*, *I. hyemalis*, *I. louisianensis*, *I. melanopoda s.l.*, *I. microvela*, *I. texana*, and *I. valida* (Singhurst et al. 2011; Weakley 2015; Brunton 2015). A basic diploid chromosome count (2n=22) plus laevigate megaspore ornamentation separates *I. mississippiensis* from all these taxa except *I. texana* and occasionally *I. melanopoda*. These species may be further separated by presence/absence of phyllopodia, difference in megaspore size, and velum coverage (Table 1). Additionally, the habitats of these species are quite different. *Isoetes mississippiensis* occurs along persistent streams, while *I. texana* is found in freshwater ponds and interdunal swales and *I. melanopoda* grows in wet prairies, soil pockets on rock outcrops, and woodland depressions (Table 1; Singhurst et al. 2011; Taylor et al. 1993).

Key to the Diploid Species of *Isoetes* of the Gulf Coastal Plain of the United States

- 1 Megaspores psilate to laevigate, rarely low tuberculate or low rugulate 2
- 2 Plants at least sometimes with darkened, often sclerified, brown-black leaf bases; velum coverage generally <15%..... ***I. melanopoda s.l.***
- 2' Plants never with darkened leaf bases; velum coverage usually >15% 3
- 3 Megaspores 280-380 mm; velum coverage 15-30% ***I. mississippiensis***
- 3' Megaspores 350-405 mm; velum coverage 100% ***I. texana***
- 1' Megaspores tuberculate, reticulate, cristate, or rugulate..... 4
- 4 Velum coverage 75-100%; microspores papillose ***I. flaccida s.l.***
- 4' Velum coverage less than 75%; microspores echinate 5
- 5 Megaspore ornamentation of tubercles or ridges; velum coverage less than ca. 25%..... ***I. melanopoda s.l.***
- 5' Megaspore ornamentation broken reticulate; velum coverage between ca. 25 and 75% ***I. valida***

Conservation

Isoetes mississippiensis is known from only two locations along approximately 2 miles of the Lotts Creek—Moody Branch waterway. Neither of these populations is located on

Table 1. Comparison of Gulf Coastal Plain *Isoetes*.

Character	<i>I. mississippiensis</i>	<i>I. texana</i>	<i>I. flaccida</i> s.l.	<i>I. melanopoda</i> s.l.	<i>I. valida</i>
Ploidy	2n=22	2n=22	2n=22	2n=22	2n=22
Habitat	Persistent streams	Persistent freshwater ponds, intertidal swales	Springs, stream bottoms, river bottoms, ditches	Ephemeral wet prairies, open graminoid swales, woodland pools, soil pockets on rock outcrops	Woodland seepages
Megaspore Ornamentation	Laevigate	Smooth to obscurely rugulose	Low tubercles to broad, interconnected mounds	Low tubercles or ridges	Broken reticulate
Megaspore Size (mm)	280–380 (\bar{x} =340)	350–405 (no mean reported)	250–500 (no mean reported)	280–440 (\bar{x} =380–410)	\bar{x} =450
Microspore Ornamentation	Spinulose/echinate	Papillose	Papillose	Spinulose/echinate	Spinulose/echinate
Microspore Size (mm)	25–30	25–30	25–33	20–30	27
Velum Coverage (%)	15–33	100	80–100	5–15	45–70
Character	<i>I. louisianensis</i>	<i>I. hyemalis</i>	<i>I. appalachiana</i>	<i>I. boomii</i>	<i>I. microvela</i>
Ploidy	2n=44	2n=44	2n=44	2n=66	2n=66
Habitat	Creeks, streams	Blackwater streams	Creek banks, woodland pools, lakes	Slow-flowing woodland streams	Persistent streams in deciduous swamp forests
Megaspore Ornamentation	Irregularly reticulate	Broken reticulate to sub-echinate	Broken reticulate	Cristate to reticulate	Densely reticulate with irregular crests and thin tubercles
Megaspore Size (mm)	500–625 (no mean reported)	400–580 (=522)	450–611 (=534)	460–610 (no mean reported)	=527
Microspore Ornamentation	Spinulose/echinate	Spinulose/echinate	Psilate to low tuberculate	Papillose/aculeate	Psilate to low tuberculate
Microspore Size (mm)	25–35	20–31	29–32	25–30	30
Velum Coverage (%)	<50	10–20	20–25	30–50	10

preserved land. Extensive field work is needed to search for additional populations in the nearby Pearl River Wildlife Management Area and Bogue Chitto National Wildlife Refuge.

