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Pantoporate pollen in the Asteraceae (Vernonieae)

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Abstract

Pantoporate pollen, which occurs sporadically in the Monocots and Dicots, has now been found in Asteraceae in two apparently related genera of the tribe Vernonieae, *Polydora* Fenzl and *Oocephala* H.Rob. Disposition of pores in *Polydora* seems more asymmetric than in *Oocephala*. Based on the known relationships within the Vernonieae, some conjectures are made regarding development of the pantoporate condition in the group.

Keywords

Asteraceae, Compositae, *Oocephala*, pantoporate pollen, *Polydora*

Introduction

The tribe Vernonieae is notable for remarkable variations in pollen structure, variations in sublophate and lophate forms with varying degrees of reduced perforated tectum in the exine and variations in the attachments of the outer exine to the footlayer. Now a new variation has been encountered during a study of South African Vernonieae that involves the first known examples of pantoporate pollen with non-equatorial pores in the Asteraceae. It is of some interest that one of the genera involved, *Polydora* (as *Crystallopollen*) was one in which pollen was first used as a taxonomic character in the Asteraceae by Steetz (1864). The new variants are occasion for some discussion of the positioning of pores in the pollen of Angiosperms.

Already known in the Tribe Vernonieae are the only examples of pollen in the Asteraceae with perforated tectum partially or completely lacking in non-colpar areas. Also unique to the tribe in the family is the six-porate form of pollen in the southeast Asian genus *Camchaya* Gagnep., where the pores occur equatorially in three pairs (Bunwong and Chantaranothai 2008, Robinson and Skvarla 2010). There is also a great deal of variation in lophate patterns in pollen of the tribe. The principle mechanism marking orientation of poles and pores and offering the most obvious provision for expansion of the grains when wet, the colpi, are lost in a set of exclusively paleotropical subtribes. As a result, many of the genera of the Vernonieae can be distinguished by the form of their pollen (Robinson and Skvarla 2010). Now, for the first time in the Vernonieae or Asteraceae we report a further variation involving pollen with pores that are pantoporate (global distribution), that is, not all equatorial in position.

Materials and methods

Specimens examined are from the U.S. National Herbarium in Washington, D.C. Examination of pollen with a light microscope was insufficient to show the position of the pores. Pollen grains in most illustrations were treated with acetolysis (Erdtman 1960), followed by staining with osmium thiocarbohydrazide solutions and sputter coating with gold-palladium (Robinson and Skvarla 2006, 2007, Robinson et al. 2008). Unacetolyzed grains were rehydrated in water or alcohol directly from herbarium sheets and similarly sputter-coated. Observations were made with a JEOL 880 (Samuel Roberts Microscopy Laboratory at the University of Oklahoma) scanning electron microscope (SEM) or a Leica 440 (United States National Museum of Natural History in Washington scanning electron microscope, both equipped with lanthanum hexaboride (LaB_6) electron sources. To achieve limited increased breakage, material gathered at the base of a centrifuge tube was given a few jabs with a dissecting needle.

Results

The two genera in which the pantoporate pollen is now being reported are both restricted to sub-Saharan Africa. The two genera, *Oocephala* and *Polydora*, are evidently closely related to each other according to the pollen similarity, and both have pedunculate heads, a characteristic of many genera. Nevertheless, the two genera are easily distinguished from each other. *Polydora* has an ordinary broadly campanulate capitulum, and an ordinary capillary pappus. *Oocephala* (egghead) has an egg-shaped capitulum and a plumose pappus.

Examined material (Table 1) includes three species of *Oocephala*, ***Oocephala centauroides*** (Klatt) H.Rob. & Skvarla, comb. nov. [basionym: *Vernonia centauroides* Klatt, Bull. Herb. Boissier 4: 824. 1896] (Fig. 1A–F); ***Oocephala staehelinoides*** (Harv.) H.Rob. & Skvarla, comb. nov. [basionym: *Vernonia staehelinoides* Harv., Thes.

Table 1. Specimens studied.

433	*Oocephala centauroides* (Klatt) H.Rob. & Skvarla, Regio oriente et Mosambique, Delagoa Bay, *Schlechter 18138* (US).
474	*Oocephala staehelinoides* (Harv.) H.Rob. & Skvarla, Transvaal, Mar. 1972, *Liebenberg 8848* (US).
475	*Oocephala stenocephala* (Oliv.) H.Rob., Zambia, *Christensen & Chisumpa 1508* (US).
451	*Polydora angustifolia* (Steetz) H.Rob. (as *P. erinacea*), Malawi, Zomba District, Likangala, Phalombe Road, 3000 ft., 3/ 12/ 1984, *Christensen & Patel GMC 1457* (US).
461	*Polydora angustifolia* (Steetz) H.Rob., *Brass 16090* (US), isoneotype.
462	*Polydora bainesii* (Oliv. & Hiern) H.Rob., Zimbabwe, *West 7266* (US).
463	*Polydora bainesii* (Oliv. & Hiern) H.Rob., Zambia, *C. Earle Smith & Richards 4671* (US).
464	*Polydora bainesii* (Oliv. & Hiern) H.Rob., Malawi, *Salubeni & Kaunda 4187* (US).
465	*Polydora chloropappa* (Baker) H.Rob., Tanzania, *Bidgood & Vollesen 7082* (US).
466	*Polydora chloropappa* (Baker) H.Rob., Zambia, *Loveridge 845* (US).
467	*Polydora jelfiae* (Moore) H.Rob., Zambia, *Christensen & Chisumba 1512* (US).
473	*Polydora poskeana* (Vatke & Hildebr.) H.Rob., Tranvaal, *Koekemoer 234* (US).
468	*Polydora serratuloides* (DC.) H.Rob., Burundi, *Lualla 4640* (US).
469	*Polydora serratuloides* (DC.) H.Rob., Tanzania, *Groomany 7869* (US).
470	*Polydora steetziana* (Oliv. & Hiern) H.Rob., S. Africa, *Koekemoer 2189* (US).
471	*Polydora steetziana* (Oliv. & Hiern) H.Rob., Namibia, *Seydel 2828a* (US).
472	*Polydora sylvicola* (Pope) H.Rob., Zambia, *Christensen & Chisumpa GMC 1526* (US).

Cap. 2: 36. 1863, "stahelinoides"] (Fig. 2A–F); *Oocephala stenocephala* (Oliv.) H.Rob. (Fig. 3A, B); and eight species of *Polydora*, *P. angustifolia* (Steetz) H.Rob. (Figs 3C, 4); *P. bainesii* (Oliv. & Hiern) H.Rob. (Fig. 5A–D); *P. chloropappa* (Baker) H. Rob; *P. jelfiae* (S. Moore) H.Rob.; *P. sylvicola* (G.V. Pope) H.Rob. (Fig. 5E, F); *P. poskeana* (Vatke & Hildebr.) H.Rob. (Fig. 6A–C); *P. steetziana* (Oliv. & Hiern) H.Rob. (Fig. 7A–C); and *P. serratuloides* (DC.) H.Rob. (Fig. 6D–E).

The pollen of both genera has a lophate exine pattern that is nearly spherically symmetrical. The pattern consists of a mixture of pentagonal and hexagonal lacunae. Perforated tectum is essentially absent leaving totally exposed muri and their subtending columellae. Both genera also share a mural structure that has been referred to as rhizomate (Robinson 1999) (Figs 1F, 2F, 3C, 4C, 5B, D, 6C, E). In these muri, the columellae, instead of being firmly attached to the footlayer at their bases, are attached basally to each other by a lower horizontal structure (rhizome) that is itself weakly attached to the footlayer. Such a structure is not unique to the two genera studied, but occurs in many lophate, triporate, non-colpate pollen grains in the subtribes Centrapalinae and Erlangeinae that are native to the Paleotropics. A note of interest is the possible difference in the chemical make-up of these muri, since they have been seen to survive the degrading effects of chloral hydrate more completely than the muri and tectum of other Vernonieae when mounted in Hoyer's solution (Anderson 1954).

Positions of the pores are often difficult to determine in lophate pollen of the Centrapalinae and Erlangeinae. The lacunae in which the pores occur are totally undifferentiated in any other way, being either pentagonal or hexagonal, even in the polar

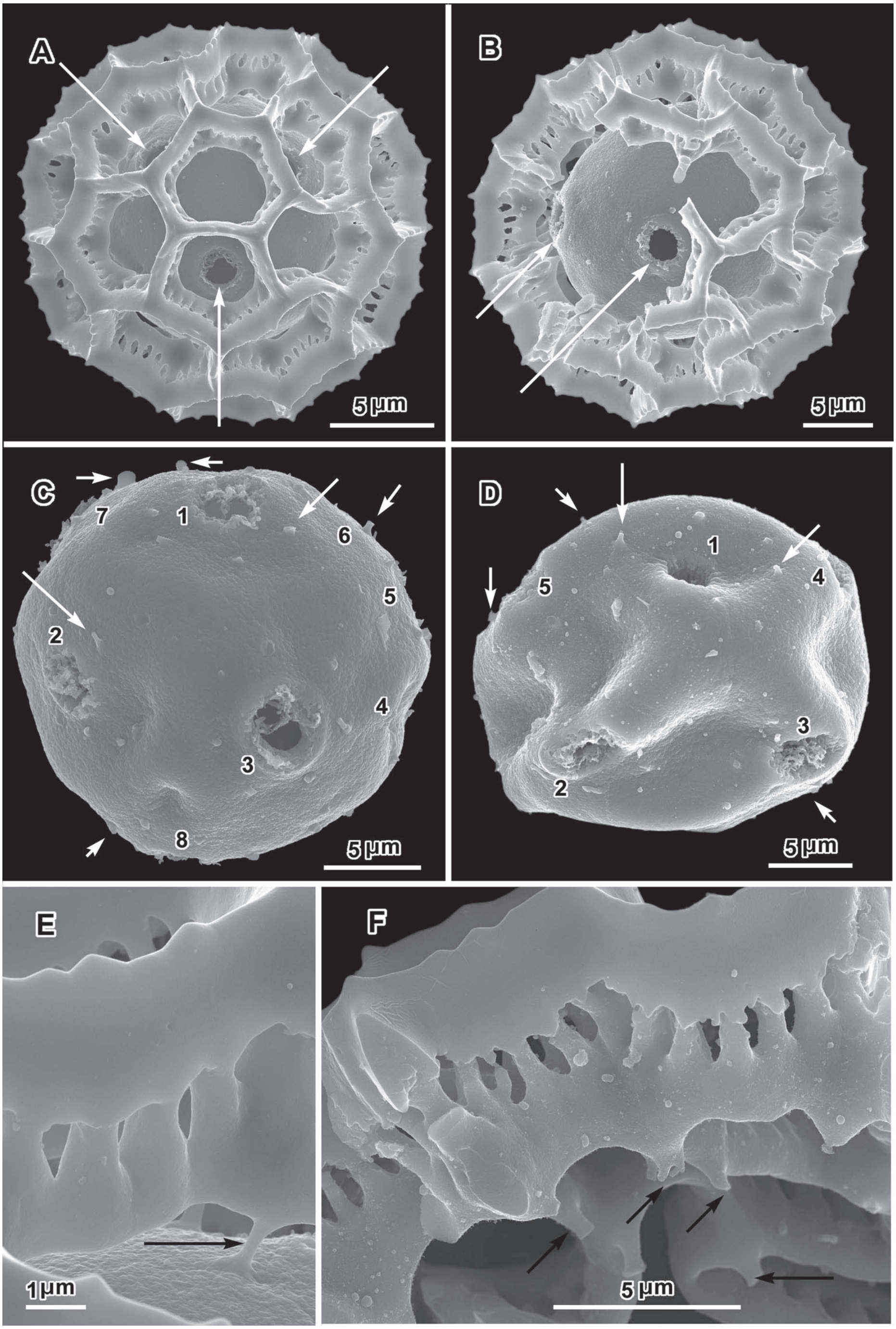

Figure 1. Scanning electron micrographs of *Oocephala centauroides* (*Schlechter 18138*). **A, B** pollen grains with muri of outer exine mostly ot totally intact, arrows showing visible pores **C, D** grains stripped of muri, with pores or possible pores numbered, arrows showing scars of muri attachment **D** distorted **E, F** pieces of muri showing rhizomate structure and stubs of attachments to footlayer.

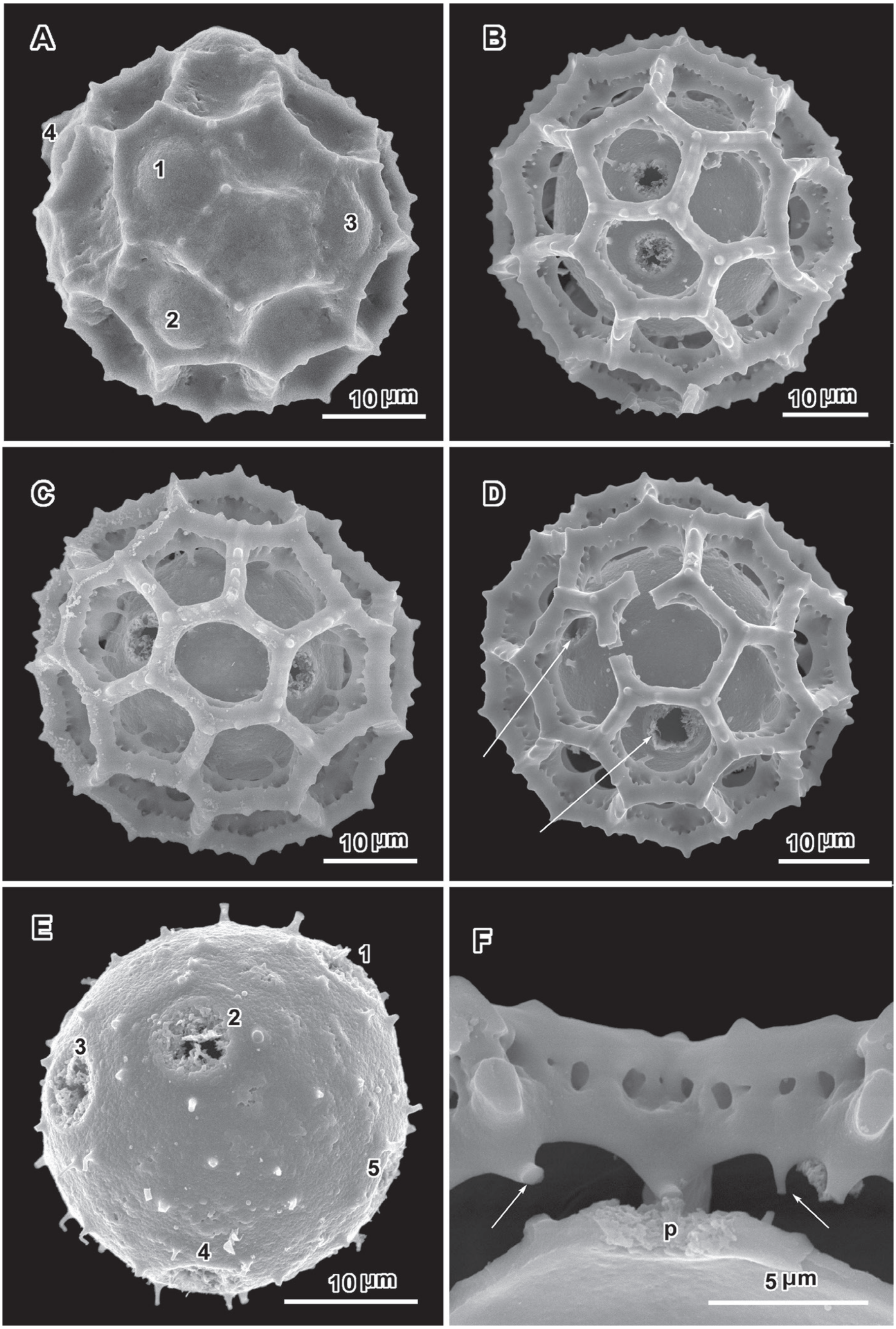

Figure 2. Scanning electron micrographs of *Oocephala staehelinoides* (**A–D** and **F** from *Liebenberg 8848*; E from *Liebenberg 8843*). **A** unacetylized grain showing three pores with caps intact, two pores in adjacent lacunae **B–D** intact or nearly intact grains showing pores in both pentagonal and hexagonal lacunae **B** with pores in adjacent lacunae **E** grain stripped of muri showing five pores and stubs of muri attachments **F** segment of muri showing rhizomate structure and remnants of weak basal attachments to footlayer.

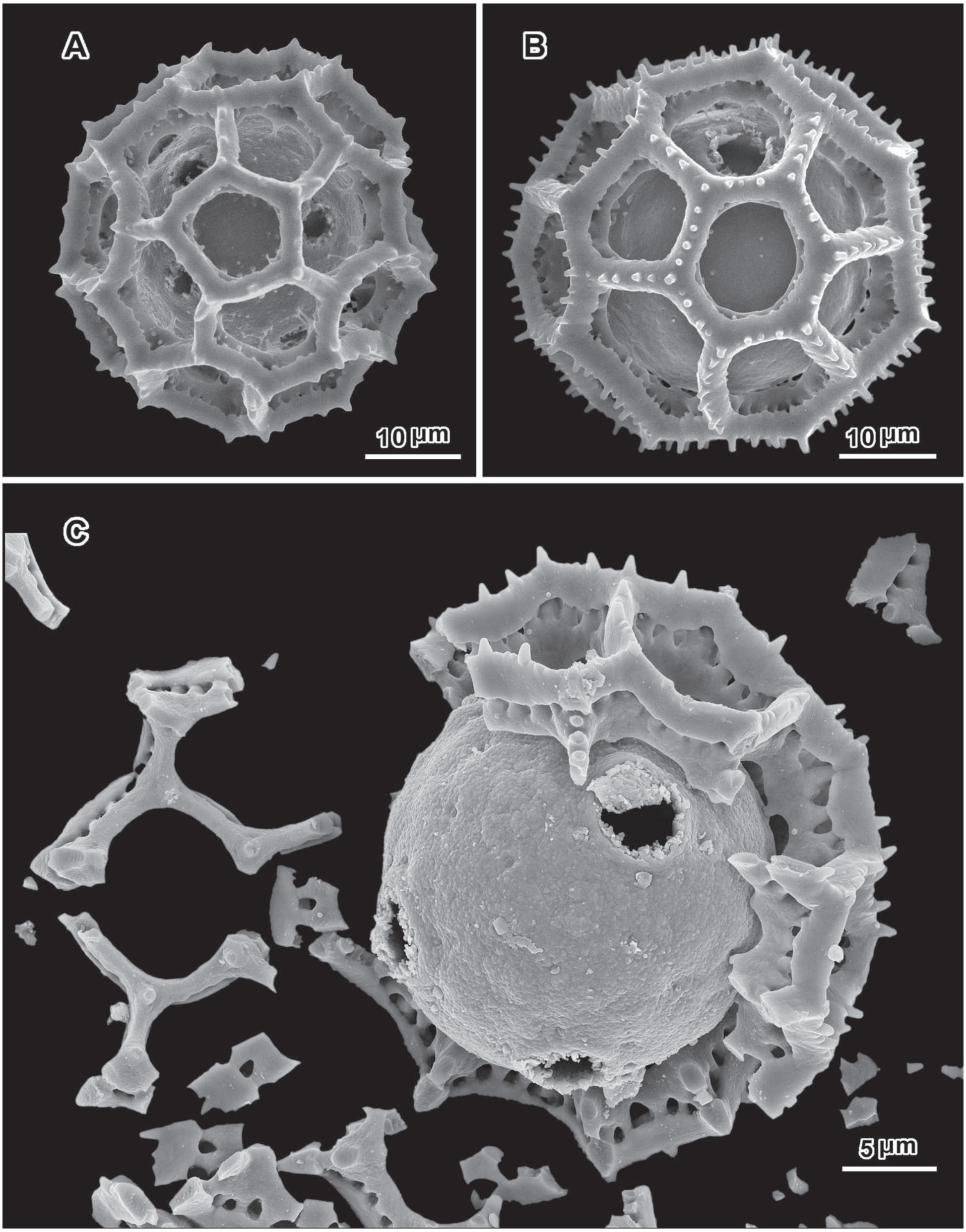

Figure 3. Scanning electron micrographs of *Oocephala stenocephala* (**A–B** from *Christensen & Chisumpa 1508*) and *Polydora angustifolia* (**C** from *Christensen & Patel 1457*). **A** intact grain with four visible pores **B** intact grain with one visible pore **C** grain partially stripped of muri showing three pores in pantoporate positions.