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Two new infraspecific taxa of *Verbascum delphicum* (Scrophulariaceae, Scrophularieae) from mainland Greece and the island of Evvia

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Abstract

Verbascum delphicum Boiss. & Heldr. subsp. *cervi* Zografidis (Scrophulariaceae, Scrophularieae) is described as a subspecies new to science and illustrated. It is narrowly distributed in the Greek National Park of Mt Parnitha (Attica, Greece) with a very small population size. The new subspecies is a seldom-collected taxon, previously overlooked and misidentified as consubspecific with the autonomous subspecies, an endemic of the island of Evvia (Greece). Also described in this study is a new variety of subsp. *delphicum* from Mt Ochi of southern Evvia.

Keywords

Verbascum, new subspecies, endangered taxon, Mt Parnitha

Introduction

Comprising more than 360 species, *Verbascum* L. (Scrophulariaceae) is the largest genus of the predominantly northern temperate tribe Scrophularieae Dumort. (= Verbasceae Dumort.) and is chiefly represented by rosulate, biennial or perennial herbs with yellow-flowered, thyrse or racemose inflorescences (Fischer 2004; Oxelman et al. 2005). Although the genus is widely distributed in Eurasia and North Africa, species

diversity is mostly concentrated in a region encompassing Anatolia, Caucasus, north-western Iran, the Levant and the southern Balkans (Murbeck 1939). In Greece, *Verbascum* is among the 10 most species-rich and the 10 most range-restricted-rich genera with a total of 76 species and an endemism rate of 32% (Dimopoulos et al. 2013).

Verbascum was extensively studied by the Swedish botanist Svante Murbeck who published two monographs on *Verbascum* and *Celsia* L. —now merged in *Verbascum*— and a series of two additional, supplementary and interpretative studies on the genus (Murbeck 1925; 1933; 1936; 1939). Since his era, several other species have been discovered and described, principally but not exclusively from Anatolia (Al-Hemaid 2001; Aytaç and Duman 2012; Bani et al. 2010; Çeçen et al. 2015; Davis 1951; 1952; Firat 2015; Greuter and Rechinger 1972; Huber-Morath 1939; 1949; 1955; 1960; 1965; 1967; 1971; 1973; 1974; 1975; 1976; 1979; 1981; 1983; Karavelioğullari 2015; Karavelioğullari et al. 2011; Karavelioğullari et al. 2004; Karavelioğullari et al. 2009; Karavelioğullari et al. 2008; Karavelioğullari et al. 2014; Kaynak et al. 2006; Parolly and Eren 2008; Parolly and Tan 2007; Ranjbar and Nouri 2015; Sotoodeh et al. 2015; Sotoodeh et al. 2016; Stefanova-Gateva 1979) and a modified classification system of “*informal, partly artificial groups*” has been utilized by Arthur Huber-Morath for the Turkish taxa (Huber-Morath 1978). Both taxonomies of Murbeck and of Huber-Morath are still widely cited and used today in studies of new species; however, it should be noted that a first assessment of molecular data suggests these schemes are non-natural and that the genus has potentially been subjected to taxonomic inflation (Ghahremaninejad et al. 2014).

Verbascum delphicum Boiss. & Heldr. was discovered by Theodor von Heldreich on Mt Dirfi of the island of Evvia (West Aegean Islands, Greece) and was subsequently jointly described by himself and Edmond Boissier in Boissier’s *Diagnoses plantarum Orientalium novarum* (Boissier 1856). The autonymous subspecies is a nemoral, short-lived perennial or biennial herb with often impressive, sizeable basal leaves. Knowing the taxon well from my excursions on the mountains of central and south Evvia I was surprised to find on Mt Parnitha (Attica, Sterea Ellas, mainland Greece) on May 2013 a small population of a closely related, yet distinct and undescribed as it appeared to be taxon. The population consisted of biennial plants with noticeably smaller and more or less differently shaped leaves than those of the insular *V. delphicum*. Inspection of the mainland population in the past recent years and comparison with the insular populations revealed some additional deviating traits for the taxon on Mt Parnitha. Taking into consideration overall morphology and the common habitat and phenology of the two taxa, as well as the phytogeographic connection between Sterea Ellas and Ins. Evvia, I propose that collectively the differences indicate distinction at the subspecies rank.