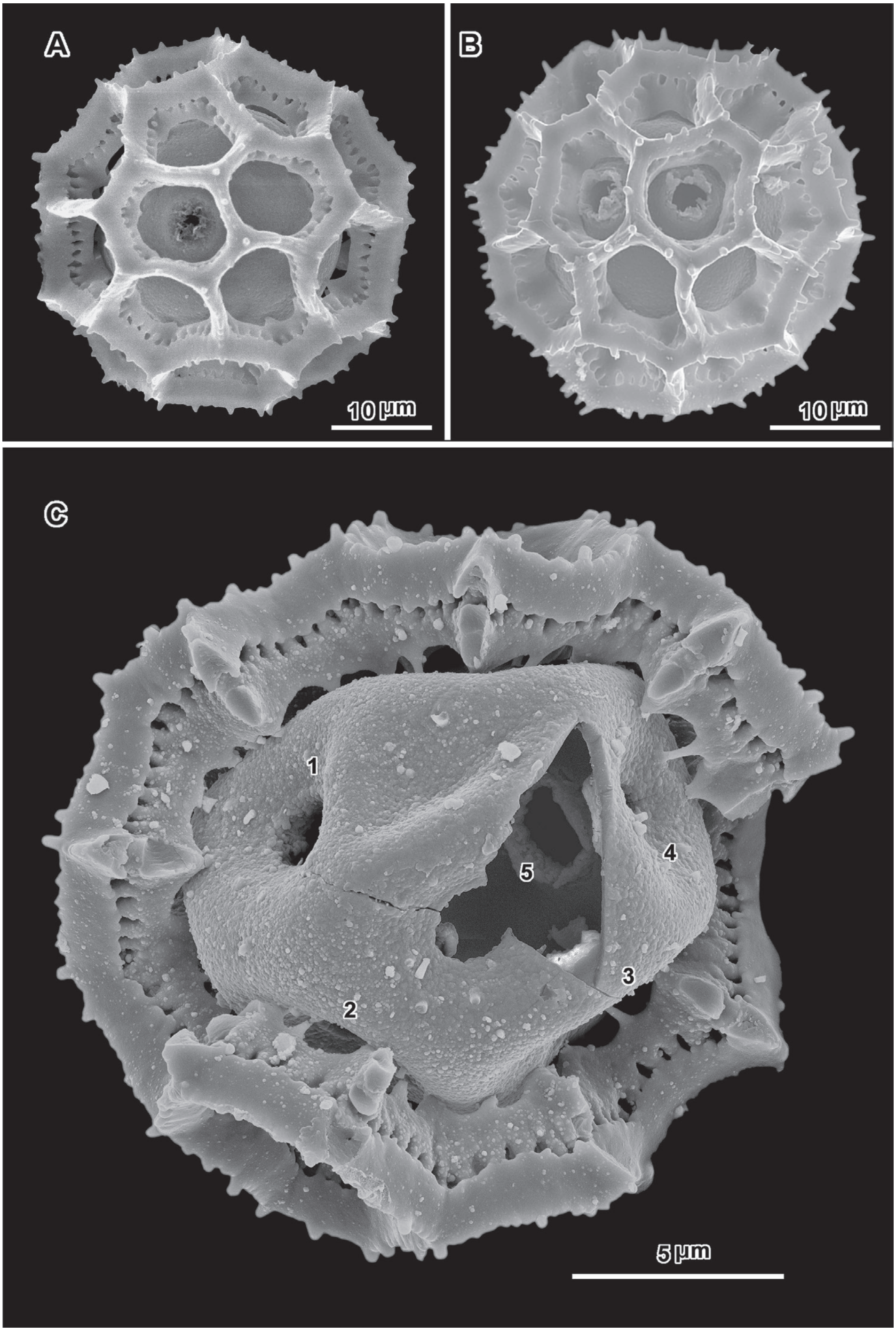

Figure 4. Scanning electron micrographs of *Polydora angustifolia* (**A** from *Brass 16090*; **B–C** from *Christensen & Patel 1457*). **A** intact grain with visible pore **B** intact grain with two visible pores in adjacent lacunae **C** grain with muri partially removed showing distorted inner surface and five pores.

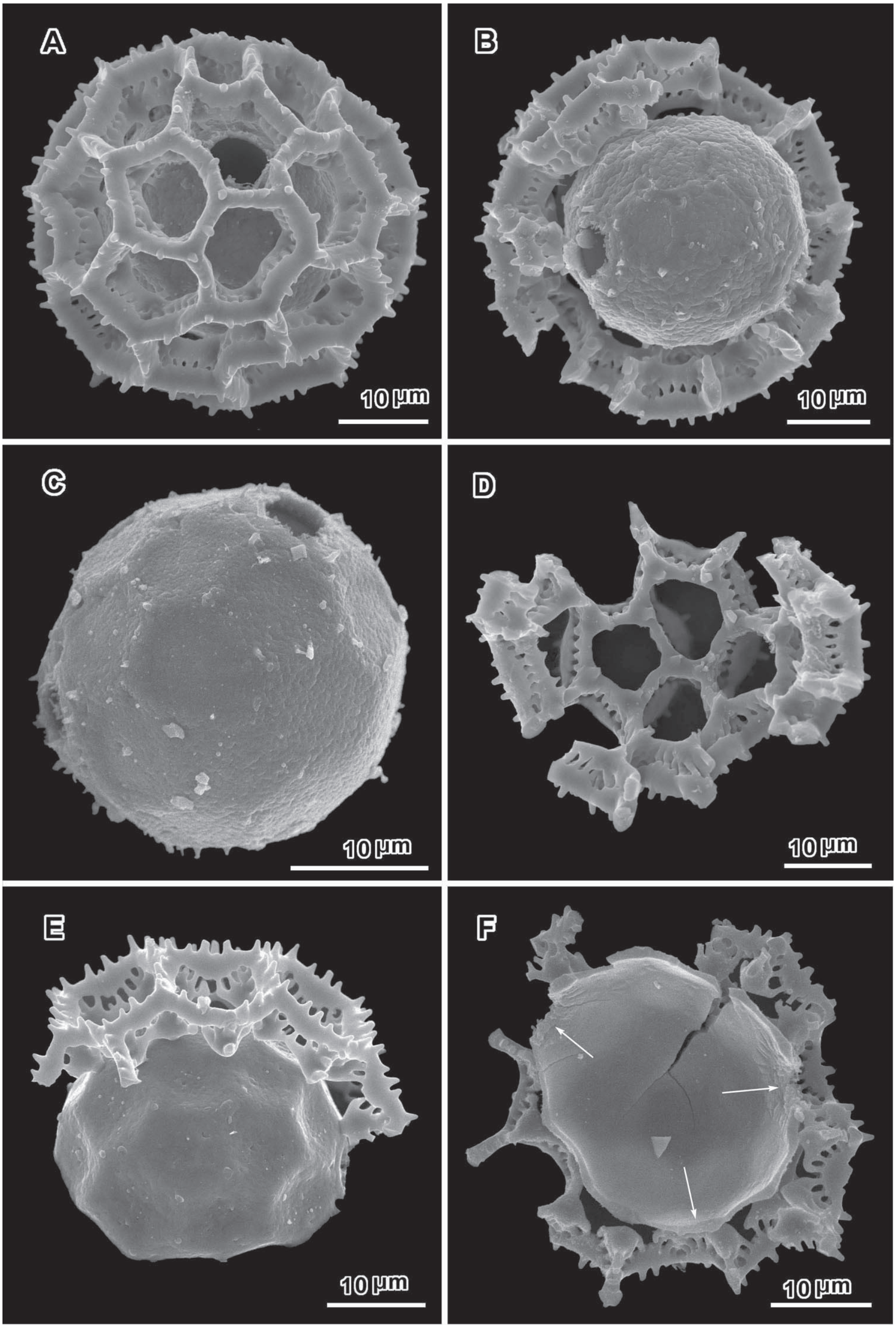

Figure 5. Scanning electron micrographs of *Polydora bainesii* (**A–D** from *Smith & Kaunda 4187*) and *Polydora silvicola* (**E–F** from *Christensen & Chisumpa 1526*). **A** intact grain with one visible pore **B, C** grains partially and completely stripped of muri **D** segment of outer exine showing how muri can detach in large units **E, F** broken grains **F** split grain with three pores (arrows) **B, C, E** grains showing asymmetry with large areas lacking pores.

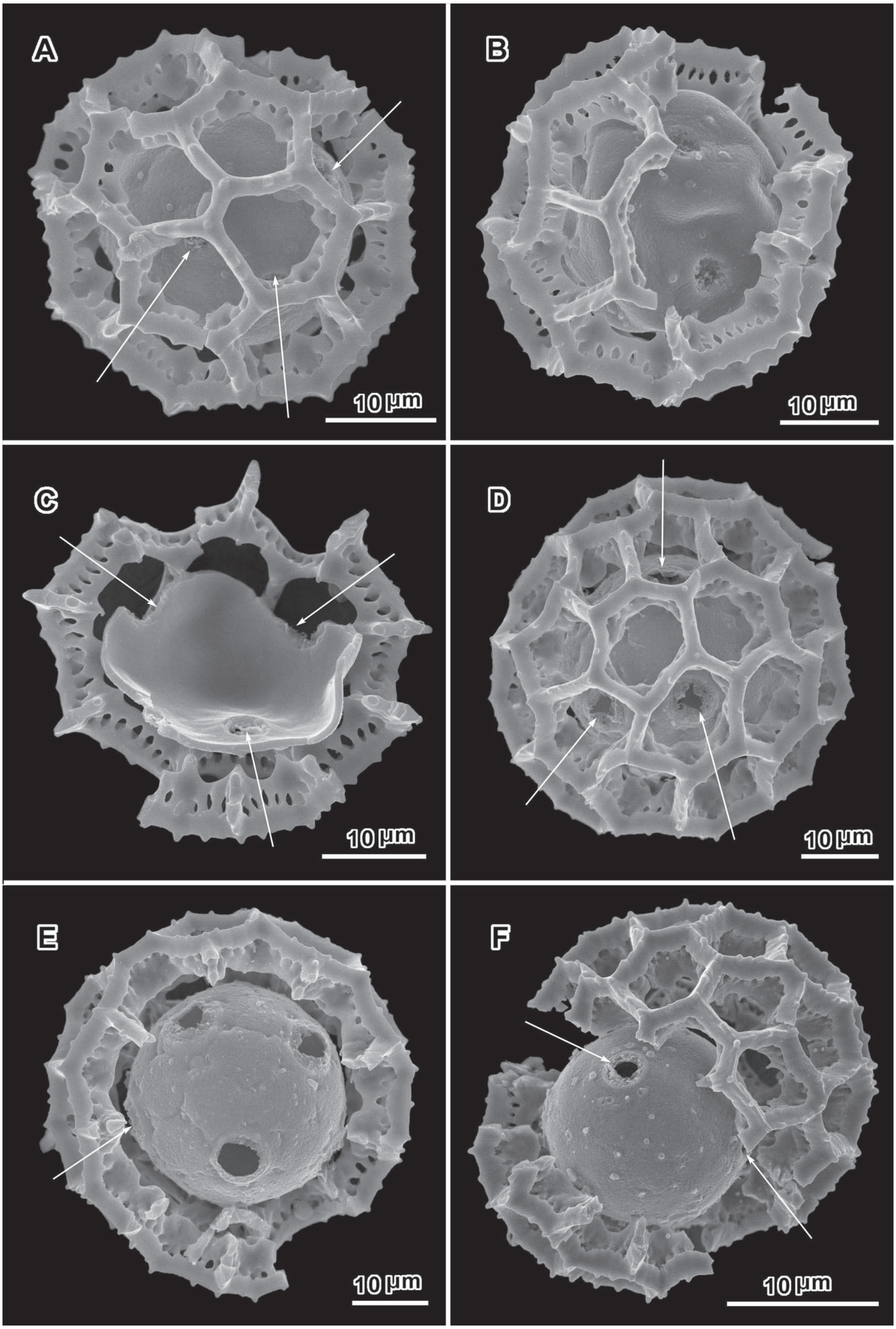

Figure 6. Scanning electron micrographs of *Polydora poskeana* (**A–C** from *Koekemoer 234*) and *Polydora serratuloides* (**D–F, D** and **E** from *Lualla 4640*, **F** from *Groomany 7869*). **A** intact grain with pore and incipient pores (arrows) **B** grain partially stripped of muri showing three visible pores **C** grain stripped of muri with three visible pores **D** intact grain with three visible pores, two in adjacent lacunae **E, F** broken grains with four and two pores visible.

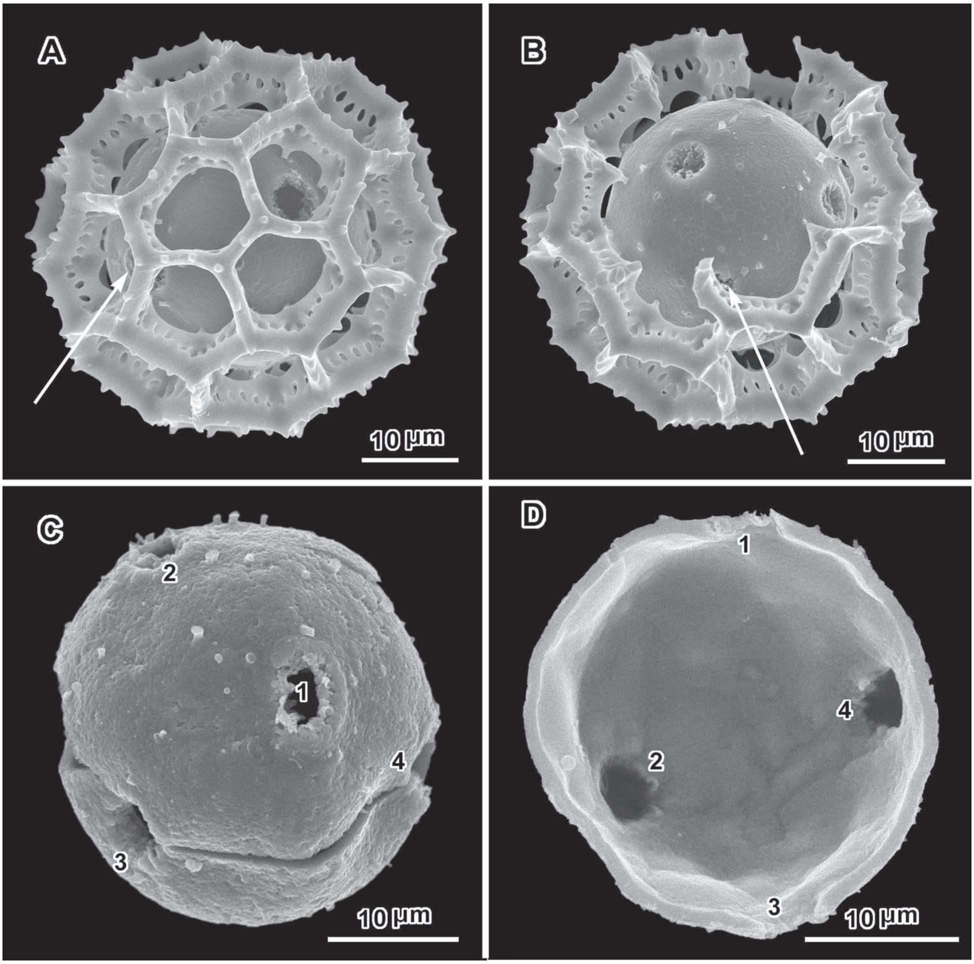

Figure 7. Scanning electron micrographs of *Polydora steetziana* (**A** and **B** from *Seydel 2828a*, **C** and **D** from *Koekemoer 2189*). **A** intact grain with two visible pores **B** broken grain with three visible pores **C** grain stripped of muri with four pores visible **D** broken grain with four pores visible from inside.

regions. The depths of the lacunae usually prevent seeing more than one pore at a time unless the grains are unacetylized and the caps on the pores are preserved (Fig. 2A) (Robinson and Skvarla 2009). Thus, the easily dehiscent muri of *Oocephala* and *Polydora* are particularly helpful. The totally exposed sphere of the pollen footlayer shows the pores very well (Figs 1C, D, 2E, 3C, 4C, 6C, 7C, D). In this way, positions and numbers of pores on the grains can be more accurately seen (Figs 1C, D, 2E, 7C,7D). To help in the estimates, a toy ball was obtained from the museum shops that showed a pattern of pentagons and hexagons that was a very close approximation of the pattern of lacunae in the pollen grains of *Oocephala* and *Polydora*. It was study of the toy ball that led to the conclusion that the pollen of *Oocephala* could characteristically have seven or eight pores. (Figs 1C, 2E).

An exact count of the pores can never be certain, since there is evidence of some uneven distribution of pores in some grains. In a few cases, in *Oocephala,* even in grains with the muri present, pores can be seen in adjacent lacunae (Figs 2A, B, 3A, 4B, 6D). In other cases in *Polydora* (Figs 3C–7C), expanses can be seen that have no pores (Fig. 5B, C, E). The total number of pores may never be more than the five or six that can be seen in some views of *Oocephala* (Figs 1C, D, 2E), and asymmetry is probably even more extreme in *Polydora* (Fig. 5C, E), but pantoporate non-equatorial distribution of pores is certain in both genera, and at least some asymmetry is certain.

Discussion

Two basic porate conditions of Angiosperm pollen are well known (Walker 1974). The forms derived generally from the tetragonal or "cruciate" division of the pollen mother cell that is found in Gymnosperms, Monocots and basal Dicots. The alternative tetrahedral or decussate division of the pollen mother cell is basic to the Eudicots, a sort of reversion to the spore mother-cell pattern of division found in most Cryptogams. The polyporate (pantoporate) condition is found sporadically in all three Angiosperm groups, or as stated by Harley (2004) "known from all three major groups of Angiosperms, although infrequently in the monocots and even less frequently in the basal dicots". In monocots (Harley 2004, Nadot et al. 2006) It is reported in some Bromeliaceae, Alismataceae and Araceae. In basal dicots polyporate pollen is mentioned only from the Trimeniaceae (Sampson 2000, Harley 2004). In the eudicots , Harley mentions Caryophyllales, Ranunculales, Podostemaceae, Linaceae, Zygophyllaceae and Geraniaceae as achieving the polyporate condition by multiplication of simple furrows that are reduced to pores. In other families such as Malvaceae, Sterculiaceae, Thymelaeaceae, Euphorbiaceae and Malpighiaceae a spiralization of a line joining centers of apertures is suggested. All of these are in derived groups, and polyporate pollen is not basic to any group.

There have been no previous reports of pantoporate pollen in the Asteraceae, and suggestions here are based on observations of the pollen of related members of the family in the tribe Vernonieae.

The Asteraceae has pollen that is basically tricolporate, a condition that seems basic to all the tribes including the Vernonieae (Blackmore et al. 2009). The most important evidence comes from the fact that the polyporate condition in the Asteraceae is found in the tribe Vernonieae which has the some of the most destabilized pollen formation of any tribe in the family. The pantoporate pollen has developed within the subgroup of the Vernonieae that already has the most spherically symmetrical forms of pollen in the tribe, the subtribal pair, Erlangeinae and Centrapalinae. It is in these subtribes that the colpi are totally suppressed, and orderly arrangement of the lacunae, even at the poles, is completely lost. These features that have become so spherically symmetrical in these subtribes are among the last layers laid down as the pollen grain matures. The position of the pores is much more basic, being established in some of the innermost and earliest laid down layers of the pollen. It is the contention here that the loss of radial symmetry in the Vernonieae pollen started with the outermost and most belatedly deposited layers of the grains, and progressed eventually to the inner and earlier deposited layers.

There is even a developmental basis for the asymmetry in the distribution of the pores, more obvious in *Polydora* and less evident in the more specialized *Oocephala*. This could trace to the fact that the developing pollen grain has a distal surface that faces outward in the pollen mother cell, and a proximal surface that faces inward toward the center of the tetrad of pollen grains. Thus, the distribution of the pores is influenced by early stages in pollen development, beginning with position in the tetrads or mother cell.

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We wish to thank W.F. Chissoe who operated the University of Oklahoma SEM. We also wish to thank Carol Kelloff who operated the USNM SEM, and Scott Whittaker supervisor of the USNM SEM Laboratory. March 2, 2014, after completion of this manuscription but before its submission, John Skvarla unexpectedly died. Two messages that he had send to me recently are worth citing. First looked forward to seeing the reaction to this paper, and second, he wish he had started working on the Vernoniae earlier in his career.

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The use of Optical Character Recognition (OCR) in the digitisation of herbarium specimen labels

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Abstract

At the Royal Botanic Garden Edinburgh (RBGE) the use of Optical Character Recognition (OCR) to aid the digitisation process has been investigated. This was tested using a herbarium specimen digitisation process with two stages of data entry. Records were initially batch-processed to add data extracted from the OCR text prior to being sorted based on Collector and/or Country. Using images of the specimens, a team of six digitisers then added data to the specimen records. To investigate whether the data from OCR aid the digitisation process, they completed a series of trials which compared the efficiency of data entry between sorted and unsorted batches of specimens. A survey was carried out to explore the opinion of the digitisation staff to the different sorting options. In total 7,200 specimens were processed.

When compared to an unsorted, random set of specimens, those which were sorted based on data added from the OCR were quicker to digitise. Of the methods tested here, the most successful in terms of efficiency used a protocol which required entering data into a limited set of fields and where the records were filtered by Collector and Country. The survey and subsequent discussions with the digitisation staff highlighted their preference for working with sorted specimens, in which label layout, locations and handwriting are likely to be similar, and so a familiarity with the Collector or Country is rapidly established.

Keywords

OCR, Digitisation, Data entry, Specimen, Label, Herbarium

Introduction

There is an increasingly urgent need to document and make available the specimens held in herbaria and other natural history collections, particularly with the current biodiversity crisis (Berendsohn et al. 2010, Hardisty et al. 2013, Purves et al. 2013). The digitisation of the collections makes the data accessible for a wide range of taxonomic and ecological research being carried out around the world (e.g. Elith et al. 2006, Bebber et al. 2010, Lees et al. 2011, Lavoie 2013). The size of the collections held in major herbaria means that complete digitisation of the specimens they hold is often unfeasible, especially with the decreased funding at the present time.

At the Royal Botanical Garden, Edinburgh (RBGE), a large-scale project to digitise the collections has been running in which specimens are minimally databased (Haston et al. 2012a). Minimal data includes filing name and geographical region, as well as a barcode to act as a unique identifier. The high resolution, zoomable images of these specimens are made available through the online Herbarium Catalogue, accessed through the RBGE website (www.rbge.org.uk). They are also accessible via other online resources including Europeana (www.europeana.eu/) and Genbank (www.ncbi.nlm.nih.gov/genbank/) using a stable URI system (Hyam et al. 2012). Whilst additional label data are not initially captured, they can be accessed by examining the specimen online. There are approximately 3 million specimens in the herbarium at RBGE; of these 630,000 have been databased with 30% only having minimal data attached.

A similar approach is being used at the New York Botanic Garden Herbarium which holds an estimated 7.3 million specimens, where they have been databasing and imaging the collection for 17 years (Tulig et al. 2012). Based on the work already completed they recently estimated that it would take a further 600,000 hours to completely database and image the remaining approx. 6 million specimens. They have brought in new protocols for partially databasing specimens, increasing the speed of processing from an average of 10 per hour to 125 per hour.

Whilst further information can be found through looking at images, data that are useful for biodiversity studies and other research are not easily available, and cannot be extracted from the database for use. These data can include location, habitat and a description of the plant. The next step in the process of databasing specimens must be to find ways of creating more complete and useful records, whilst minimising the need for a large investment in staff hours.

It is only recently that Optical Character Recognition (OCR) has started to be used more widely to aid with the digitisation of natural history collections (Moen et al. 2008, Heidorn and Wei 2008, Nelson et al. 2012) and literature relating to these collections such as the Biodiversity Heritage Library (Biodiversity Heritage Library 2014) which uses OCR output to help navigate the literature. As the quality of the software has improved, OCR has become a viable option, more able to cope with the complex tasks which can be presented by natural history objects; e.g. distinguishing between labels and plant material on a herbarium specimen. Another contributing factor to the increased viability of OCR could be that there is now a large enough body of imaged specimens to make investment in OCR software worthwhile.

Several software applications have been developed to make use of OCR outputs easier. SALIX (Lafferty and Landrum 2008, Barber et al. 2013) and HERBIS (Beaman et al. 2006) parse the OCR output to a database, in a semi-automatic way, with the process being watched and facilitated by a user. Another approach (Heidorn and Wei 2008) has been to mark-up the output from the OCR, for input into the Darwin Core. Silver Biology (2013) is currently testing a site for enabling a citizen science initiative to database herbarium specimen labels. The OCR output is tagged with the relevant fields (e.g. Collector) and then parsed into Darwin Core fields. The use of OCR is also being explored by the AugmentOCR working group as part of Integrated Digitized Biocollections (iDigBio), the National Resource for Advancing Digitization of Biodiversity Collections (ADBC) funded by the National Science Foundation.

At RBGE we have been exploring how OCR processing can be used to add data to the minimal entries already created for specimens.

Whilst we have only just started to make use of data from OCR, the process of gathering this information has been integrated into the digitisation workflows since 2010. The workflows at RBGE have been developed in such a way that they are 'modular' (Haston et al. 2012b), to allow flexibility in the stages of digitising specimens. All specimen images are passed through ABBYY Recognition Server (Abbyy 2014) which provides the OCR output in the form of a text file. The unparsed text is automatically entered into a single field within a MySQL database. A PDF file with the OCR output overlaid on the image of the specimen is also saved.

The aims of this investigation are to examine how we can incorporate the OCR output into the workflows to make the digitisation process more efficient.

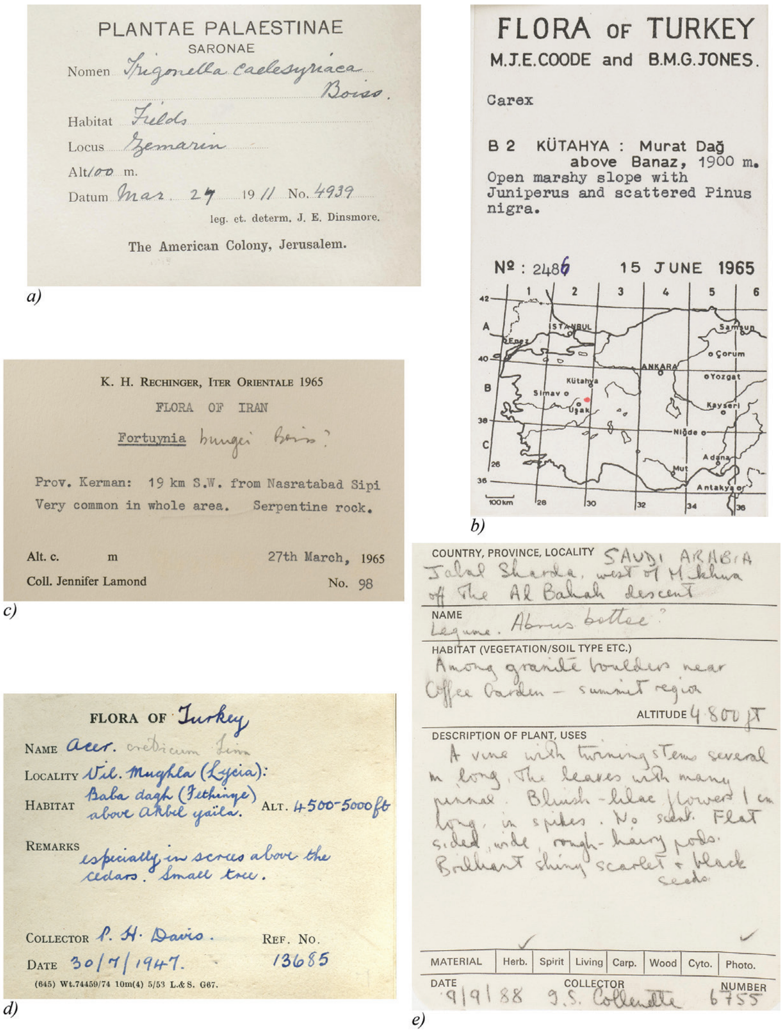
In particular we hope to be able to answer the following questions:

1. Can OCR speed up the digitisation process, whilst maintaining data quality?
2. Is OCR worth the investment in time and software?

Methods

To investigate how data extracted from OCR process can aid in the addition of data to minimal database records, a series of trials were carried out by six members of the digitisation team at RBGE.

The specimens used in this study were collected in Southwest Asia and the Middle East from the early 19th century to the present day. The earlier specimens are generally handwritten, but some have printed headings (Figure 1a). Later specimens are generally type-written or printed (Figure 1b and 1c). Specimens include those used in the writing of the Flora of Turkey (Davis 1985), and also the ongoing work on the Flora of Arabia (Miller 1996). This is a key focus region for research at RBGE and there are several members of staff who have considerable experience of collections from this area



a)

PLANTAE PALAESTINAE
SARONAE
Nomen Trigonella caelesyriaca Boiss.
Habitat Fields
Locus Ezemarin
Alt 100 m.
Datum Mar. 27 1911 No. 4939
leg. et. determ. J. E. Dinsmore.
The American Colony, Jerusalem.

b)

FLORA OF TURKEY
M.J.E.COODE and B.M.G.JONES.
Carex
B 2 KÜTAHYA : Murat Dağ
above Banaz, 1900 m.
Open marshy slope with
Juniperus and scattered Pinus
nigra.
№ : 2486 15 JUNE 1965

c)

K. H. RECHINGER, ITER ORIENTALE 1965
FLORA OF IRAN
Fortuynia bungei Boiss?
Prov. Kerman: 19 km S.W. from Nasratabad Sipi
Very common in whole area. Serpentine rock.
Alt. c. m 27th March, 1965
Coll. Jennifer Lamond No. 98

d)

FLORA OF Turkey
NAME Acer. creticum Linn
LOCALITY Vil. Mughla (Lycia):
HABITAT Baba dagh (Fethiye) above Akbel yaila. ALT. 4500-5000 ft
REMARKS especially in screes above the cedars. Small tree.
COLLECTOR P. H. Davis. REF. No. 13685
DATE 30/7/1947.
(645) Wt.74459/74 10m(4) 5/53 L.&S. G67.

e)

COUNTRY, PROVINCE, LOCALITY SAUDI ARABIA
Jalal Sharda, west of Mikhwa
off the Al Bahah descent
NAME
Legume. Abrus bottae?
HABITAT (VEGETATION/SOIL TYPE ETC.)
Among granite boulders near
Coffee Garden – summit region
ALTITUDE 4 800 ft
DESCRIPTION OF PLANT, USES
A vine with twining stems several
m long. The leaves with many
pinnae. Bluish-lilac flowers 1 cm
long, in spikes. No scent. Flat
sided, wide, rough-hairy pods.
Brilliant shiny scarlet + black
seeds.

MATERIAL	Herb.	Spirit	Living	Carp.	Wood	Cyto.	Photo.
	✓						✓

DATE 9/9/88 COLLECTOR J.S. Collenette NUMBER 6755

Figure 1. Example labels: **a** Pre-printed label with handwritten details **b** and **c** mixed labels with pre-printed and typed information **d** Mainly handwritten label, with printers mark **e** Mainly handwritten label with unusual phrasing.

and so they offer a valuable resource, being able to offer advice on difficult handwriting, cryptic notes on labels and terms to use when searching OCR text.

These specimens have been imaged and minimally databased as part of an ongoing project to image and digitise RBGE herbarium specimens. The digitisation workflow includes the routine processing of all specimen images through ABBYY Recognition Server software, and the unparsed text output is stored within the images database.

For this study 20,000 specimen records were exported from the main database into a temporary Access database. The data included the minimal data fields, the image file location and the OCR data. The OCR output was searched for Countries and Collector names, which were considered to be the most useful additional fields, as well as being the most likely to be easily 'read' by the OCR software. A short SQL script in Access was used to search for a selected word within the OCR text and, when present, to copy the word to a new field. As the specimens were from a limited geographical area, it allowed a list of Countries and major Collectors to be developed.

As well as carrying out simple searches for Country and Collector, other keywords and phrases were found to be peculiar to a particular Collector or Country. These included printers marks (Figure 1d) on otherwise handwritten labels, unusual wording (Figure 1e) or abbreviations used within pre-printed label headings. Common 'reading' errors made by the OCR software (e.g. the OCR software reading Turbey instead of Turkey), variations in spellings of provinces, states or cities were also useful in attaching an initial Country or Collector to a specimen.

The specimen records were then sorted by either Country or Collector, to enable verification of the data. This could be done rapidly using IrfanView (2014) a freeware graphic viewer, which was able to use the image file locations to create a slideshow of specimen images. This allowed specimens to be rapidly checked and the Collector and/or Country to be verified.

Once the Collector and Country had been verified, these data were added to the original specimen records using a batch process facility. This allowed a large number of records to be rapidly updated.

Trial format

The updated records were then used as the basis of a series of trials to assess how the data extracted from the OCR could be utilised in the wider digitisation effort at RBGE. The trials were set-up to look at rates for data entry with and without OCR data being used to aid the process.

The digitisation staff used the institutional database for data entry, allowing full use of the look up tables for collectors, countries and their top-level divisions, as well as a short-cut for repeat entry of fields. They were provided with two screens, one landscape and one portrait to allow for easy viewing of specimen images and organisation of other programmes required.

Each trial consisted of two protocols. These protocols differed in the amount of data being captured. The Complete Protocol involved the capture of all data on the specimen, including the original label as well as any additional determinations and annotations. The Partial Protocol limited the capture of data to a pre-determined standard set of fields including collector, collection number and date, locality information, and the taxon name under which it was originally collected. Twenty-four batches of records, each comprising 50 specimens, were created using a series of filters. These batches were then given to the team of digitisers.

Table 1. Format of the trials.

Trial	'Filter'	Protocol	Number of repeats/person	Total specimens/person
1.	Random	Complete	2	100
		Partial		100
2.	Collector	Complete	2	100
		Partial		100
3.	Country	Complete	2	100
		Partial		100
4.	Collector & Country	Complete	2	100
		Partial		100
5.	Collector & Country(OCR)	Complete	2	100
		Partial		100
6.	Random	Complete	2	100
		Partial		100

The six 'filters' used were:

1. Pre-study control (Random)
2. Collector only
3. Country only
4. Collector and Country
5. Collector and Country, with full OCR output
6. Post-study control (Random)

Trial 1: Pre-study control

This first trial was used as a control and provided a baseline for the testing. The digitisers were each given two batches of randomly selected specimens which only contained minimal data.

Trial 2: Collector only

The digitisers were each given two batches of specimens which had been selected using a filter which ensured that all specimens in the batch had been collected by the same collector or collector group.

Trial 3: Country only

The digitisers were each given two batches of specimens which had been selected using a filter which ensured that all specimens in the batch had been collected in the same country.

Trial 4: Collector and Country

The digitisers were each given two batches of specimens which had been selected using a filter which ensured that all specimens in the batch had been collected in the same country and by the same collector or collector group.

Trial 5: Collector and Country, with full OCR output

The digitisers were each given two batches of specimens which had been selected using a filter which ensured that all specimens in the batch had been collected in the same country and by the same collector or collector group. In addition, a full OCR output was also provided. For this study the type of OCR output used was one where a PDF of the OCR output, layered over the top of the specimen image where text was detected. The digitisers were then asked to copy the OCR data into the appropriate fields and correct it for spelling and punctuation errors.

Trial 6: Post-study control

This final trial was used as a second control to assess how using the other methods, and increased familiarity with the process affected timings. The digitisers were each given two batches of randomly selected specimens which only contained minimal data.

The digitisers were asked to keep a record of the time it took to complete each set of specimens, excluding breaks.

Analysis

The results of the tests were collated and an Analysis of Variance (ANOVA) was carried out in R. The digitisers were also asked to complete a short survey which explored the 'people' side of the work, asking about preferred workflows, their perception of time taken to complete tests and what resources may be of benefit to aid similar work in the future. The online questionnaire was followed up with an informal discussion of the trials, allowing points mentioned in the survey to be discussed further and also to discuss some of the wider implications of digitising specimens.

Results

The results of the study show significant differences in the average time taken for the trials to be completed. The level of variation observed between the trials differed between the Complete and Partial Protocols. Significant variation was observed between the trials completed using the Partial Protocol.

The results are summarised in Table 2.

Diagnostic plots were used to check that the data were normally distributed. There was evidence for some heteroscedascity in the data, so we cannot assume a normal distribution. A Poisson distribution was tested and compared with a normal distribution using AIC, which suggested that a normal distribution model fits the data better than a Poisson distribution model. We therefore present the results from the analyses based on a normal distribution.

Table 2. Average time taken to complete trials.

Trial	'Filter'	Number of completed batches per Protocol	Average Complete Protocol (minutes)	% time saved (compared with Random 1)	Average Partial Protocol (minutes)	% time saved (compared with Random 1)
1.	Random 1	10	313	0%	226.9	0%
2.	Collector	10	259.5	17.1%	220.2	2.7%
3.	Country	10	345.7	10.5% increase	192.6	15.2%
4.	Collector & Country	10	262.8	16.1%	105.3	53.6%
5.	Collector & Country (OCR)	10	252.6	19.3%	125.7	44.7%
6.	Random 2	10	283.9	9.3%	219.9	3.1%

The data were analysed to investigate the effect of Person on the trials, since this would have an impact on the analysis used. Firstly a linear regression was carried out treating each person as a factor. This suggested that the variation observed is explained by the Trial rather than the Person. Secondly co-plots were used to visualise the interactions of the person and the trials. These showed no significant effect of the person on the results, and the major effects were related to Trial. As a result of these analyses it was decided that one of the datasets should be excluded from the analyses as an outlier.

The Analysis of Variance (ANOVA) showed significant variation between the 12 trials.

Table 3. Result of ANOVA for the 12 trials.

	Df	F Value	Pr (>F)	Significance
Trial	11	13.03	4.11e-14	*** (0)
Residuals	85			

The filters appear to have greater impact in the trials using the Partial Protocol. The Partial Protocol is used as the standard for the majority of databasing at RBGE. Therefore these trials were analysed further to explore this impact and the results are illustrated in the box plots (Figures 2 and 3).

Partial protocol

The trials completed using the Partial Protocol show a significant reduction in the average time taken to add data to specimens which had been filtered by Country, by Collector and Country and by Collector and Country with OCR.

The greatest reduction in average times was seen in those specimens filtered by Collector and Country. The Country filter appeared to have the greatest impact on reducing the time.

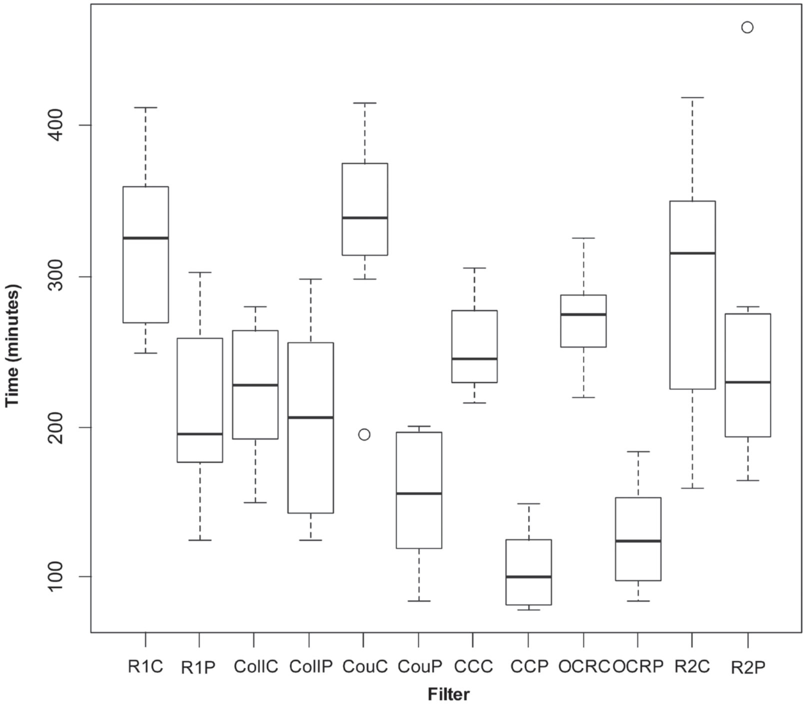


Figure 2. Box plot of Complete and Partial Protocol results. R1C – Random 1 complete; R1P – Random 1 Partial; CollC – Collector only Complete; CollP – Collector only Partial; CouC – Country only Complete; CouP – Country only Partial; CCC – Collector & Country Complete; CCP – Collector & Country Partial; OCRC – Collector & Country OCR Complete; OCRP – Collector & Country OCR Partial; R2C – Random 2 Complete; R2P – Random 2 Partial.