The new subspecies *V. delphicum* subsp. *cervi* Zografidis described and illustrated in this work was apparently overlooked and misidentified by Murbeck as consubspecific with subsp. *delphicum* based on material collected by Heldreich and Bassilios Tuntas from Mt Parnitha. The differences between the two subspecies are presented and discussed. A new, distinct variety of subsp. *delphicum* from Mt Ochi, south Evvia is also described.

Methods

For the cultivated material current-year seeds were sown in early October (2013 & 2015), in small pots filled with Compo® Bio Anzucht- und Kräutererde substrate. Two-weeks old plants were individually transferred in plastic pots 7 cm of diameter and were transplanted every c. 8 weeks two additional times in successively larger plastic pots, 15 and 24 cm of diameter. The plants were kept outdoors, daily receiving 5 hours of direct sunlight on average, whereas the substrate was kept moist but not soggy.

Measurements were performed either with a common ruler or under a stereo-microscope (Zeiss, Stemi 2000-C) equipped with a camera and ImagePro software. Because the population size of the new subspecies is extremely small the measurements were either performed *in situ* without damaging the plants, or, when this was not feasible, only small plant-parts were collected for subsequent assessment under the stereo-microscope. In particular, two flower-clusters (glomerules) of the middle part of the inflorescence were removed from 20 individual plants i) at flowering and ii) at fruiting. Statistical significance was assessed with two-tailed T-tests for two independent means ($p < 0.01$) and two-tailed Mann-Whitney U-tests ($p < 0.01$).

Taxonomy

Verbascum delphicum Boiss. & Heldr. subsp. *cervi* Zografidis, subsp. nov.

urn:lsid:ipni.org:names:77158533-1

Figures 1, 2; Suppl. material 1

Diagnosis. subsp. *cervi* can be distinguished from subsp. *delphicum* by a combination of the following characters: lamina of larger rosette-leaves 6–22 × 3–11 cm (vs. 16–40 × 11–24), 1.5–3.7 of length to width ratio (vs. 1.2–1.9), obtuse-cuneate at the base (vs. obtuse-truncate to cordate); indumentum of abaxial surface of rosette-leaves thinner; indumentum of adaxial surface of first-year mature rosette-leaves ± harsh (vs. soft); stamen filaments greenish-white (vs. orange).

Type. GREECE. Attica: Mt Parnitha, 38°09'N, 23°43'E, limestone slope with *Abies cephalonica*, 1100 m, 22 June 2015, *A. Zografidis* 109. (Holotype: ATH, Isotype: ATHU)

Description. Monocarpic, eglandular- and minutely glandular-hairy biennial herb —or rarely short-lived perennial bicarpic— producing a well-branched taproot and a basal leaf-rosette in the first year of vegetative growth, followed by the production of additional rosette-leaves (in the same rosette) and an erect, terete, leafy flowering-stem in the second year of vegetative and reproductive growth. Eglandular hairs dendritic, 0.2–0.8 mm of length, more or less covering the whole aerial part of the plant; glandular hairs minute, sparse, present on leaves, bracts, bracteols and calyx segments, visible by microscopy; fully developed first-season rosettes yellowish- to brownish- and harshly-tomentose above, grayish- or yellowish- to brownish-



Figure 1. *Verbascum delphicum* subsp. *cervi* Zografidis: **A** habit **B** first year mature leaf-rossette, bar = 10 cm **C** partial inflorescence, bar = 1 cm **D** capsules, bar = 5 mm **E** seeds, bar = 2 mm.

and \pm harshly-tomentose beneath; rosette-leaves few to several (up to 50 in cultivated specimens), petiolate; petiole 1–10 cm of length; lamina ovate-elliptic to oblanceolate, 1.5–3.7 of length to width ratio, obtuse-cuneate at the base, crenate, obtuse at apex; larger leaf laminae 6–22 \times 3–11 cm; second year mature rosette-leaves and lower cauline-leaves similar but \pm glabrescent on adaxial surface; middle cauline-leaves progressively smaller, shortly petiolate, obtuse at the base, obtuse or subacute at the apex; upper cauline-leaves, small, sessile, obtuse at the base, subacute at the apex; all cauline leaves alternate; stem 40–160 cm of height, green to reddish-black, glabrescent but \pm persistently tomentose below; Inflorescence 25–60 cm of height, simple or sparingly branched at the base with short, sub-erect branches and then inflorescence narrowly pyramidal in outline; flowers arranged in clusters of pedicellate, compacted cymes (glomerules), \pm crowded at least above, consisting of 3–12 flowers; bracts 3–7 \times 2–4 mm, ovate-lanceolate, acute to acuminate, glabrescent; bracteoles present, similar to

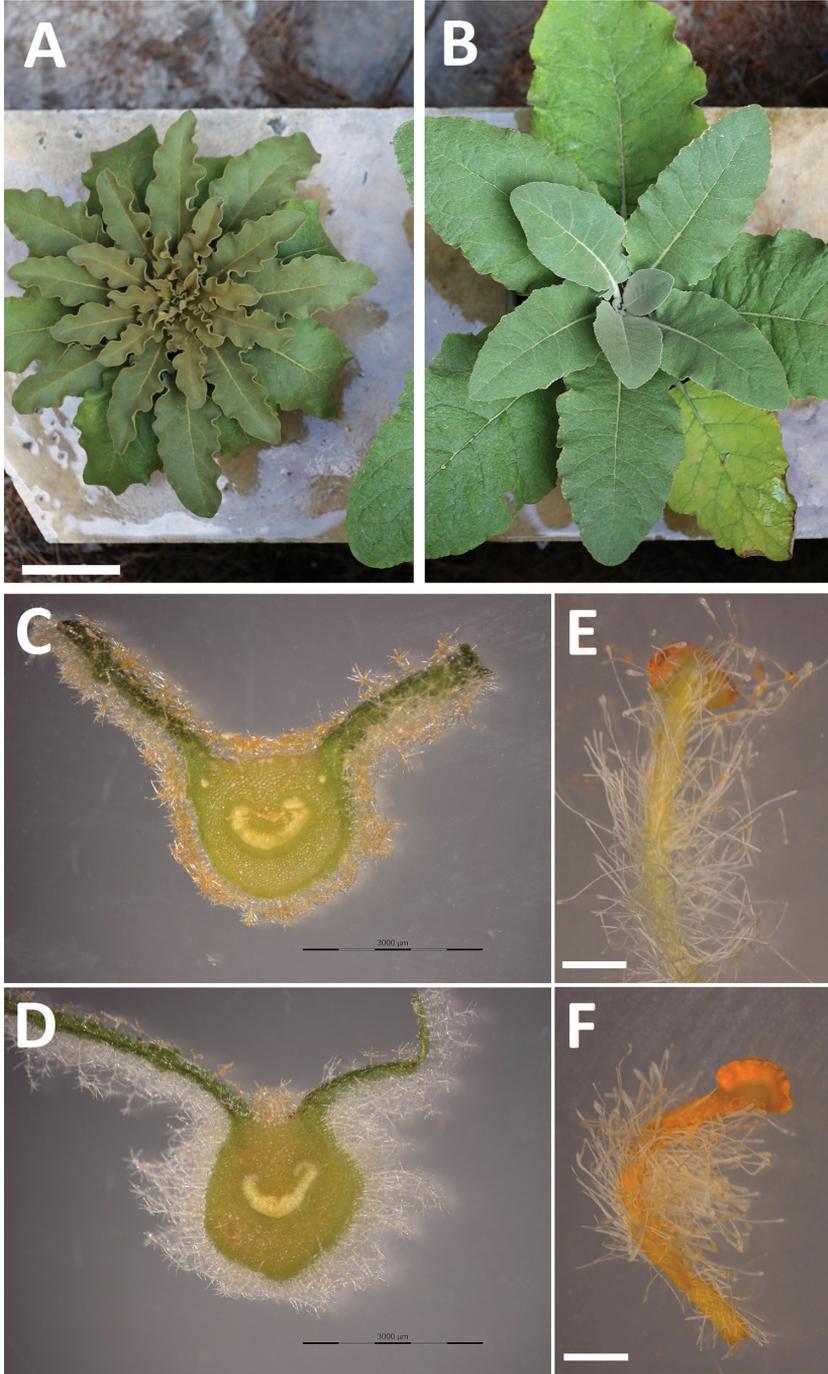


Figure 2. Comparative illustration of *V. delphicum* subsp. *cervi* and subsp. *delphicum* differential traits: **A, C, E** subsp. *cervi* **B, D, F** subsp. *delphicum* **A, B** first-year mature rosette-leaves of cultivated plants, bar = 10 cm **C, D** cross section of leaves indicating the shorter and darker indumentum of subsp. *cervi*, bars = 3 mm **E, F** anterior stamens, bars = 1 mm;