Table 4. Result of ANOVA using Protocol 'pairs' (Complete and Partial).

Trial		Df	F Value	Pr (>F)	Significance
Partial	Trial	5	6.487	0.0013	** (0.001)
	Residuals	18			

The results of the ANOVA for the 6 trials are shown in Table 4. These were calculated using the Protocol 'pairs' (Complete and Partial). Three of the trials were found to have a result which was significant to greater than 0.001.

Survey

The survey was completed by all those who took part in the trials. The first five questions asked the digitisers to assign a value of 1-5 to each of tests, based on speed, ease of use, accuracy and preference.

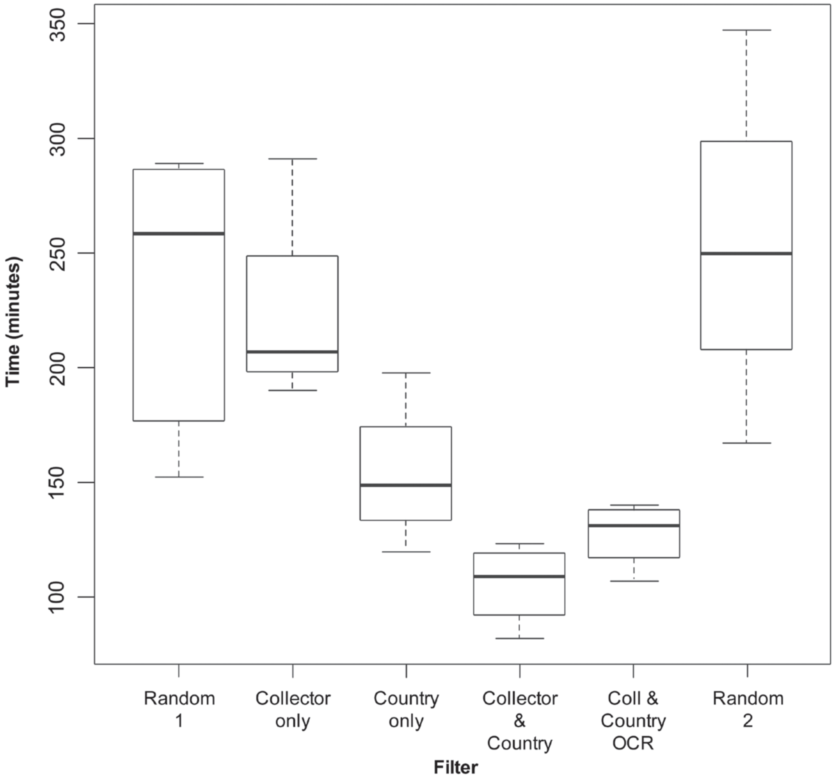


Figure 3. Box plot of Partial Protocol results.

Question 1: speed

The participants perceived the trials filtered by Country and Collector to be the fastest (66.7%) and the two random trials to be the slowest (66.7%).The use of OCR data to filter the specimens was perceived to be slightly faster than the Country only filter.

Question 2: ease of use

A similar result was found for the question asking the participants to rate the filters by their relative ease of use. Collector and Country was perceived to be the easiest to use (100%) and the hardest were the two random filters (66.7%).

Question 3: accuracy

Again the Collector and Country filter was perceived to be the least likely to lead to mistakes (83.3%) and the random filters were perceived to be the most likely to lead to mistakes (66.7% and 50%).

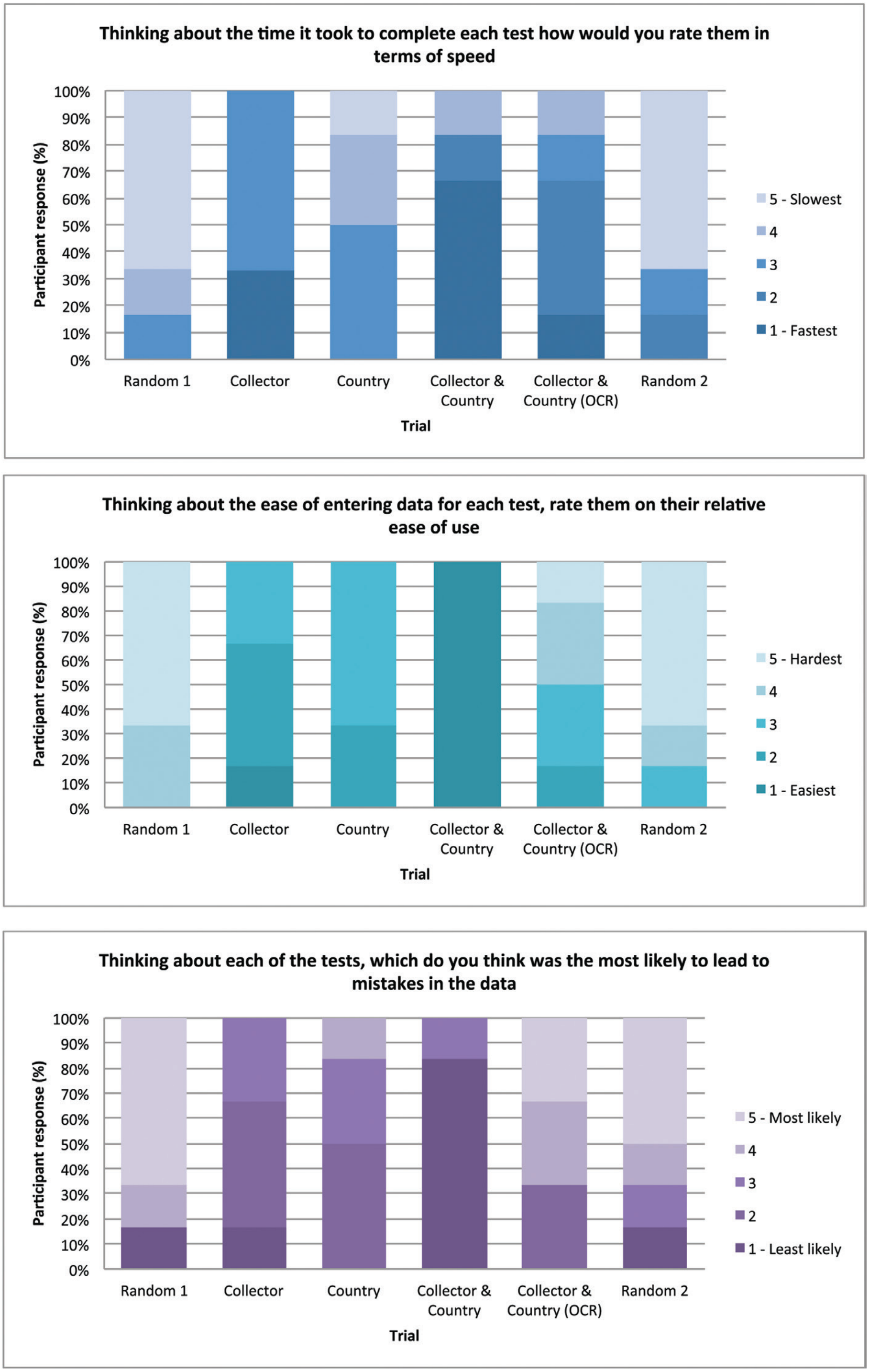


Figure 4. Digitiser responses to questions 1, 2 and 3 of survey

Questions 4 and 5: preference

The digitisers were asked which of the workflows would be preferred for digitising 50 and 1000 specimens. For 50 specimens there was a clear preference for the Collector and Country filter, with all participants selecting this filter. However when considering larger numbers of specimens the number selecting Collector and Country dropped, with 2 selecting the Country only filter.

Discussion

Summary

This study investigated how data extracted from OCR can be used to sort specimens prior to databasing and aid in the addition of data to minimal database records. Of the methods tested here, the most successful in terms of efficiency used the Partial Protocol, filtered by Collector and Country. This method was on average 20 minutes (8.9%) faster per batch of 50 records than the next most efficient method.

Protocols: Complete and Partial

As expected, the Complete Protocol which requires a larger quantity of data to be entered for each record resulted in a significant increase in the time taken to enter data. In particular, the need to enter multiple specimen determinations may often involve the creation of additional name records not already held in the database which can be time consuming. The amount of data on a label to be entered is a balance between usefulness and cost. For most users, we believe that the Partial Protocol, which places more emphasis on the geographical data, captures the highest priority information from the label.

Filters: Collector and Country

Prior to the trials, there had been an expectation that filtering the records by Collector would have the greatest impact. This was not borne out during the trials. In fact, the greatest impact came from filtering the records by Country. From the feedback it was apparent that a familiarity with the geography of a country aids the digitisation process more than familiarity with a Collectors label style and handwriting. However, a combination of the Country filter with the Collector filter was found to be most effective in speeding up the data entry process.

This was also reflected in the feedback from the digitisation team, who all identified this combined filter as the preferred option for digitising 50 specimens, and the majority would prefer this filter when digitising 1000 specimens. However, occasionally working with a large batch of similar records from a particular collector or country which were difficult in terms of legibility or geography resulted in reduced job satisfaction.

Variability

Whilst some of the trials showed a much greater variation in times to complete than others, the lack of variation between the preliminary random trial and the final random trial suggests that there was little 'learning effect'.

Direct use of OCR data

The direct use of OCR output seems to have had very little effect on the time it took to digitise images. This may be due in part to the format of the output which did not allow users to copy multiple lines of text easily. More suitable output formats may increase the impact of the OCR output in the future.

The OCR output was most useful for long sections of text, often descriptions of the habitat and plant. However, some of the digitisers also found the output useful for shorter sections of texts, particularly place names.

In general, care needs to be taken in using the OCR output directly, as there can be some errors in punctuation, spelling and spacing. It is currently only of use for typed and printed labels, and not yet able to pick up hand-written ones, and so wasn't available for all specimens encountered. In some cases the quality of the OCR output was so poor (spelling errors etc.) that it was quicker to type even the longer sections of text.

The Human factor

The results of the questionnaire and the subsequent discussion with the digitisers resulted in several interesting and unexpected points.

Preference for working with physical specimens

There was a clear preference expressed for working with physical specimens. One interesting point which was raised during the discussion with the digitisers, and which the authors hadn't previously considered, was the preference for working with the actual specimen as opposed to the image of the specimen. Two main reasons for this came out of the discussion. Firstly they found that using a screen to view, read and interpret the label information can cause more strain on the eyes than looking at a physical specimen. Secondly they felt that the images of the specimens took more time to manipulate and access the label information. The software we had provided the digitisers did not allow an easy zoom to the area of interest, whereas they felt that a physical specimen can be manipulated more easily and moved to make the label easier to read.

Working 'methods'

The digitisers also expressed the view that it was desirable for two people to work on similar sets of specimens since this gave them the opportunity to discuss and help each other. This was something which was not designed as part of these trials, but which came about because of the selection of specimen sets. This was more apparent for one set of specimens in which the handwriting on the labels was particularly difficult to read.

For the purpose of the trials we pre-filled some of the fields in the institutional database: Collector, Country or both, depending on the trial. The work carried out in the preparation of the batches which allowed the pre-filling of these fields meant that some issues, such as difficult handwriting of a collector's name, did not have to be handled by the digitisers. This was seen as an advantage by the digitisation team.

In the questionnaire we asked the digitisation team to complete, we asked whether they thought any filters would lead to an increase, or reduction in mistakes in the data. Whilst this is something we haven't quantified by checking the data entered during this investigation, it is interesting to note that the Collector and Country filter was felt to be least likely to lead to mistakes in the data.

Future work

This feedback from the digitisers has influenced how the next phase of the digitisation of the collection will develop. Where appropriate the digitisers will work in pairs enabling sharing of learning and expertise, and allowing discussion of problems encountered. Further to this, the digitisers felt it would be beneficial to have a resource which provided examples of collector's hand-writing and locations for old or difficult names. There is also a need to take in to consideration the well-being of the digitisation staff, particularly with reference to the physical environment for repetitive tasks, something we will consider when developing the digitisation process in the future.

The use of OCR data will continue to be expanded for the digitisation of the collections in general. In particular this output is also likely to be of high quality for many of the more recent specimens, as they have clear type-written labels. For families like the Zingiberaceae where the labels often have very long descriptions, partly because floral characters are lost once the specimen is pressed, access to the OCR output of the label would allow the full label to be easily added to the specimen record through a simple cut and paste. A future study of how working with physical versus virtual specimens and how this affects work flows for the digitisation process may be carried out in the future to help optimise practices at RBGE.

We are exploring other elements we could extract from the OCR output. These include numerical elements such as the Collection Number, Date, Latitude and Longitude, and Altitude. There is also potential to extract additional levels of locality information.

Some of the processes for pre-sorting herbarium specimens described here may be used in the future as part of crowd-sourcing projects. Opening up the data entry process beyond the trained digitisation staff would require the implementation of quality control checks which have not been carried out in this study.

Whilst we have found that the quality of OCR output to be variable depending on the condition of the label, it is expected that the software will continue to improve, allowing increasing amounts of data to be extracted.

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RESEARCH ARTICLE

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Dorstenia triseriata (Moraceae) a new and endangered species from Brazil

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Abstract

A new species of Moraceae is described, illustrated and compared to its close morphological relatives. *Dorstenia triseriata* presents similarities with *Dorstenia turnerifolia* but distinguished by size of peduncle, diameter of receptacle, number of bract rows, color of marginal bracts, and by an indistinct fringe on inflorescence. A conservation assessment based on IUCN criteria determines the new species to be vulnerable (VU).

Keywords

Atlantic rainforest, Dorsteniae, neotropics, taxonomy

Introduction

Dorstenia L. currently includes approximately 105 species and is the second largest genus of Moraceae (Berg 2001). This genus has a mostly herbaceous habit, marked by the absence of tepals in the pistillate flowers, simple interfloral bracts, and an expanded receptacle (the coenanthium) containing many grouped, diminutive flowers (De Granville 1971, Berg 2001).

Dorstenia sect. Lecania Fisher & Meyer comprises approximately 24 species, which are endemic to the rainforests of eastern Brazil. The species of section Lecania are characterized by herbaceous to suffrutescent plants usually with unbranched stems, long internodes, broad to subulate stipules, and inflorescences mostly orbicular to elliptical in shape (Carauta 1978, Berg 2001). The new species described here belongs to this section according to description adopted by Carauta (1978) and Berg (2001).

Taxonomic treatment

Dorstenia triseriata A.F.P.Machado, Fontella & Carauta, sp. nov.

urn:lsid:ipni.org:names:77138784-1
http://species-id.net/wiki/Dorstenia_triseriata

Type. Brazil. Espírito Santo: Município de Santa Teresa, Parque Natural Municipal São Lourenço, 19°56'09"S, 40°36'00"W. 28 oct 2008. TT Carrijo 1508 & AFP Machado (holotype: R!) Fig. 1 A–F; 2A–C.

Dorsteniae turnerifoliae similis, sed pedunculo elongato (in vicem brevi), receptaculo rotundato cum una serie bracteis submarginalibus viridibus etiam duabus seriebus bracteis marginalibus violaceis (nec tantum una serie bracteis) et fimbria non distincta (in vicem fimbria distincta) differt.

Herb to subshrub up to 40 cm tall; rhizome short; stem 3–5 mm thick, hirtellous with straight and uncinate hairs, internodes up to 1(-2.0) cm long. Leaves spiraled, lamina oblong to lanceolate, or subovate to subobovate, 3–7(-9) × 1.5(-2.5) cm long, chartaceous, apex acute, base rounded, margin dentate; indumentum rough on both surfaces, of uncinate hairs, plus simple and elongated hairs on veins, lateral veins 5–8 pairs, prominent on the abaxial surface, tertiary venation reticulate; petiole 1–2 cm long, pilose; stipules persistent, subulate, 1–2 mm long, coriaceous, deflexed. Inflorescences greenish, margin purplish; peduncle 1.0–3.5 cm long, pubescent with simple and elongated hairs; receptacle circular, 0.3–0.8 cm in diameter, margin dentate, fringe not distinct; submarginal bracts green in 1 row, ovate, up to 0.5 mm long; marginal bracts purplish in 2 rows; staminate flowers at the periphery of inflorescence, tepals 3, stamens 2, filaments as long as the perianth; pistillate flowers sessile, tepals 2–3, ovary free, stigmas 2 subequal in length; fruit a dehiscent drupe rough, 2 mm.

Etymology. The specific epithet is an allusion to number of marginal bracts rows, arranged in three vertical rows.

Distribution and habitat. *Dorstenia triseriata* inhabits the states of Espírito Santo, Bahia, and Minas Gerais in Brazil.

Observations. *Dorstenia triseriata* is closely related to two other species: *Dorstenia romaniucii* A.F.P.Machado & M.D.M. Vianna and *Dorstenia turnerifolia* Fisch. & C.A. Mey. From *D. romaniucii* both other species are differentiated by the staminate flowers disposed peripherally at the inflorescence. *Dorstenia triseriata* is distinguished

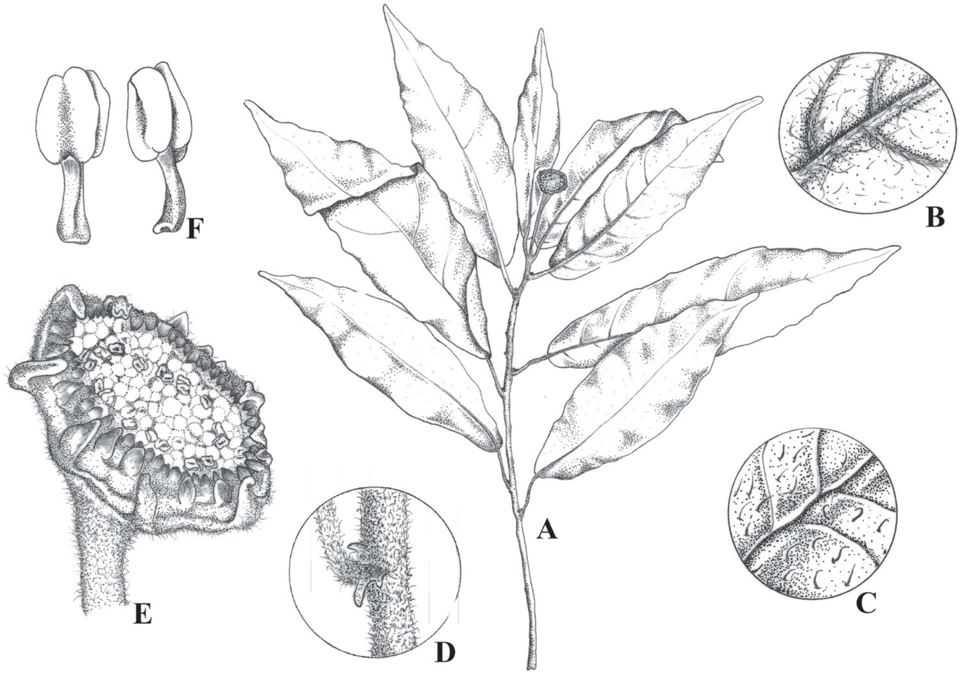

Figure 1. *Dorstenia triseriata*. **A** Habit **B** Leaf abaxial detail **C** Leaf adaxial detail **D** stipule **E** Inflorescence receptacule **F** Stamens (based on Carrijo & Machado 1508, Holotype).