bracts but smaller; longer pedicels 3–8 mm of length, tomentose, ± glabrescent; calyx divided almost to the base into 5 lanceolate to lanceolate-linear, acute segments, 3.5–6 × 1.1–1.7 mm; abaxial surface of calyx tomentose, ± glabrescent; corolla rotate, flat, 1.6–3.6 cm of diameter, light yellow, often with purple marks on the throat, with pellucid glands, divided to c. 3/4 into 5 broadly-obovate, subequal lobes; abaxial surface of corolla partially tomentose, adaxial surface often ciliate near the throat, otherwise glabrous; tube of corolla ± infundibuliform, 1–2.7 mm of length, 1.5–2.9 mm of diameter; stamens 5, free, densely ciliate with white, clavate hairs which reach the connective of anthers; three posterior stamens 5–9.5 mm, two anterior stamens 7–12 mm; stamen filaments greenish-white, occasionally with a purple tinge; all five anthers reniform, mediofix, papillose on adaxial surface, 0.6–1.5 mm; style tomentose at the base, 6–10 mm, clavate at the apex; stigma hemispherical; capsule (excl. rostrum) 3.5–7.5 × 3–5.4 mm, ovoid to broadly ovoid, densely tomentose on early development, later glabrescent, with a rostrum 1–1.5 mm; seeds numerous, chestnut brown to dark brown, 0.7–1 × 0.5–0.7 mm, obpyramidal to ovoid-oblong, irregularly prismatic, faveolate with 3–7 pits in each longitudinal series.

Etymology. Name derives from the genitive of the Latin word “cervus” in reference to the red deer of the National Park which were often observed in the subspecies habitat. The popular animals are a considerable threat to their own *Verbascum* as they consume the young inflorescences.

***Verbascum delphicum* Boiss. & Heldr. subsp. *delphicum* var. *filictorum* Zografidis, var. nov.**

urn:lsid:ipni.org:names:77158534-1

Figure 3; Supplementary file 2.

Diagnosis. Variety *filictorum* differs from typical subsp. *delphicum* in that it produces sterile stems up to c. 80 cm of height instead of basal leaf-rosettes.

Type. GREECE. Ins. Evia. Above the settlement of Ag. Dimitrios, 38°06'N, 24°26'E, in patches of *Pteridium aquilinum*, 500 m, 4 July 2015, A. Zografidis 113. (Holotype: ATH, Isotype: ATHU)

Description. Polycarpic eglandular- and minutely glandular-hairy short-lived perennial herb —or less often monocarpic biennial— producing a well-branched taproot and a sterile, erect or ascending, terete, leafy stem in the first year of vegetative growth, followed by the production of an additional sterile stem and a terete flowering-stem in each of the succeeding few years of vegetative and reproductive growth. Eglandular hairs dendritic, 0.4–2 mm of length, more or less covering the whole aerial part of the plant; glandular hairs minute, sparse, present on leaves, bracts, bracteols and calyx segments, visible by microscopy; fully developed first-season leaves whitish- to yellowish- and softly-tomentose above, grayish-white and softly tomentose beneath; sterile stems up to 80 cm in height; fertile stems 40–180 cm of height, green to reddish-black, glabrescent but ± persistently, tomentose below; lower cauline-leaves petiolate;



Figure 3. *Verbascum delphicum* subsp. *delphicum* var. *filictorum* Zografidis: Habit. A sterile stem is discernible next to the flowering stem.

petiole up to 15 cm of length; lamina ovate to widely ovate, 1.2–1.9 of length to width ratio, obtuse-truncate to cordate at the base, crenate, obtuse at apex; larger leaf laminas 16–40 × 11–24 cm; middle cauline-leaves similar but progressively smaller and often subacute at the apex, shortly petiolate; upper cauline-leaves small, sessile,