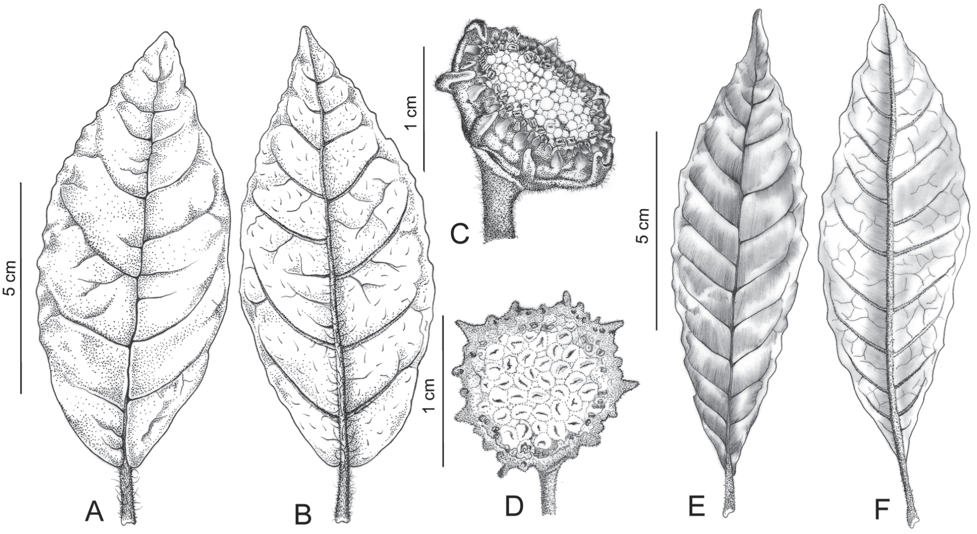

Figure 2. *Dorstenia triseriata*. **A** leaf adaxial surface **B** leaf abaxial surface **C** Inflorescence lateral view. *D. turnerifolia* **D** Inflorescence **E** leaf adaxial surface **F** leaf abaxial surface. (**A–C** based on Carrijo & Machado 1508; **D–F** based on A.F.P. Machado 1081, HUEFS).

Table 1. Comparative morphology of *Dorstenia triseriata* and its related species.

Characters *Taxa*	Leaf blade (cm long)	Lateral veins	Peduncle (cm)	Receptacle	Marginal bracts (rows)	Fringe
D. triseriata	3–7(–9)	5–8 pairs	1.5–3.0	Rounded (0.3–0.8)	3 (1 green + 2 purple)	Not distinct
D. romaniucii	2–13(–17)	14–16 pairs	1–1.5	slightly angular (1–1.3)	2 (green)	Not distinct
D. turnerifolia	5–7(–17)	(7–)10–17 pairs	0.5–1.0	Orbicular to rounded (1–2)	1 (green)	Distinct

from *D. turnerifolia* by its elongated peduncle (vs. short), purplish and circular receptacles (vs. green and angular receptacles), fringe not distinct (vs. fringe distinct) and marginal bracts in three rows 1green and 2 purplish (vs. 1 row). submarginal bracts green in 1 row, ovate, up to 0.5 mm long; marginal bracts purplish in 2 rows

The circumscription of *D. turnerifolia* adopted by Berg and Hijman (1999) and Berg (2001) is too broad and covers many taxa. However, the analysis of classical collections, original description, and the plant material collected by the first author at the type locality allows the recircumscription of *D. turnerifolia* (Fig 2D, E, F and Table 1) and allows us to recognize *D. triseriata* as a new species.

In *Dorstenia* the vegetative characters can be very variables specially when observed in a herbarium material. However, the reproductive characters are most reliable. The new species belongs to a group of species with similar habit and similar vegetative structures. The specimens of this group are commonly identified at herbaria as *D. turnerifolia*. Despite this they can easily separated with a criterious analysis of reproductive structures. The main differences between these taxa are also showed in Fig. 2 and Table 1.

Conservation status. According to IUCN (2001) criteria, this species is considered Vulnerable (VU B2a; B2bi, ii, iii). Area of occupancy estimated to be less than 2000 Km² with a decrease in area of occupancy, extension of occurrence, and habitat quality.

Key of *Dorstenia triseriata* and its related species

1 Receptacle slightly angular with two rows of marginal bracts. Staminate flowers intermixed with pistillate flowers .... ***D. romaniucii***

– Receptacle rounded or orbicular. Marginal bracts in 1 or 3 rows. Staminate flowers grouped peripherally at the inflorescence **2**

2 Peduncle 0.5–1 cm, receptacle 1–2 cm diam. Marginal bracts green disposed in one row. Fringe distinct.. ***D. turnerifolia***

– Peduncle 1–3.5 cm, receptacle 0.3–0.8 cm diam. Marginal bracts disposed in three rows (1 green + 2 purplish). Fringe not distinct ...***D. triseriata* sp. nov.**

Additional specimens examined. BRAZIL. Espírito Santo. Santa Teresa, 28 May 2008, *Machado* 937 (R); l.c., Santa Teresa, Parque Natural Municipal São Lourenço, 29 Mar. 2007, *Monteiro et al.* 368 (R); l.c., Santa Teresa, Parque Natural Municipal

São Lourenço, *Machado* 936, l.c., Santa Teresa, *Carrijo*, 1507. May 2008 (R). Bahia. Itanhaém, 17°8'17"S, 40°25'34"W. 29 Dec 2004, *Amorim et al.*, 4629 (HUEFS). Minas Gerais. Itabira, Fazenda do Quilombo, 19°37'10"S, 43°13'36"W. 27 Jan. 1943, *Magalhães s.n.* (HUEFS 118735)

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Revision of endemic Marquesas Islands *Bidens* (Asteraceae, Coreopsideae)

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Abstract

During the preparation of the *Vascular Flora of the Marquesas Islands* four new species of *Bidens* (Coreopsideae, Asteraceae) have come to light and are described herein: *B. woodii* W.L. Wagner, J.R. Clark & Lorence, **sp. nov.** from Ua Pou, and *Bidens microcephala* W.L. Wagner, J.R. Clark & Lorence **sp. nov.**, *B. evapelliana* W.L. Wagner, J.R. Clark & Lorence, **sp. nov.,** and *B. wichmanii* W.L. Wagner, J.R. Clark & Lorence, **sp. nov.** from the undercollected island of Fatu Hiva. In addition to these new species, we recognize the following six species of *Bidens* previously described from the Marquesas Islands: *Bidens beckiana* (F. Br.) Sherff (Eiao and Hatutaa), *B. bipontina* Sherff and *B. cordifolia* Sch. Bip. (both in Nuku Hiva), *B. henryi* Sherff (Hiva Oa, Tahuata), *B. uapensis* (F. Br.) Sherff (Ua Pou), and *B. polycephala* Sch. Bip. (Nuku Hiva, Ua Huku, Hiva Oa, Tahuata, and Mohotani). Two names are reduced to synonymy under *B. polycephala*: *B. collina* Degener & Sherff, **syn. nov.** and *B. jardinii* Sch. Bip., **syn. nov.** *Bidens polycephala* has the widest distribution of the Marquesan species on five of the islands and exhibits considerable variation.

Keywords

Bidens, Asteraceae, Coreopsideae, Marquesas Islands, French Polynesia, conservation

Introduction

The Flora of the Marquesas Islands project is a collaborative program, primarily between the Smithsonian Institution and the National Tropical Botanical Garden, intended to further knowledge of the flora of this remote archipelago. In 1997 the first publications of new species and revisions of genera with more than one endemic species were initiated (Florence and Lorence 1997; Wagner and Lorence 1997). Since that time a series of publications has enumerated and revised a number of genera (for summary see Lorence and Wagner 2011). After the 2011 issue in PhytoKeys there were only two major groups in the Marquesas Islands flora for which revisions had not been completed. The first, *Cyrtandra* J.R. Forst. & G.Forst. (Gesneriaceae), is now complete with 11 species (Wagner et al. 2013). The present revision of the Marquesas species of *Bidens* L. completes the precursor publications required to finalize the data in the online Flora of the Marquesas Islands website (Wagner and Lorence 2002 and onward; http://botany.si.edu/pacificislandbiodiversity/marquesasflora/index.htm). The new species described in these precursor publications have increased the known native flora in the Marquesas Islands by about 25%.

The genus *Bidens* is the largest genus of the tribe Coreopsideae with 150–235 species (Sherff 1937; Strother and Weedon 2006); most research on various groups within the genus suggest numbers at the lower end of the range are probably more accurate (e. g. Ganders and Nagata 1990). The genus has had a long, complex taxonomic history summarized by Sherff (1937) in his revision of the genus. Sherff's revision remains the only modern study of the entire genus as presently delimited in which he treated 235 species, many with one to several varieties. Most of the species occur in the Americas and Africa, while Sherff (1937) accepted 59 species in the Hawaiian Islands and southeastern Polynesia, but our current estimate is there are about 40 species. There are only a few indigenous species in Europe and northern Asia. The taxonomy of the genus remains confused despite a growing number of individual groups within the genus having been the subject of detailed studies (Ganders et al. 2000). Species of related genera such as *Coreocarpus* Benth., *Coreopsis* L., *Cosmos* Cav., *Dahlia* Cav., and *Thelesperma* Less. have had a tangled history with *Bidens*, and it has been one of the most difficult to define. Relationships among the 20+ genera within the tribe Coreopsideae are poorly understood, but recent phylogenetic studies using molecular data as well as morphological and anatomical traits are helping to resolve monophyletic groups within the tribe and the relationships among them (Ganders et al. 2000; Kimball and Crawford 2004; Crawford et al. 2009; Knope et al. 2012; Funk et al. unpubl.). These recent molecular phylogenies have also indicated that some Coreopsideae genera are not monophyletic, especially in the broadly sampled (multiple species in 19 genera) study by Kimball and Crawford (2004). These studies have resolved a number of well-supported lineages; however, the two largest genera, *Bidens* and *Coreopsis,* were determined to be non-monophyletic in their present delimitation. One alternative at this stage of the phylogenetic understanding of the various clades is that a broadly circumscribed genus *Bidens* (or *Coreopsis*), inclusive of much of the tribe, would be the best taxonomic solution to the problem. The alternative would be to segregate out numerous relatively small genera reflecting morphologically identifiable monophyletic groups. If this latter course were to be followed for the Pacific species, which are in a clade containing *B. pilosa* L. and other New World species, the correct generic name would seem to be the obscure name *Kerneria* Moench.

In the Marquesas Islands Schultz (1856) described four species, *B. cordifolia, B. jardinii, B. polycephala,* and *B. serrulata*, in his enumeration of plants collected by Jardin. *Bidens jardinii* is here considered to be a synonym of *B. polycephala,* and *B. serrulata* is a homonym. Sherff as part of his overall multiyear efforts to study the genus provided *B. serrulata* with the new name, *B. bipontina*. Forest Brown (1935) described two additional species in the genus *Campylotheca* Cassini, *C. beckiana* and *C. uapensis*. These were transferred later to *Bidens* by Sherff, who also described three additional species himself, *B. henryi*, *B. collina,* and *B. ahnnei* (the latter two here considered synonyms of *B. polycephala*). Additional names in *Bidens* from the Marquesas are *Bidens hivoana* Degener & Sherff (1934), described from the island of Hiva Oa, and *Bidens teikiteetinii* Florence and Stuessy (1988). With subsequent study both have been transferred to *Oparanthus* (Shannon and Wagner 1997). To the previously described six species we here add four species from two underexplored islands: *B. woodii*, from the summit of Ua Pou, and *B. microcephala, B. evapelliana*, and *B. wichmanii* from Fatu Hiva (Table 1). We have arranged the species in the taxonomic section according to an unpublished phylogeny by Funk et al. See Fig. 1 for map of the Marquesas Islands showing the geographic relationships among the islands.

When evaluated using the IUCN criteria for endangerment (IUCN 2001, see also www.iucnredlist.org/info/categories_criteria2001), most of the Marquesan species of *Bidens* fall into the Endangered (EN) or Critically Endangered (CR) categories, which designate species facing the highest risk of extinction in the wild. Marquesan species of *Bidens* meet these IUCN criteria by having known ranges less than 100 km^2, an area of occupancy of less than 10 km^2, and continuing decline in the quality of habitat across the Marquesas Islands.

Due to the small areas involved on oceanic islands, many single island endemics have a geographic range of less than 100 km^2 and some less than 10 km^2. Therefore they will fall automatically into the Critically Endangered (CR), Endangered (EN), or Vulnerable (VU) category, or in other words into extremely high (CR) to lower (VU) risk of extinction categories despite the fact that they may have relatively small natural

Table 1. Island distribution of Marquesas species of *Bidens*. Islands arranged from oldest to youngest.

Species / Island	Eiao	Hatutaa	Nuku Hiva	Ua Huka	Ua Pou	Hiva Oa	Tahuata	Fatu Hiva
B. henryi						X	X	
B. polycephala			X	X		X	X	
B. uapensis					X			
B. microcephala								X
B. woodii					X			
B. evapelliana								X
B. wichmanii								X
B. bipontina			X					
B. cordifolia			X					
B. beckiana	X	X						
Totals	1	1	3	1	2	1	2	3

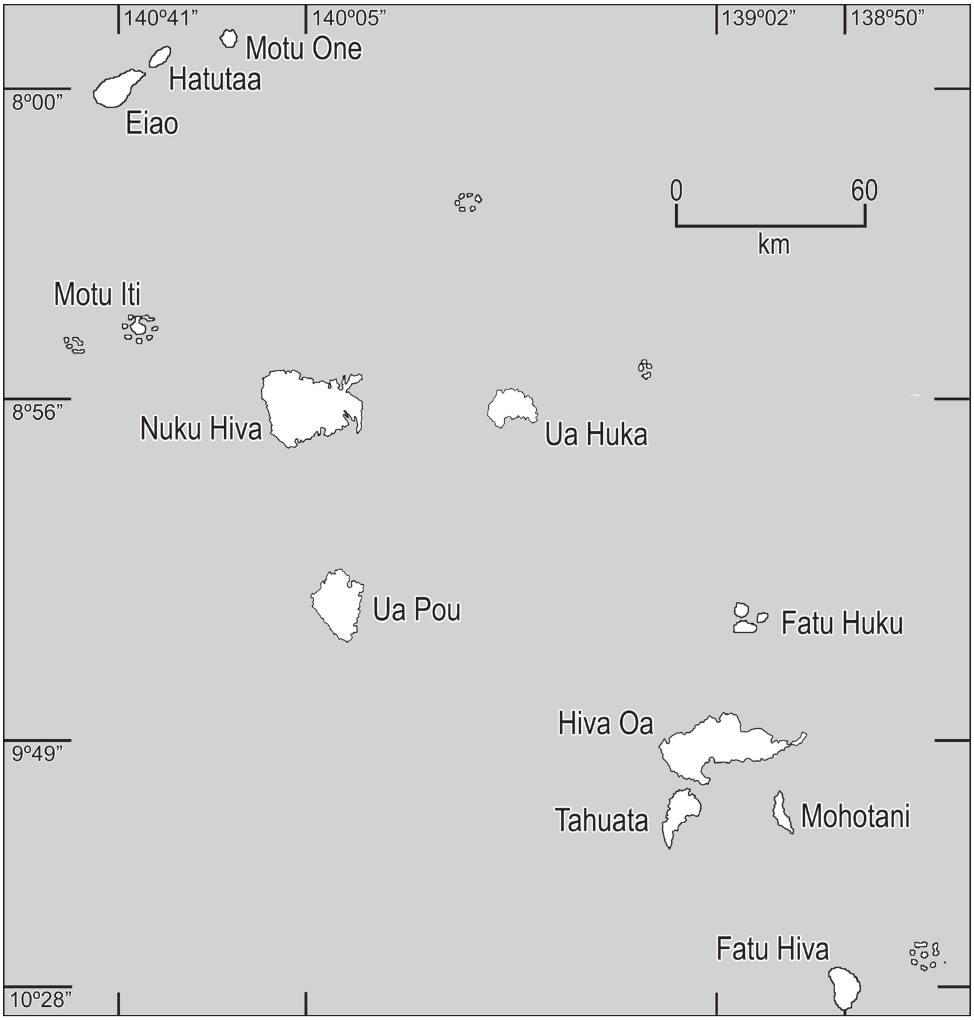

Figure 1. Map of the Marquesas Islands.

ranges and may be relatively common locally with healthy, regenerating populations. Some will fall into the Data Deficient (DD) category, simply because we know so little about their actual population size, status, and range. Although the IUCN evaluations are not ideally suited for islands, for the sake of consistency we use them herein for Marquesas *Bidens* and where appropriate have added qualifying comments under Conservation Status for species that seem extremely at risk and those that are more common.

All measurements given herein are taken from dried herbarium specimens, although certain features such as shapes were supplemented with information from alcohol-preserved flowers and fruits, field notes, and color slides or digital photos. Measurements are presented in the descriptions as follows: length × width, followed by units of measurement (mm or cm). Specimens from the following herbaria were studied: AD, BISH, BKL, BR, CBG, CHR, F, K, L, MO, MPU, NSW, NY, P, PAP, PTBG, OS, TEX, UBC, US, and WU. We have examined all collections cited except for the four types of the Schultz (1856) names for which we studied images of them sent by P. Lowrey.

Taxonomic part

Artificial key to species of Marquesas *Bidens*

1 Ray florets absent; disk florets 1–10; heads < 2 mm in diameter .... 4. ***B. microcephala***

– Ray florets present; disk florets 12–50; heads > 2 mm in diameter **2**

2 Plant prostrate; leaf blades 1–2.8(–5.5) cm .... 6. ***B. evapelliana***

– Plant ascending to erect; leaf blades (1–)3–12 cm **3**

3 Leaves thick and coriaceous, veins raised on lower surface, blades ovate .... 5. ***B. woodii***

– Leaves membranous to chartaceous, veins not conspicuously raised, blades lanceolate to elliptic, rarely narrowly ovate **4**

4 Leaf blades with a tuft of hairs at base on lower surface .... 3. ***B. uapensis***

– Leaf blades glabrous or sometimes pubescent, but not with hairs in a tuft **5**

5 Heads 8–15 mm in diameter; disk florets ca. 50 .... 7. ***B. wichmanii***

– Heads 2–15 mm in diameter; disk florets 12–34 .... **6**

6 Outer involucral bracts 1–4.5 mm long; disk florets 12–25; rays 3–12 mm long .... 2. ***B. polycephala***

– Outer involucral bracts (4–)5–13 mm long; disk florets 30–34; rays 9–20 mm long **7**

7 Heads 2–5 mm in diameter; rays 13–20 mm long; leaf apex long-acuminate to caudate .... 8. ***B. bipontina***

– Heads 5–15 mm in diameter; rays 9–15 mm long; leaf apex acute to acuminate or sometimes caudate **8**

8 Outer involucral bracts recurved; plant glabrous except sometimes a few hairs on the involucral bracts .... 1. ***B. henryi***

– Outer involucral bracts erect to ascending; plant pubescent, at least along the petiole or involucral bracts, but often also on leaves **9**

9 Outer involucral bracts similar to inner ones and tapering at base; leaves simple, glabrous or pubescent toward the base and in a line along the petiole .... 10. ***B. beckiana***

– Outer involucral bracts well differentiated from inner ones and pales, not tapering at the base; leaves trifoliolate or sometimes simple, moderately pubescent, especially on lower surface, midrib, veins, and in a line along the petiole .... 9. ***B. cordifolia***

1. *Bidens henryi* Sherff, Bot. Gaz. (Crawfordsville) 76: 164. 1923.

http://species-id.net/wiki/Bidens_henryi
Fig. 2D–F

Campylotheca henryi (Sherff) F. Br., Bernice P. Bishop Mus. Bull. 130: 355. 1935.

Type. Marquesas Islands. Hiva Oa: Atuona Valley ridge on route to Hanamenu, 3500–4000 ft [1065–1220 m], December 1917, C. Henry s.n. (holotype: F-474749!).

Description. Erect subshrubs to shrubs 1–2 m tall. Leaves simple, 2.5–13 cm long including petiole, blades lanceolate or elliptic-lanceolate, 1.8–9.5 × 0.5–3.8 cm, glabrous, margins serrate, apex acuminate. Heads (1–)3–4(–7), in diffuse cymes terminating main stem and lateral branches, 5–15 mm in diameter excluding rays, peduncles 1.2–9.5 cm long, glabrous; outer involucral bracts 4–13 mm long, linear, well differentiated from inner bracts, recurved, apex erose, sometimes with few short hairs; ray florets ca. 13, sterile, rays yellow, 12–15 × 2–5 mm; disk florets ca. 30–32, perfect, corollas yellow. Achenes black, straight, 8–10 × 1–2 mm, glabrous or with few inconspicuous setae near the apex; pappus of 2–3 antrorse barbed awns.