ovate-cordate, subacute at the apex; all cauline leaves alternate; Inflorescence 25–60 cm of height, simple or sparingly branched at the base with short, sub-erect branches and then inflorescence narrowly pyramidal in outline; flowers arranged in clusters of pedicellate, compacted cymes (glomerules), \pm crowded at least above, consisting of 3–12 flowers; bracts 3–7 \times 2–4 mm, ovate to lanceolate, acute to acuminate or cuspidate, glabrescent; bracteoles present, similar to bracts but smaller; longer pedicels 4–10 mm of length, tomentose, \pm glabrescent; calyx divided almost to the base into 5 lanceolate to lanceolate-linear, acute segments, 3.5–6 \times 1.1–1.7 mm; abaxial surface of calyx tomentose, \pm glabrescent; corolla rotate, flat, 1.5–2.8 cm of diameter, yellow, with or without indistinct purple marks on the throat, with pellucid glands, divided to c. $3/4$ into 5 broadly-obovate, subequal lobes; abaxial surface of corolla partially tomentose, adaxial surface sometimes ciliate near the throat, otherwise glabrous; tube of corolla \pm infundibuliform, 1–2.3 mm of length, 1.5–2.2 mm of diameter; stamens 5, free, ciliate with white, clavate hairs which reach the connective of all anthers or do not reach the connective of the anterior stamens; three posterior stamens 5–8 mm, two anterior stamens 6–10 mm; stamen filaments orange; all five anthers reniform, mediofix, papillose on adaxial surface, or glabrous on adaxial surface of the connective of anterior stamens, 0.8–1.4 mm; style tomentose at the base, 6–9 mm, slightly clavate at the apex; stigma hemispherical; capsule (excl. rostrum) 3.5–7 \times 3–5 mm, ovoid to broadly ovoid, densely tomentose on early development, later glabrescent, with a rostrum 1–1.5 mm; seeds numerous, chestnut brown to dark brown, 0.7–1.1 \times 0.5–0.7 mm, obpyramidal to ovoid-oblong, irregularly prismatic, faveolate with 4–8 pits in each longitudinal series.

Etymology. Name is in reference to the often abounding in ferns habitat of the variety.

***V. delphicum* specimens examined.** subsp. *cervi*: GREECE. Attica: In regione abietina montis Parnethis, 5–18 June 1911, Tuntas s.n. (GB)

subsp. *delphicum*: GREECE. Ins. Evvia: In rupibus ad cacumen m. Delphi, 5000', 19 August 1948, Heldreich, 2040 (G-BOISS); In regione sylvatica & superiore montis Dirphyis (Delphi hod.) usque ad cacumen, 3000'–5500' 31 July–5 August 1858, Heldreich 799 (K, P); Insula Evvia meridionalis, Montes Ocha, in valle infra Hagios Dimitrios, ca. 600 m, 21 May 1955, K. H. Rechinger, 17181 (W); Insula Evvia meridionalis, Montes Ocha, in querceto-castanetis versus Kallianou, ca. 600 m, 22 May 1955, K. H. Rechinger, 17220 (W); Insula Evvia meridionalis, 3 km a promontorio Kaphireos occidentem versus, 22 June 1958, K. H. Rechinger, 18953 (W).

Results and discussion

The differences between *V. delphicum* subsp. *cervi* and subsp. *delphicum* are presented in Table 1, whereas a comparative illustration is presented in Figure 2. A three-year field survey of both insular and mainland populations and examination of cultivated plants confirmed the constancy of the distinctive features. Subspecies *cervi* is characterized by

Table 1. Diagnostic characteristics of *V. delphicum* subsp. *cervi* and subsp. *delphicum*. Numbers in brackets indicate mean and standard deviation values.

	<i>V. delphicum</i> subsp. <i>cervi</i>	<i>V. delphicum</i> subsp. <i>delphicum</i>
Life cycle	Monocarpic biennial, rarely polycarpic short-lived perennial	Polycarpic short-lived perennial or monocarpic biennial
Indumentum of first year mature rosettes on adaxial surface of leaves	Yellowish to brownish, harsh	Grayish-white to yellowish, soft
Indumentum of rosette leaves on abaxial surface	Grayish-white or yellowish to brownish, thin	Grayish-white, thick
Dendritic hairs (mm)	0.2–0.8	0.4–2
Length to width ratio of leaf-lamina (rosette leaves)	1.5–3.7 [2.5 ± 0.5]	1.2–1.9 [1.6 ± 0.2]
Lamina of larger leaves, (cm)	6–22 [14.7 ± 4.4] × 3–11 [6.2 ± 1.9]	16–40 [26.6 ± 7.1] × 11–24 [17 ± 3.5]
Base of lamina	Obtuse-cuneate	Obtuse-truncate to cordate
Stamen filaments	Greenish-white	Orange
Hairs on connective of anterior stamens (adaxial surface)	Present	Frequently absent