Distribution. Marquesas Islands, occurring on Hiva Oa and Tahuata, (400-) 620–1200 m.

Habitat. *Bidens henryi* is known from ridges and summit areas in montane wet shrubland or low forest with *Metrosideros collina* (J.R. Forst. & G. Forst.) A. Gray and *Weinmannia marquesana* F. Br. with fern understory along with other shrubs and trees such as species of *Cheirodendron, Coprosma, Crossostylis, Cyrtandra,* and *Myrsine*.

Conservation status. Proposed IUCN Red List Category **Endangered** (EN), criteria B2a, B2b (i–iii): B2: total area of occupancy less than 500 km^2 (ca. 378 km^2); B1a, severely fragmented; B1b (i–iii), habitat continuing decline inferred. The suitable habitat for *Bidens henryi* on Hiva Oa (ca. 315 km^2), and Tahuata (ca. 61 km^2) is restricted to mountain slopes and summits, indicated as an endangered environment that is threatened by human activity (deforestation and fire), feral animals, and invasive plants, thus reducing the extent of the forest. It is relatively common locally in some areas, however, and consequently vulnerable (VU) might be an alternative category (Butaud, pers. comm. 2014).

Specimens examined. Marquesas Islands. Hiva Oa: Chemin d'Atuona à Hanamenu par Feani, crête Hanamenu, 1090 m, 12 Feb 1975, Schäfer 5192 (K, US); Chemin d'Atuona à Hanamenu par Feani, côté Atuona, 1010 m, 13 Feb 1975, Schäfer 5205 (K, MPU); Feani ridge to upper slopes of dry side of island, 1150 m, 12 Feb 1975, Oliver & Schäfer 3122 (BISH, MO, P, PTBG, US); Feani, trail from Atuona to Hanamenu, 1190 m, 10 Feb 1975, Oliver & Schäfer 3105 (BISH, P, PTBG, US); Feani, vieux sentier d'Atuona à Hanamenu, crête côté Hanamenu, 900 m, 5 Mar 1975, Schäfer & Oliver 5271 (K, MPU, US); Puamau, chemin vers Atuona, après la bifurcation vers Hanaupe, lieu-dit Keiani, 650 m, 26 Mar 1975, Schäfer 5382 (K, MPU, US); A l'est de la piste d'aviation, 7 Mar 1974, Hallé 2117 (US); Mt. Ootua, central part, 785 m, 28 Jul 1977, Gagné 1200 (BISH, US); Mt. Ootua, central part, 800 m, 27 Jul 1977, Gagné 1166 (BISH, US); Rim

Figure 2. *Bidens bipontina* Sherff (**A–C**). **A** Distal part of plant **B** Head post-flowering showing involucral bracts and apex of achenes **C** Head showing rays and apex of disk florets. Drawn from Perlman & Wood 15028 (US), except B from Wood and Perlman 4601 (US). Images used to augment illustration from field shots of Wood and Perlman 4601 and Perlman and Wood 15021. *Bidens henryi* Sherff (**D–F**). **D** Distal part of plant **E** Head post-flowering showing involucral bracts **F** Head showing rays and disk florets. Drawn Wood 10038 (US), except F from Perlman 14868 (US). Images from field shots used to augment illustration of Wood 10038, Wagner 6219 and Lorence & Price 8932.

of Puamau valley along trail from main road, 650 m, 9°46"26.8'S/138°54"24.8'W, 20 Feb 2003, Perlman 18488 (BISH, P, PAP, PTBG, US); NE slopes Mt. Temetiu, 700 m, 23 Feb 1929, Mumford & Adamson 49 (BISH); Atuona V., 700 m, 6 Oct 1930, Pacific Ent. Survey EX 49 (BISH [2]); Feani, 900 m, 15 Dec 1921, Brown 1084 (BISH); Road from Atuona to Puamau, just below Mt. Ootua, 700 m, 22 Jan 1975, Sachet, Oliver & Schäfer 2131 (BISH, PTBG, US); Ootua, 800 m, 15 Dec 1921, Brown & Brown 1018 (BISH); Atuona-Feani Trail, upper part of trail, exposed slope, 900–1000 m, 24-26 Sep 1963, Sachet & Decker 1122 (BISH, NSW, MO, P, US); Teavaimataii, N side Mt. Ootua, 800 m, 6 May 1929, Mumford & Adamson 351 (BISH [2]); Hanaiapa, 800 m, 30 Oct 1922, Quayle 1600 (BISH); Road from Atuona to Puamau, just below Mt. Ootua, 660–690 m, 22 Jan 1975, Sachet, Oliver & Schäfer 2129 (BISH, CBG, CHR, K, MO, NSW, L, P, PTBG, US); Entre Hanamenu et la crête de Feani, lieu-dit Teho’o-ho’o, 750 800 m, 27 Jul 1975, Schäfer 5629 (MPU); Hava Iafa, 700 m, 29 Oct 1922, Jones 1600 (BKL); Atuona-Feani Trail, upper part of trail, just below crest of ridge, 1200 m, 24–26 Sep 1963, Sachet & Decker 1141 (BISH, PTBG, US); Where trail toward Hanamenu turns into dry ridge, 884 m, 3 Aug 1988, Perlman 10208 (BISH, F, MO, PTBG, UBC, US); Trail to Feani and Hanamenu, 1006 m, 29 Jul 1988, Perlman, Wagner, Lorence, Florence & Montgomery 10177 (AD, BISH, F, MO, P, PAP, PTBG, UBC, US); Along old Atuona-Hanamenu Trail, on high ridge leading to Mt. Feani, 1050–1150 m, 30 Jul 1988, Lorence, Wagner, Florence, Perlman & Montgomery 6259 (PAP, PTBG); Mt. Feani, 1100 m, 11 Nov 1989, McKee 44683 (BISH, PAP); Atuona, piste de Hanamenu, 680 m, 29 Jul 1988, Florence, Lorence, Perlman & Wagner 9609 (BISH, P, PAP, US); trail from Atuona (W) to ridge leading to Mt. Feani and Temetiu, 1020 m, 29 Jul 1988, Wagner & Lorence 6219 (BISH, PTBG, US); Atuona, piste de Hanamenu, crête centrale, 1010 m, 29 Jul 1988, Florence, Lorence, Perlman & Wagner 9617 (BISH, P, PAP, US); Base camp, near Vaitumete to ridge crest south of Teakatau, 1200 m, 9°48"S/139°4"W, 29 Jan 2003, Lorence, Dunn & Price 8932 (BISH, P, PAP, PTBG, US)[used in molecular study, Funk et al.], cult from Lorence et al. 8932, Lorence 9175 (BISH, PTBG, US); Temetiu region, drainages to southeast of Vaimete et Vaiumioi (source), headwaters of Hanamenu, 1067 m, 29 Jan 2003, Wood 10038 (BISH, NY, P, PAP, PTBG, US); Trail to Hanamenu, along summit crest, 1000 m, 9°47"9.29'S/139°4"56.7"W, 1 Aug 2005, Perlman 19759 (PAP, PTBG); Road from Atuona to Puamau, just below Mt. Ootua, spur ridge above road below Ootua peak, 720 m, 23 Nov 1974, Sachet & Decker 1923 (BISH, CBG, CHR, K, MO, MPU, NSW, L, P, PAP, PTBG, US); Eiaone-Piamau divide, crest approx. 0.5 km from pass, 400 m, 5 Dec 1963, Decker 973 (BISH, MO, NSW, PTBG, US); Atuona-Feani Trail, Feani ridge, 1000 m, 24–26 Sep 1963, Sachet & Decker 1195 (US); Mt. Ootua, off road between Airport and Puamau, on E side of summit, 811 m, 21 Aug 1995, Perlman & Wood 14868 (BISH, MO, P, PAP, PTBG, UBC, US); Eiaone–Piamau divide, crest approx. 0.5 km from pass, 400 m, 5 Dec 1963, Decker 973 (BISH, MO, NSW, PTBG, US).**Tahuata:** Vaitahu, crête d’Amatea, début de la montée raide vers la partie haute, 620 m, 10 Apr 1975, Schäfer 5519 (MPU); Ridge between Amatea & Haaoiputeomo, summit crest of island, 823 m, 12 Jul 1997, Perlman, Wood & Luce 15989 (MO, P, PAP, PTBG, US); Summit of ridge above Vaitahu, near Haaoiputeomo, on ridge near antenna, along ridge crest between Vaitahu & Hanatetena, 823 m, 1 Sep 1995, Perlman, Wood & Luce 14917 (MO, P, PAP, PTBG, US); Along top of ridge from Amatea to Haaoiputeomo, over Hanatetena village, Summit crest of island above Vaitahu, 866 m, 11 Jul 1997, Perlman, Wood & Luce 15958 (P, PAP, PTBG, US); Région du sommet de Tahuata, 17 Mar 1974, Hallé 2186 (US); de Hamatea à la crête centrale de l'île, 750–850 m, 26 May 1975, Thibault 54 (BISH, US); Mt. Ootua, summit area and along trail from road cut, 732 m, 9°46"10'S/138°58"31.4'W, 19 Jul 2004, Perlman & Wood 19207 (BISH, P, PAP, PTBG, US).

Discussion. *Bidens henryi* has conspicuous linear, recurved outer involucral bracts.

2. *Bidens polycephala* Sch. Bip., Flora 39: 360. 1856.

http://species-id.net/wiki/Bidens_polycephala

Figure 3E–F

Coreopsis polycephala (Sch. Bip.) Drake, Ill. Fl. Ins. Mar. Pac. 209. 1890.

Type. Marquesas Islands. Nuku Hiva, D.E.S.A. Jardin 40 (holotype: P).

Bidens jardinii Sch. Bip., Flora 39: 360. 1856.

Coreopsis jardinii (Sch. Bip.) Drake, Ill. Fl. Ins. Mar. Pac. 209. 1890.

Type. Marquesas Islands. Nuku Hiva, D.E.S.A. Jardin 41 (holotype: P).

Bidens ahnnei Sherff, Bot. Gaz. (Crawfordsville) 76: 165. 1923.

Type. Marquesas Islands. Nuku Hiva, Hakaui, December 1916, C. Henry s.n. (holotype: F [452364]!; isotype: F!).

Bidens collina Deg. & Sherff, Bot. Gaz. (Crawfordsville) 96: 144. 1934; Publ. Field Mus. Nat. Hist., Bot. Ser. 16: 79. 1937.

Campylotheca collina (Deg. & Sherff) F. Brown, Bernice P. Bishop Mus. Bull. 130: 354. 1935.

Type. Marquesas Islands. Hiva Oa: Tehutu, 100 m, 19 May 1929, E.P. Mumford & A.M. Adamson 400 (holotype: NY-00162622!; isotype: BISH!).

Description. Erect subshrubs 0.5–2 m tall. Leaves simple or very rarely (Nuku Hiva) compound and trifoliolate, 3–15.5 cm long including petiole, blades lanceolate to elliptic-lanceolate, 2–11 × 1.2–5 cm, glabrous or lower surface occasionally pubescent, especially on young leaves, margins variably serrate to serrulate or subentire, apex acuminate or occasionally acute or caudate (Nuku Hiva). Heads 10–80(–100+), glabrous to sparsely pubescent at base, in diffuse cymes terminating main stem and lateral branches, main inflorescence axis up to 6.5 cm, heads 2–5 mm in diameter excluding rays, peduncles 0.1–5 cm long, glabrous or sparsely pubescent; outer involucral bracts 1–4.5 mm long, well differentiated from inner bracts, glabrous to sparsely ciliate; ray florets 3–12 per head, sterile, rays yellow, 3–12 × 1–4 mm, apex rounded, entire or bi- or trilobed; disk florets ca. 12–25, perfect. Achenes gray to black, straight or slightly curved, 3–8 × 0.5–1 mm, margin setose; pappus of 0–2 short awns. $n = 36$ (Gillett 1972).

Distribution. Marquesas Islands, occurring on Nuku Hiva, Ua Huka, Hiva Oa, Mohotani, and Tahuata, 10–800(–1080) m. The occurrence on Mohotani is based on observation by Jean-François Butaud (pers. comm., 2014), but should be verified by collections.

Habitat. *Bidens polycephla* is known from slopes and ridges to windswept cliffs, in mesic forests with *Freycinetia impavida* (Gaudich. ex Hombr.) B. C. Stone, *Metrosideros collina*, and *Dicranopteris linearis* (Burm. f.) Underw., or *Hibiscus tiliaceus* L. and *Pandanus tectorius* Parkinson ex Du Roi forest.

Conservation status. Proposed IUCN Red List Category **Endangered** (EN), criteria B2b i–iii): B2, total area of occupancy less than 500 km² (ca. 50 km²); b (i–iii), habitat continuing decline inferred. The suitable habitat for *Bidens polycephla* on Nuku Huka (ca. 340 km²), Ua Huka (ca. 83 km²), and Tahuata (ca. 61 km²) is indicated as an endangered environment, threatened by human activity (deforestation), feral animals, and invasive plants, thus reducing the extent of the forest. However, *B. polycephala* has been observed to be locally common in some areas with considerable regeneration, and alternatively it might be considered Near Threatened (NT) (Butaud, pers comm. 2014).

Specimens examined. Marquesas Islands. Nuku Hiva: Hakaui, ridge, 800 m, 7 May 1921, Brown 405B (BISH); Between Taiohae Bay and Hooumi Bay, 900 m, 20 Jul 1977, Gagné 1155 (BISH, US), Gagné & Montgomery 1162 (BISH); Terre Deserte, Haatuatua Valley, 1050 m, 1 Aug 1988, Gagné & Montgomery 2463, 2471 (BISH); Route Toovii–Terre Deserte, km 4 après le col, 940 m, 8°50"S/140°10"W, 9 Dec 1982, Florence 4353 (BISH, K, NY, P, US); Route Toovii–Terre Deserte, km 1 après le col, 960 m, 8°52"S/ 140°10"W, 10 Dec 1982, Florence 4390 (BISH, P, PAP); Moyenne Taipivai, sous le captage de la cascade de Teuakueenui, 440 m, 8°51"S/140°6"W, 4 Aug 1987, Florence 8471 (BISH, P, PAP, US); Taipi Vai, 500 m, 7 May 1921, Brown 405A (BISH); Piste Aakapa–Pua, sous le col de Taahui, 260 m, 8°49"S/140°9"W, 7 Aug 1987, Florence 8502 (PAP), 180 m, 8502(PAP); Toovii, face SE du Mt. Tuhokia, 1080 m, 8°50"S/140°8"W, 10 Mar 1986, Florence 7516 (PAP); Moyenne vallée de Hakaui, secteur central, 240 m, 8°54"S/ 140°9"W, 23 Jul 1987, Florence 8387 (BISH, P, PAP); Hakaui Valley, 61 m, 26 Jun 1988, Perlman 10010 (BISH, PAP, PTBG); Toovii, épaulement au-dessus du réservoir, 1020 m, 8°52"S/140°9"W, 7 Dec 1982, Florence 4332 (BISH [2], K, NY, P, US); Route Toovii–Terre Deserte, 2 km après le col, 960 m, 8°52"S/140°10"W, 4 Jun 1984, Florence 6895 (BISH [2], P, PAP); South spur of the summit ridge of the island, between Hakui and the Tapuaooa shelter on the Toovii Plateau, 1070 m, 21 Jul 1970, Gillett 2194 (BISH, US); Mountain near Hakaui, s.d., Sherff 3090 (BISH); 22 Dec 1919, Sherff 3084-b (BISH [2]); 17 Sep 1919, Sherff 3084-a (BISH); Ridge, 800 m, 18 Oct 1922, Quayle 1588 (BISH); Partie S de Toovii, 750 m, 11 Jul 1975, Thibault 143 (BISH, P, US); Taipivai, Teuakueenui Falls area, 351 m, 8°51"2'S/140°6"10'W, 25 Jun 1997, Wood, Meyer & Luce 6356 (BISH, HAST, MO, NY, P, PAP, PTBG, UBC, US). **Ua Huka:** Ridgecrest south of central Vaipae'e Valley, approx. 2 km E of bend, 450 m, 18 Mar 1964, Decker 1877 (BISH, MO, PTBG, US); central crest of island N of Vaipae'e, 550-600 m, 16 Mar 1964, Decker 1868 (US); seacliffs just before the village of Hokatu, road from Hane to Hokatu, 12 m, 1 Jul 1997, Perlman, Wood & Meyer 15878 (MO, NY, P, PAP, PTBG, UBC, US, WU); Hitikau region, ascended

Figure 3. *Bidens beckiana* (F. Br.) Sherff (**A–B**). **A** Distal part of plant **B** Head post-flowering showing involucral bracts and apex of achenes. Drawn from Florence 9368 (US) [A] and Perlman 10064 (US) [B]. *Bidens cordifolia* Sch. Bip. (**C–D**). **C** Distal part of plant **D** Head post-flowering showing involucral bracts. Drawn from Wood & Perlman 4600 (US). *Bidens polycephala* Sch. Bip. (**E–F**). **E** Distal part of plant **F** Head post-flowering showing involucral bracts and apex of achenes. Drawn from Perlman 15878 (US). Image from field shots used to augment illustration of Wood 10504.

via the Matukuoha Ridge over-looking Hane, constitutes the summit of the single crater of Ua Huka, 730 m, 5 Dec 2003, Wood 10495 (PTBG); Hane valley, ridge and cliffs above Tiki marae, back of valley on west side, 518 m, 8°54"50.6'S/138°31"51.5'W, 12 Jun 2004, Perlman, Lorence, Dunn & Wood 19009 (BISH, P, PAP, PTBG, US); Ridgecrest about 1 km N of Tahoatikikau crater, 300 m, 23 Mar 1964, Decker 1918 (BISH, CHR, K, MO, P, US); Hanahouua Valley, back of valley, cliffs near ridge between Hanahouua and Hanaei, 488 m, 8°54"46.7'S/139°30"8.68'W, 28 Jul 2005, Perlman & Meyer 19750 (BISH, MPU, NY, P, PAP, PTBG, US) [used in molecular study, Funk et al.]; Summit of Hitikau, crest of island, at very summit, 853 m, 28 Jun 1997, Perlman, Wood & Meyer 15847 (PTBG); Vaipaee, upper valley, Aunoa property, 60 m, 8°54"40'S/139°34"11'W, 9 Dec 2003, Wood 10504 (AD, BISH, BR, K, MO, NY, P, PAP, PTBG, US); Hokatu village coast, scattered along coast and cliffs from Hokatu to Tenaha to Haavahae, 31 m, 8°55"6.32'S/139°31"17.8'W, 10 Jun 2004, Perlman 19001 (BISH, P, PAP, PTBG, US); Hane/Hokatu cliff zone, 520 m, 11 Dec 2003, Wood & Meyer 10515 (BISH, P, PAP, PTBG, US); Hanahouua valley, back of valley below cliff walls, 1500 ft, 8°54"46.7'S/139°30"8.68'W, 26 Jun 2004, Perlman & Wood 19071 (BISH, P, PAP, NY, PTBG, US); Crest of ridge W of Vaipae'e Valley, approx. 3 km inland from bayhead, 280–300 m, 25 Feb 1964, Decker 1728 (BISH, MO, P, PTBG, US); Matukuoha, on ridge leading to Hitikau, 549 m, 28 Jun 1997, Perlman, Wood & Meyer 15857 (BISH, MO, NY, MPU, OS, P, PAP, PTBG, US). **Tahuata:** Near village of Hapatoni, coast to south of village, on seacliffs about .25–5 miles from Hapatoni, 46 m, 9°58"14.2'S/139°7"8.01'W, 3 Feb 2003, Perlman & Price 18376 (BISH, P, PAP, PTBG, US); Vaitahu, vers la crête d'Uuau, partie basse de la crête, 550 m, 8 Apr 1975, Schäfer 5468 (K, MPU, US); Base of cliff, above slope, about .3 km S. of Hapatoni, 150 m, 3 Feb 2003, Price 218 (BISH, P, PAP, PTBG, US) [used in molecular study, Funk et al.]; Trail from Vaitahu to Hapatoni, Tiana, the Vaitahu water catchment, 190 m, 30 Jan 1975, Oliver & Schäfer 3068 (BISH, CBG, CHR, K, MO, NSW, L, PTBG, US); Hanatetena, main valley, first deep side gulch to the north, 457 m, 2 Feb 2003, Wood 10081 (PTBG, US); Near village of Hapatoni, coast to south of village, on seacliffs about 0.25-5 miles from Hapatoni, 100 m, 9°58"23'S/139°7"8'W, 3 Feb 2003, Perlman & Price 18378 (BISH, NY, P, PAP, PTBG, US).

Discussion. *Bidens polycephala* is the most variable of the Marquesan *Bidens*, and is also the most widespread, occurring on four islands. It is similar to *Bidens henryi* but differs in having much shorter involucral bracts and in the large but variable number of heads among individuals, and it occupies drier and lower elevation habitats. Some of the collections of this species from Nuku Hiva seem to grade toward *B. bipontina* as they have more caudate leaf apices and longer rays (e.g., Florence 4332, 4353, and 4390 from Toovii Plateau area) than collections from other areas of Nuku Hiva and other islands. Specimens from the Terre Deserte, Haatuatua Valley (Gagné & Montgomery 2463, 2471) have heads on the smaller end of the variation like some other collections from Nuku Hiva, but uniformly have compound leaves. Compound leaves occurs only in Haatuatua and the adjacent Tapueahu Valleys, and they are found in all three of the species that occur there (*B. cordifolia, B. bipontina,* and *B. polycephala*).

Otherwise these species all have simple leaves. The only exception to this is the rare occurrence of compound leaves in *B. microcephala* on Fatu Hiva. This pattern could be the result of presence of compound leaves in populations of one of the three species and hybridization among them at some time in the past. Two collections are considered putative hybrids and are discussed below. Gillett (1972) used a collection (Gillett 2194) in his experimental studies of Pacific *Bidens*. He determined that *B. polycephala* was self-compatible and is capable of forming fully fertile F_1 hybrids with several Hawaiian species (*B. mauiensis* (A. Gray) Sherff, *B. menziesii* (A. Gray) Sherff, and *B. molokaiensis* (Hillebr.) Sherff).

3. *Bidens uapensis* (F. Brown) Sherff, Publ. Field Mus. Nat. Hist., Bot. Ser. 16: 115. 1937.

http://species-id.net/wiki/Bidens_uapensis
Figure 4

Campylotheca uapensis F. Brown, Bernice P. Bishop Mus. Bull. 130: 358. 1935.

Type. Marquesas Islands. Ua Pou: Mt. Tekahoipu, 810 m, 9 September 1922, E.H. Quayle 1149 (lectotype, designated by Sherff, Publ. Field Mus. Nat. Hist., Bot. Ser. 16: 115. 1937: BISH-723226!). An additional syntype is Quayle 1066 (BISH).

Description. Erect, suffrutescent perennial herbs 0.6–3 m tall. Leaves simple, 4.5–12 cm long including petiole, blades lanceolate to lanceolate-elliptic, 3–8.5 × 1–4 cm, mostly glabrous, except for a tuft of hairs on lower surface at base, margins serrulate to serrate, apex acuminate to occasionally acute. Heads 3–12(–16), in diffuse cymes, terminating main stem and lateral branches, 2–8 mm in diameter excluding rays, peduncles 0.4–7 cm long, stout; outer involucral bracts 1.5–8 mm long, well differentiated from inner bracts, margins ciliate, inner bracts often with a tuft of hairs at apex; ray florets 5–11 per head, sterile, rays yellow, 7–15 × 1.5–5 mm; disk florets ca. 23–25, perfect. Achenes gray or black, straight, 3–5 × 0.5 mm, tipped, margin setose; pappus of 2 irregularly antrorse barbed awns.

Distribution. Marquesas Islands, endemic to Ua Pou, 6–920 m.

Habitat. Ridges and slopes in openings of mesic or wet forest, with common species such as *Metrosideros collina*, *Weinmannia marquesana*, *Freycinetia impavida, Hibiscus tiliaceus, Pandanus tectorius,* and *Dicranopteris linearis*.

Conservation status. IUCN Red List Category **Endangered** (EN), criteria B2a, B2b i-iii): B2, total area of occupancy less than 500 km^2 (c. 50 km^2); B2a, fragmented populations; b (i-iii), habitat continuing decline inferred. The suitable habitat for *Bidens uapensis* on Ua Pou (c. 105 km^2) is indicated as an endangered environment, threatened by human activity (deforestation, fire), feral animals, and invasive plants, thus reducing the extent of the forest. Nevertheless, *B. uapensis* has been observed to be locally common in some areas with good regeneration (Butaud, pers. comm. 2014), and consequently an alternative category might be Least Concern (LC).

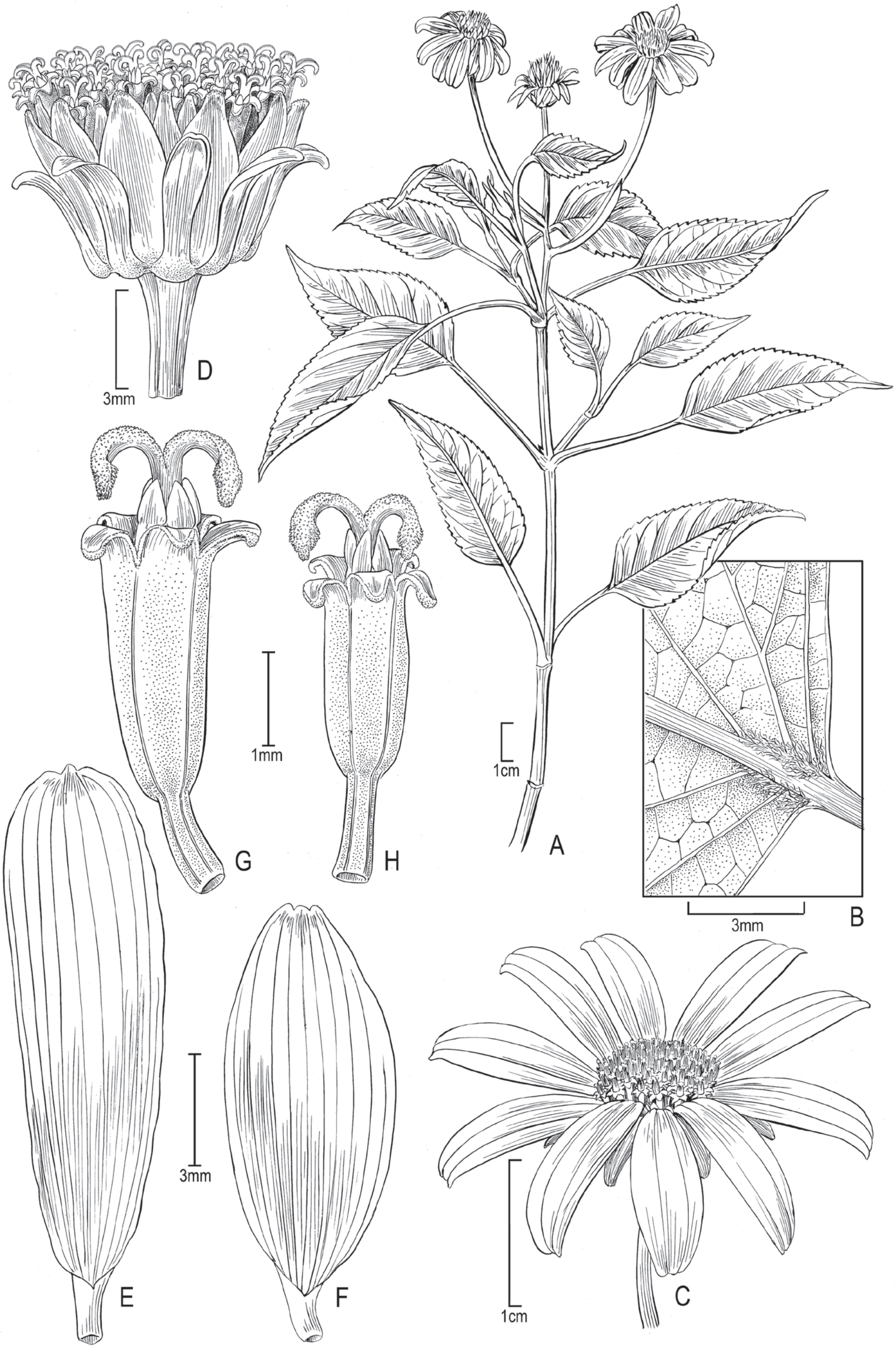

Figure 4. *Bidens uapensis* (F. Brown) Sherff **A** Distal part of plant **B** Leaf surface (underside) **C** Head showing rays and disk florets **D** Head with ray florets removed to show involucral bracts **E–F** Ray florets, showing variation **G–H** Disk florets, showing variation. Drawn from Dunn 241 (US) [**A–E, G**], Perlman & Wood 19083 US [**F, H**].

Specimens examined. Marquesas Islands. Ua Pou: Poumaka (above Hakahetau), SE facing near the base, 675 m, 9°23"38'S/140°4"53'W, 30 Nov 2003, Dunn 318 (BISH, K, MO, NY, PAP, P, PTBG, US); Along road between Hakamaii village and Hakotu valley, 300 m, 9°24"13'S/140°6"52'W, 15 Jul 2003, Lorence, Dunn, Wood & Teikiehuupoo 9098 (BISH, P, PAP, PTBG[2], US) [used in molecular study, Funk et al.]; Teavaiteaki Pass, along road to Hohoi, between Hohoi and Pass, Moukatutai, 274 m, 2 Jul 1997, Perlman, Wood, Meyer, Kautai & Kohumoetini 15883 (BISH, MO, P, PAP, PTBG, UBC, US); Toua, growing alongside a newly cut road at the pass into Hakatau valley, 550 m, 9°26"4'S/140°3"50'W, 16 Jul 2003, Dunn, Lorence & Wood 241 (P, PAP, PTBG, US) [used in molecular study, Funk et al.]; Kuata'u Mountain, near Hakahou, 6 m, 9°21"24'S/140°3"24'W, 3 Jul 1997, Wood 6443 (BISH, MO, P, PAP, PTBG, UBC, US); Hakahau, Tehutu Road, 700 m, 10 Aug 1988, Gagné & Montgomery s.n. (BISH [2]); Teavahaakiti, steep slopes of main ridge to S of Oave, N & E facing cliffs between Teavahaakiti & Tekohepu, 869 m, 5 Jul 1997, Perlman & Wood 15912 (AD, MO, NY, P, PAP, PTBG, US); Teavahaakiti, cliffs between Tekohepu & Teavahaakiti, 686 m, 4 Jul 1997, Perlman, Wood & Kautai 15894 (AD, BISH, HAST, MO, NY, P, PAP, PTBG, UBC, US); Forested ridges and slopes to the north and west of Pouakei, 701 m, 9°23"S/140°5"W, 8–9 Jul 2004, Wood & Perlman 10839 (BISH, P, PAP, PTBG, US); Pouakei and along ridge trail to Pouakei, across valley from Pou Maka and Pou Maka trail, 808 m, 9°23"9.63'S/140°4"9.81'W, 9 Jul 2004, Perlman & Wood 19184 (PTBG, US); Ridge just north of Oave, between Oave and Matahenua, high mountain peaks along main backbone ridge, 945 m, 9°23"45.5'S/140°4"43.3'W, 3 Jul 2004, Perlman & Wood 19083 (BISH, NY, P, PAP, PTBG, US); Hakahai, valle de Hakaohoka, environs du sommet du Mt. Aefiti, 400 m, 9°22"S/140°4"W, Dec 1985, Ottino s.n. (PAP); 1500 m, 7 Sep 1922, Quayle 1066 (BISH); Central Ua Pou including the summit crest regions around Oave and the near-by peak of Matahenua, 899–924 m, 9°23"S/140°4"W, 2 Jul 2004, Wood & Perlman 10820 (PTBG).

Discussion. *Bidens uapensis* can be differentiated from other species in having achenes that have pronounced barbed awns and leaf blades with a tuft of hairs on lower surface at the base, a character not seen in any of the other Marquesas *Bidens*.

4. *Bidens microcephala* W.L. Wagner, J.R. Clark & Lorence, sp. nov.

urn:lsid:ipni.org:names:77139444-1
http://species-id.net/wiki/Bidens_microcephala
Figure 5

Type. Marquesas Islands. Fatu Hiva: Angled rocks above Omoa village (Aiguilles Rocheuses), south-facing, sea cliffs, 524 m [10°31"42.8'S/138°41"17.2'W], 6 September 1995, S. Perlman & K. R. Wood 14946 (holotype: PTBG-066383; isotypes: BISH, K, MO, MPU, NY, P, UC, US).

Description. Erect, suffrutescent perennial herbs 1–1.3 m tall. Leaves simple, (4–)6–14.5(–20) cm long including petiole, rarely compound, blade lanceolate to lanceolate-elliptic, occasionally lanceolate-linear, (1.5–)3.5–9.5(–14) × (0.9–)1.3–4 cm, glabrous, margins serrate to serrulate, occasionally subentire, apex acuminate. Heads 40–50, in compact cymes, becoming diffuse at maturity, heads often in tight clusters, terminating main stem and lateral branches, main inflorescence axis 6–9 cm, heads 1–2 mm in diameter, peduncles 0.1–1.5 cm long, glabrous; outer involucral bracts 1–2 mm long, well differentiated from inner bracts; ray florets absent; disk florets (1–)5–10, perfect. Achenes gray or black, straight, 3–4 × 0.5 mm, sparsely setose; pappus absent.

Distribution. Marquesas Islands, endemic to southern and central Fatu Hiva, 10–625 m.

Habitat. On sea cliffs in mixture of native shrub and trees and alien vegetation, with native species such as *Dodonaea viscosa* Jacq., *Hibiscus tiliaceus*, *Pisonia grandis* R. Br., *Celtis pacifica* Planch., *Psydrax odorata* (G. Forst.) A.C. Sm. & S.P. Darwin, *Wikstroemia coriacea* Seem., and *Dinebra xerophila* (P.M. Peterson & Judz.) P.M. Peterson & N. Snow, and naturalized species like *Casuarina equisetifolia* L., *Coffea arabica* L., *Cordyline fruticosa* (L.) A. Chev., *Psidium guajava* L., *Miscanthus floridulus* (Labill.) Warb., and *Morinda citrifolia* L.

Etymology. The specific epithet refers to the extremely small heads, probably the smallest in the genus.

Conservation status. Proposed IUCN Red List Category **Critically Endangered** (CR), criteria B1ab, B2a,b (i–iii): B1, total extent of occurrence less than 100 km^2 (ca. 85 km^2), a, severely fragmented and b, continuing habitat decline inferred; B2a, estimated area of occupancy estimated to be less than 10 km^2; B2b (i–iii), habitat continuing decline inferred. The estimated area of occupancy for *B. microcephala* on Fatu Hiva (ca. 85 km^2) is indicated as an endangered environment, threatened by human activity (deforestation and fire), feral animals, and invasive plant species, thus reducing the extent of the suitable habitat. It is still locally common and regenerating on some cliff areas inaccessible to goats, however, so VU might be an alternative category (Butaud, pers. comm. 2014).

Specimens examined. Marquesas Islands. Fatu Hiva: Omoa, crete a l'Est du Mt Tefatutea, 625 m, 10°31"S/138°40"W, 25 Jul 1988, Florence & Perlman 9566 (P, PAP); On seacliffs of Aiguilles Rocheuses, S of Omoa village, above Tataaihoa and Tahaoa, 524 m, 6 Sep 1995, Perlman & Wood 14948 (BISH, MPU, P, PAP, PTBG, US) [used in molecular study, Funk et al.]; Tetio, seacliffs between Omoa and Hanavave, Tetio lies S of Matatu Point, about halfway to Omoa, 6–110 m, 15 Sep 1995, Perlman & Wood 14996 (BISH, MO, P, PAP, PTBG, US), cultivated plant from seed from this source, 5 Nov 1996, Lorence 7823 (BISH, PTBG, UBC, US); Hanavave Valley, cliffs below Teani, near Teeavahinenao Pass, up Uiha stream to back wall, 378 m, 16 Sep 1995, Perlman, Wood & Alexi 15009 (BISH, MO, MPU, NY, PAP, PTBG, US); Aiguilles Rocheuses, Tataaihoa side, 533-579 m, 6 Sep 1995, Wood & Perlman 4465 (BISH, K, MO, MPU, NY, P, PTBG, US); Tetio, S of Hanavave, 31-152 m, 15 Sep 1995, Wood & Perlman 4539 (AD, BISH, MO, MPU, NY, P, PAP, PTBG[2],

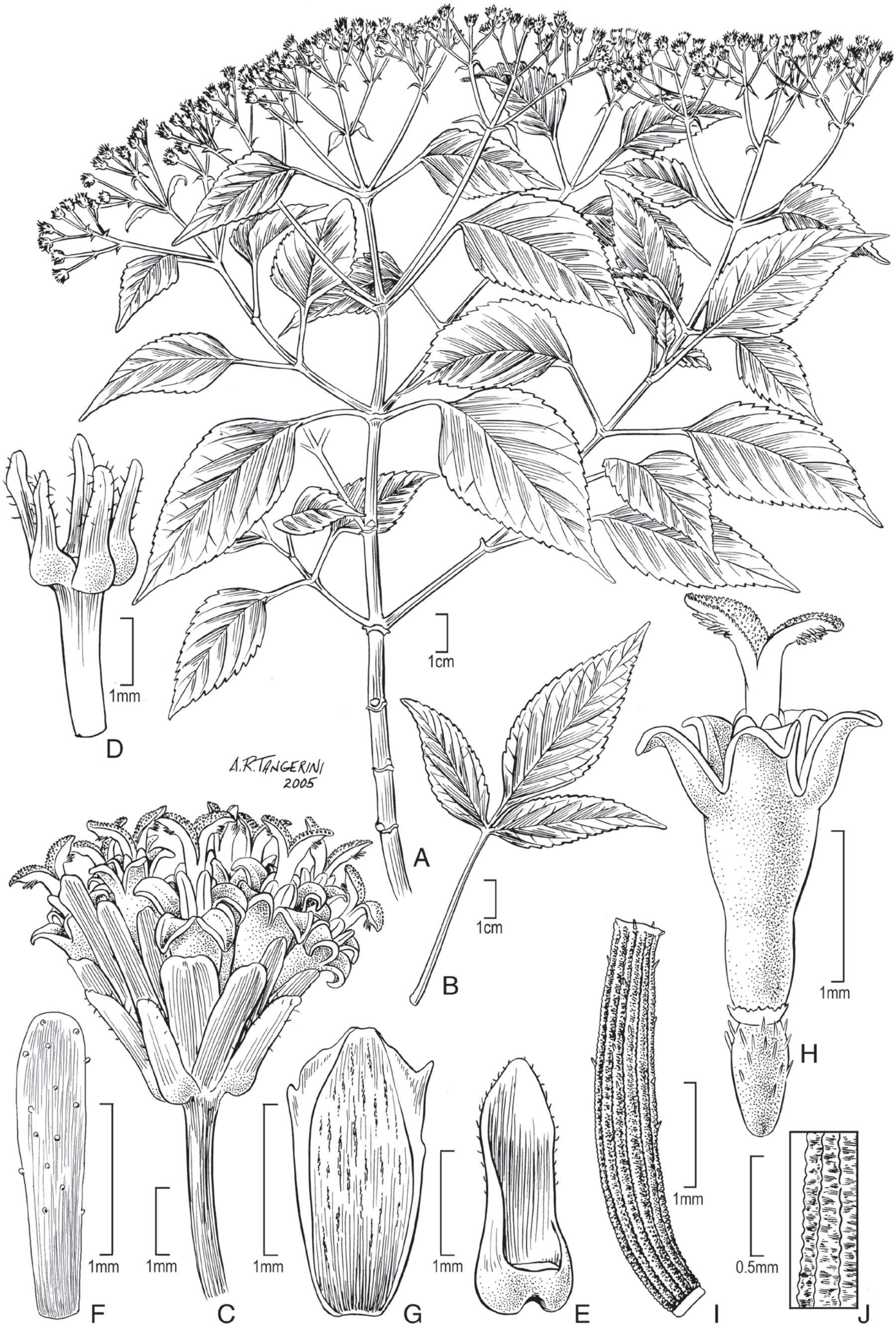

Figure 5. *Bidens microcephala* W.L. Wagner, J.R. Clark & Lorence **A** Distal part of plant **B** Compound leaf **C** Head showing bracts and disk florets **D** Outer Involucral bracts and peduncle **E** Outer involucral bract showing basal gibosity **F** Pale **G** Inner involucral bract **H** Disk floret **I** Achene **J** Inset showing achene surface. Drawn from Perlman 18444 (PTBG) [**A, C, D, G** and **H**], Perlman 18416 (unmounted) [**B**], pickled material of PTBG cult. 950676 (from Perlman & Wood 14996) [**E, I and J**], and Wood 10103 [**F**].