its smaller and more elongated leaves with the base of leaf-laminas obtuse to long-cuneate —vs. ± truncate or even cordate in subsp. *delphicum*— and by a shorter, harsher and darker indumentum. Another significant character is the color of the stamen filaments: either greenish-white in subsp. *cervi* or deep-orange in subsp. *delphicum*. I note that this character is almost lost with drying. Life-cycle is an additional interesting trait. In his *Flora Orientalis*, Boissier has cited *V. delphicum* as a biennial herb (Boissier 1856), a vague conception which has been perpetuated in various floras ever since (Ferguson 1972; Raus 1986). Although biennial individuals are indeed found among its populations, the autonymous subspecies is more frequently a short-lived perennial herb as evidenced by the concomitant existence of the flowering stem and either of an additional leaf-rosette or of a previous-year withered infructescence or of both on the same plants. On the other hand, subsp. *cervi* has clearly drifted towards the biennial life-cycle and very rarely do the plants exceed the usual two years lifespan—I have seen only two such individuals.

On Mt Parnitha and on the mountainous region of central Evvia—Mts Dirfi and Xirovouni—*V. delphicum* inhabits Greek-fir or mixed *Abies-Castanea* woodlands, flowers from early-mid-June to early-mid-August and matures seeds from July to August. On Mt Ochi of southern Evvia the species is found in open *Castanea* woodlands—*Abies* is absent from southern Evvia— or in sub-montane to montane, open shrublands dominated by thick patches of *Pteridium aquilinum* ferns. In these habitats of Mt Ochi, I have found that subsp. *delphicum* frequently produce sterile stems instead of basal leaf rosettes; the unusual trait gives a quite distinctive appearance to the plants but apart from it they are indistinguishable from typical individuals that grow in proximity. I propose this taxon to be classified as a new variety of subsp. *delphicum* (Figure 3 and Supplementary file 2). The variety might have evolved from the competition for sunlight inside the dense patches of ferns of these habitats, whereas I have never found

it in central Evvia —not even in the shadier spots where subsp. *delphicum* produces the typical basal rosettes.

Murbeck's assumption that typical *V. delphicum* existed on Mt Parnitha was based on the following material he cited in his monograph: i) a collection by Heldreich —“*Parnes, reg. abiet. occid., leg. HELDREICH 1854, n. 2902 [Hb. Berl.]*”— even though Heldreich himself never reported *V. delphicum* from mainland Greece and the date of the collection, which has unfortunately been destroyed during World War II (Th. Raus, personal communication, 27 August 2015), precedes by two years that of the original description of the species; ii) three collections by collector Basilios Tuntas —“*Parnes, prope cacumen, leg. TUNTAS 5/7/1911, n. 1247 [Hb. Hal.; Hayek].- Mt Parnes, prope cacumen, leg. TUNTAS 21/7/1907, n. 356 [Hb. Hal.]; 13/6/1909, n. 810 [Hb. Hal.]*”— which, however, were not found either in WU-Generale, WU-Halácsy-Graecum or WU-Halácsy-Europaeum (W. Till, personal communication, 15 March 2016). Perhaps the only surviving voucher is kept in the Gothenburg Herbarium and likely corresponds to the aforementioned n. 1247 specimen of the collector, although the serial number is missing. Nevertheless, on the sheet there is a label with Murbeck's name and handwriting that states “*V. delphicum*”. Having seen the specimen I have no doubt it represents subsp. *cervi* on account of the characteristic small basal leaves with an obtuse-cuneate base and the short indumentum. It is interesting to note that the aforementioned specimen includes the whole aerial part of a plant arranged on a single sheet, which is actually feasible for a medium individual of subsp. *cervi* —e.g., see the Holotype, Supplementary file 1. On the contrary, a medium individual of subsp. *delphicum* is impossible to completely fit on a voucher sheet because the basal leaves are too big. I conclude that on Mt Parnitha there exists a single infraspecific taxon of *V. delphicum*, namely subsp. *cervi*, allopatric to the insular subsp. *delphicum* which is confined to Evvia. The species had not been collected from the mainland for almost a century, but its existence was confirmed by a recent floristic study on the mountain (Aplada et al. 2007), (E. Aplada, personal communication 1 September 2016). Other reports of *V. delphicum* from the mainland —from the Peloponnese cited in (Dimopoulos et al. 2013) or from Mt Pendeli cited in (Vladimirov et al. 2012)— are in error (Th. Raus, and K. Polymenakos, personal communications respectively). The distribution map of *V. delphicum* is presented in Figure 4.

Suggested conservational status

V. delphicum subsp. *cervi* is restricted to the core of the National Park of Mt Parnitha where it apparently constitutes a single, fragmented population within an area of occupancy of less than 1 km² and a total population size of no more than 50 mature individuals (August 2016). The alarmingly rare new taxon has suffered habitat loss with the devastating fire of 2007 on the mountain and is now under direct threat by the overpopulated deer of the National Park which consume the developing inflorescences; the bitten plants respond by producing a few new small flowering shoots but seed yield is expected to be



Figure 4. Distribution map of *Verbascum delphicum*: ■ subsp. *cervi*; ●, ○ subsp. *delphicum*; ○ var. *flictorum*.

severely affected. Importantly, the population size of *V. delphicum* subsp. *cervi* has been reduced about 20% over the last three years and the taxon is apparently critically endangered according to IUCN Red list criteria C(2a(i,ii)) and D(1) (IUCN 2001).

Comments on taxonomic affinities and phytogeography

Considering the recent radiation in the genus *Verbascum* (Ghahremaninejad et al. 2014) and the strong phytogeographic connection between Ins. Evvia and Sterea Ellas (Trigas 2003), it is reasonable to assume that *V. delphicum* subsp. *cervi* represents a neoendemic taxon that has diverged from the insular subspecies through the process of allopatric subspeciation. On the other hand, the infrageneric relationships of *V. delphicum* are more difficult to infer. In particular, Murbeck places *V. delphicum* under Sect. *Bothrosperma* Murb., Subsect. *Fasciculata* Murb., B. *Isandra* Franch., p. p., a.

Bracteolata Murb., α *Umbellulifera* Murb., 1. *Adenanthera* Murb. and further groups it with the widespread in the Balkans *V. banaticum* Schrad. on account of the white stamen-hairs and the relatively long pedicels. However, the two species are very different and only doubtfully closely related —*V. banaticum* is an eglandular herb with lobed and pinnatisect at the base of the lamina rosette-leaves, freely branched, leafy, lax inflorescences and has smaller all flower parts and capsule. Rather I suspect that *Adenanthera* —i.e. having papillate connective of the anthers of the anterior stamens— is a non-monophyletic trait and that *V. delphicum* is actually more closely related to some *Leianthera* Murb. —i.e. with glabrous connective— species of the centered but not restricted to the Balkans group of *V. nigrum* L., *V. chaixii* Vill., *V. lanatum* Schrad. and *V. glabratum* Friv. These species show considerable resemblance to *V. delphicum* with respect to general leaf morphology, indumentum and habit. Moreover, additionally to their glabrous connective of anterior stamens, these species all differ from *V. delphicum* in the purple stamen-hairs and in the more or less striate stems. I should also note at this point that the connective of the anterior stamens of *V. delphicum* is often glabrous too and this is particularly evident for subsp. *delphicum* — Figure 2F shows one such stamen with the hairs not found on the connective. Intriguingly, *V. delphicum* also shows considerable phenetic resemblance with two Asiatic species, namely *V. discolor* Murb. from the Amanus Mountains and *V. antitauricum* Hub.-Mor. from the Anti-Taurus mountains, both of south-central Turkey. *V. discolor* is generally a more glabrous plant than *V. delphicum* with glabrous connective of anterior stamens, glabrous outer surface of the corolla and a more branched and laxer inflorescence. *V. antitauricum*, similarly to *V. delphicum* has either papillate or glabrous connective of anterior stamens but has bicolored stamen-hairs, glabrous corollas on the outer surface, more or less shorter pedicels and it is eglandular. In any case, the differences between *V. delphicum* and the Turkish species are not more pronounced than those between *V. delphicum* and the aforementioned Balkan species —compared individually— and thus additional data from molecular phylogenetics and/or cytological studies are needed for clarifying the topic of *V. delphicum* infrageneric affinities.

Conclusions

Both infraspecific taxa of *V. delphicum* described in this study are distinct and easily recognized, whereas the species closest relative remains unknown. Subspecies *cervi* is apparently a critically endangered taxon.

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Supplementary material 1

***Verbascum delphicum* subsp. *cervi* Zografidis subsp. nov., holotype.**

Authors: Aris Zografidis

Data type: JPEG file

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Supplementary material 2

***Verbascum delphicum* subsp. *delphicum* var. *filictorum* Zografidis var. nov., holotype.**

Authors: Aris Zografidis

Data type: JPEG file

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