US); About 1 km S of Omoa, 10 m, 31 Oct 1974, Decker 2689 (BISH, BKL, CBG, CHR, K, L, MO, MPU, NSW, NY, P, PAP, PTBG, US); Ridge to south of Omoa village at Angled Rocks (Aguilles Rocheuses), 585 m, 10°31"42.8'S/138°41"17.2'W, 11 Feb 2003, Perlman 18416 (BISH, P, PAP, PTBG, US); Coastline between Hanaui to Hanahoua, north of Omoa, 9 m, 10 Feb 2003, Wood & Price 10103 (BISH, MPU, PTBG, OS, US); Ouia valley, back of valley on south side in forest, 210 m, 10°29"10.3'S/138°37"12.9'W, 14 Feb 2003, Perlman 18444 (BISH, MPU, P, PAP, PTBG, US); Ridge from Omoa to Aiguilles Rocheuses, along ridge crest to Tefatutea Peak, sea cliffs of Needle Rocks above Tahaoa, 594 m, 22 Jul 1988, Perlman 10156 (AD, BISH, MO, MPU, P, PAP, PTBG, US) ; about 1 km along coast N. of Hanaui, 10 m, 10 Feb 2003, Price & Wood 231 (PAP, PTBG, US) [used in molecular study, Funk et al.]; Chemin d'Omoa à Hanavave, au-dessus de la vallée de Teatapu, 550 m, 18 Sep 1975, Schäfer 5747 (BISH, MPU, P, PAP, PTBG, US).

Discussion. *Bidens microcephala* exhibits the most reduced heads of all Marquesan *Bidens*, generally having 10 or fewer disk florets per head and completely lacking in ray florets. In several specimens (Price & Wood 231, Wood & Perlman 4539, Wood & Price 10103, Perlman & Wood 14996), this reduction is even more extreme; flower heads in these specimens contain consistently fewer than 4 florets each, often only two or even occasionally one. These latter specimens also universally exhibit entire to subentire leaf margins and might represent yet another evolutionary lineage worthy of formal recognition (e.g., in Lorence 7823, specimen from cultivated plant grown from seed from Perlman 14996).

5. *Bidens woodii* W.L. Wagner, J.R. Clark & Lorence, sp. nov.

urn:lsid:ipni.org:names:77139445-1
http://species-id.net/wiki/Bidens_woodii
Figure 6

Type. Marquesas Islands. Ua Pou: Central Ua Pou including the summit crest regions around Oave and the nearby peak of Matahenua, 899–924 m, 9°23"S/140°4"W, 2 Jul 2004, Wood & Perlman 10806 (holotype: US-3547652; isotypes: BISH, P, PAP, PTBG) [used in molecular study, Funk et al.].

Description. Erect, suffrutescent perennial herbs 0.5–1 m tall. Leaves simple, 5–7 cm long including petiole, petiole stout, blades thick and coriaceous, ovate to broadly ovate, 3–4.5 × 1.8–2.5 cm, glabrous, the veins on lower surface conspicuously raised, margins serrate, apex short-acuminate. Heads 1–2, in compact cymes terminating main stem and lateral branches, 4–5 mm in diameter excluding rays, peduncles ca. 2 cm long, stout, glabrous; outer involucral bracts ca. 3–4 mm long, broad, well differentiated from inner bracts; inner bracts dark purple, erose and with a few short hairs; ray florets ca. 6–8, sterile, rays yellow, obovate, 10–12 × 4–7 mm, apices often bi- or tri-lobed; disk florets ca. 30–34, perfect, corollas yellow; pappus absent. Achenes not seen.

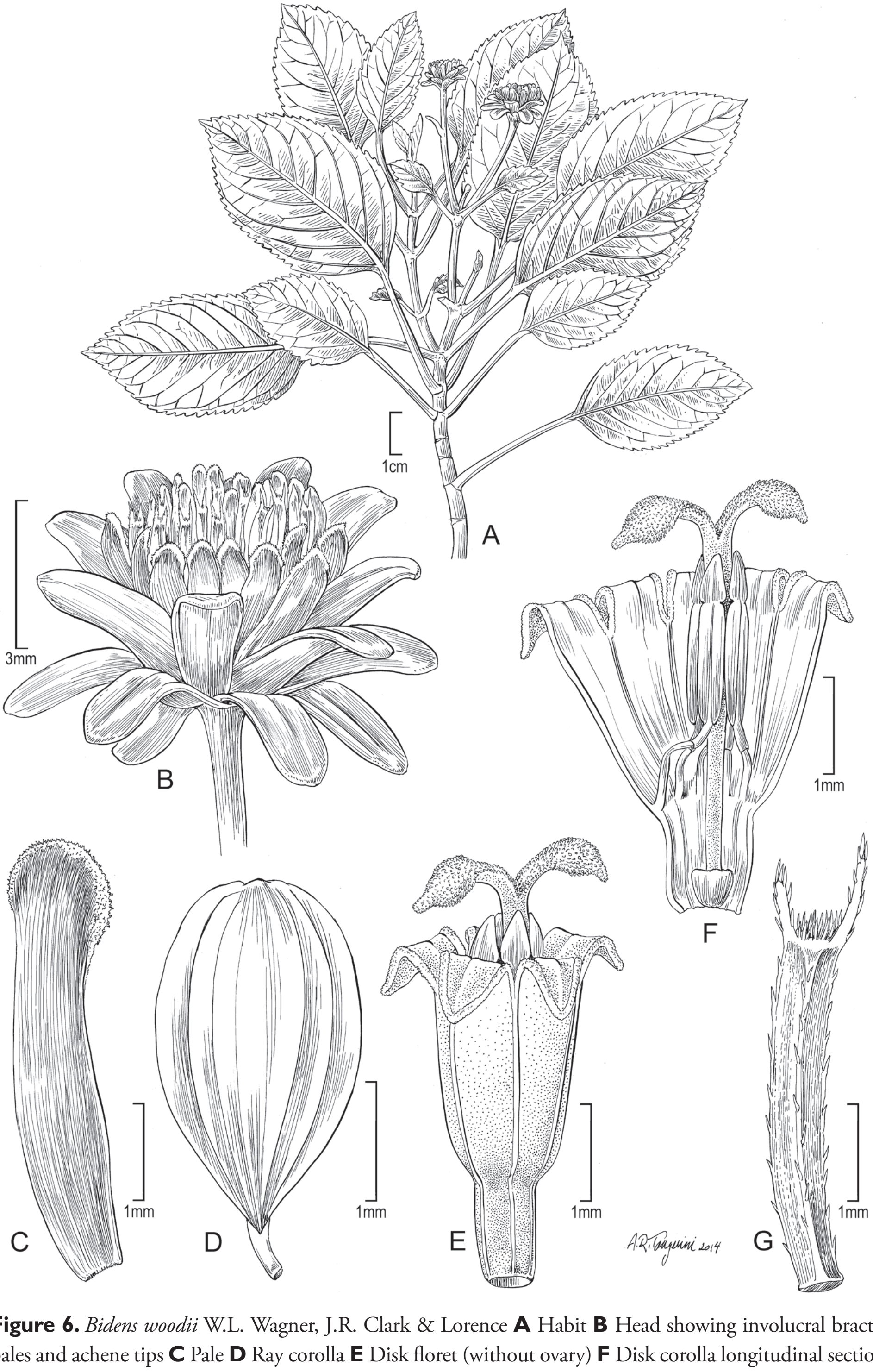

Figure 6. *Bidens woodii* W.L. Wagner, J.R. Clark & Lorence **A** Habit **B** Head showing involucral bracts, pales and achene tips **C** Pale **D** Ray corolla **E** Disk floret (without ovary) **F** Disk corolla longitudinal section **G** Achene. Drawn from Wood & Perlman 10806 (holotype, US).

Distribution. Marquesas Islands, Ua Pou, known only from the type on the summit crest around Oave and the nearby peak of Matahenua, ca. 920 m.

Habitat. Occurs in low shrubland of *Metrosideros collina* with *Dicranopteris linearis* on the windswept and cloud-shrouded summit area.

Etymology. This new species is named for Kenneth R. Wood, who made the only known collection of it and who has contributed greatly to our knowledge of the flora of the Marquesas and Hawaii through his collections, excellent photography, and field observations.

Conservation status. IUCN Red List Category **Endangered** (EN), criteria B2a, B2b i-iii: B2, total area of occupancy less than 500 km^2 (c. 50 km^2); B2a, fragmented populations; b (i-iii), habitat continuing decline inferred. The suitable habitat for *Bidens woodii* on Ua Pou (c. 105 km^2) is indicated as an endangered environment, threatened by human activity (deforestation, fire), feral animals, and invasive plants, thus reducing the extent of the suitable habitat.

Discussion. *Bidens woodii* is most similar to *B. evapelliana* but can be differentiated by its habit (erect versus prostrate, and 0.5–1 m versus 0.3–0.5 m tall stem), leaves with raised venation, and obovate rays. It is known only from the type collection.

6. *Bidens evapelliana* W.L. Wagner, J.R. Clark & Lorence, sp. nov.

urn:lsid:ipni.org:names:77139446-1
http://species-id.net/wiki/Bidens_evapelliana
Figures 7, 8

Type. Marquesas Islands. Fatu Hiva: Slopes of Mounanui, on open ridge, 10°28'656"S/138°38'149"W, 730 m, 16 Jul 2005, Perlman 19665 (holotype: PTBG-066395; isotypes: BISH, MO, P, US).

Description. Prostrate, suffrutescent perennial herbs up to 0.3–0.5 m tall. Leaves simple, coriaceous, 1.3–3.6(–7) cm long including petiole, petiole relatively short, blades elliptic to ovate, 1–2.8(–5.6) × 0.7–2(–3.5) cm, glabrous, margins serrate, apex rounded to acute. Heads 1–3, in compact cymes terminating main stem and lateral branches, 4–8 mm in diameter excluding rays, peduncles 1–2.5 cm long, glabrous; outer involucral bracts 4–6 mm long, broad, well differentiated from inner bracts; ray florets normally 3–6 per head, sterile, rays yellow, ca. 8 × 2–5 mm; disk florets ca. 23–25, perfect. Achenes tawny to gray, straight, ca. 5 × 1 mm, slightly keeled, glabrous; pappus of 2 irregular antrorse barbed awns.

Disribution. Marquesas Islands, known only from the south-central part of Fatu Hiva from Mt. Natahu and Teavapuhiau Pass to Mounanui and Touaouoho, 700–850 m.

Habitat. Scattered on ridgetops and cliffs, in scrubland or low forest of *Metrosideros collina, Freycinetia impavida, Crossostylis biflora* J.R. Forst. & G. Forst., *Hibiscus tiliaceus, Pandanus* sp., *Weinmannia marquesana,* and *Dicranopteris linearis*.

Etymology. This species is named in honor of Eva Pell, Under Secretary for Science at the Smithsonian Institution upon her retirement. She served in this position from 2010 to 2014 during which time she worked to strengthen science across the

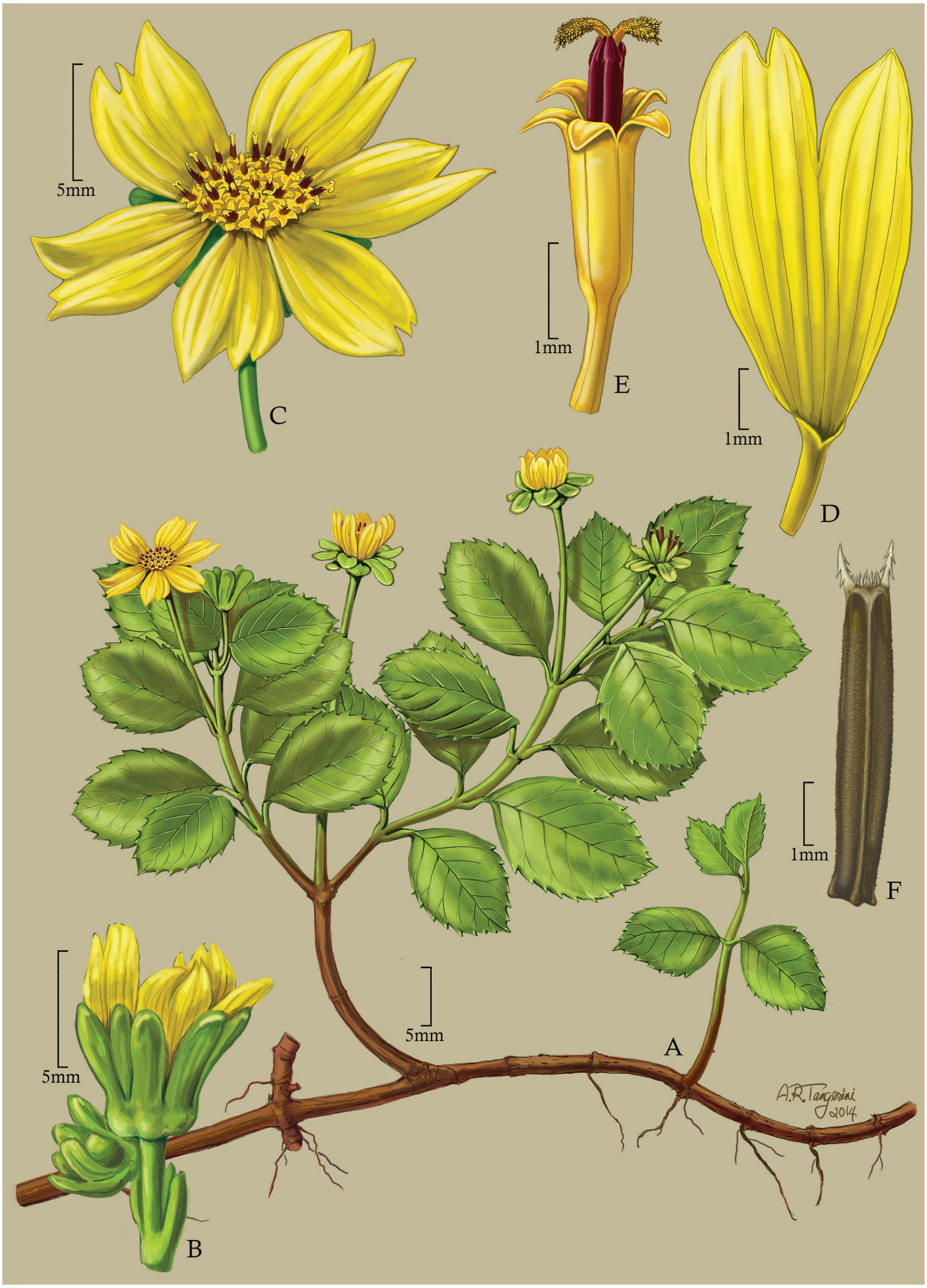

Figure 7. *Bidens evapelliana* W.L. Wagner, J.R. Clark & Lorence **A** Habit **B** Young head showing pre-flowering florets **C** Head showing ray and disk florets **D** Ray corolla **E** Disk corolla **F** Achene. Drawn from Perlman 19665 (isotype, US) and field images of collection [**A, B**], and Florence & Perlman 9590 (US) [**C–F**].

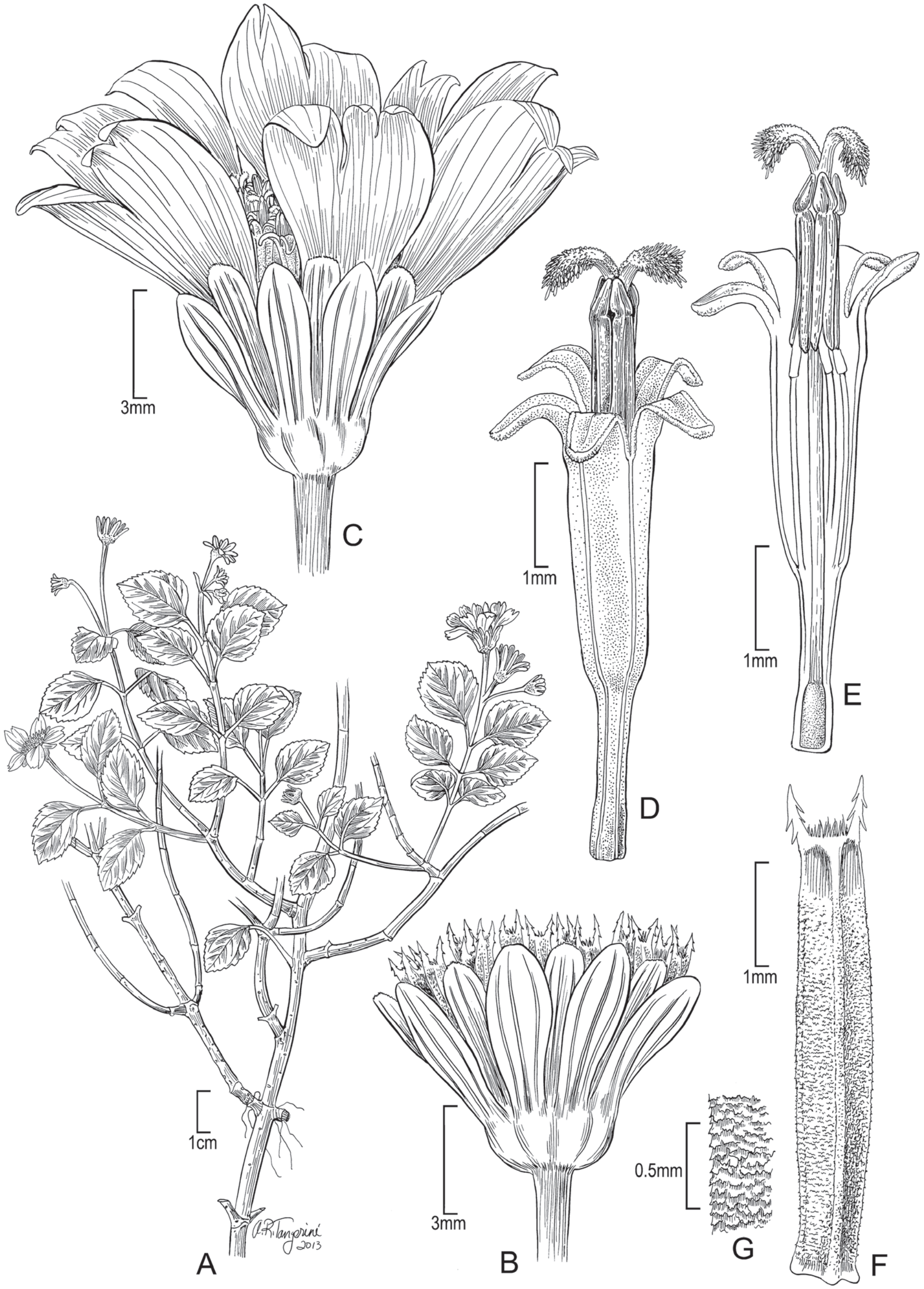

Figure 8. *Bidens evapelliana* W.L. Wagner, J.R. Clark & Lorence **A** Habit **B** Head post-flowering showing involucral bracts and apex of achenes **C** Young head showing immature rays and involucral bracts **D** Disk corolla **E** Disk corolla longitudinal section **F** Achene **G** Inset showing achene surface. Drawn from Perlman 10166 (PTBG) [**A**], Perlman 19665 (isotype, US) [**B**], and Florence & Perlman 9590 (US) [**C–G**].

institution. Her accomplishments include creation of the four "Grand Challenges Consortia," which have been instrumental in developing interdisciplinary collaborations across the Smithsonian. She also played a key role in creating the Smithsonian's Tennenbaum Marine Observatories Network, the first worldwide network of coastal field sites to standardize measurements of biological change in marine environments.

Conservation status. Proposed IUCN Red List Category: **Critically Endangered** (CR), criteria B1ab, B2a,b (i–iii): B1, total extent of occurrence less than 100 km² (less than 10 km²); a,b, known from a single location; B2a, area of occupancy estimated to be less than 10 km²; B2b (i–iii), habitat continuing decline inferred. The estimated area of occupancy for *B. evapelliana* on Fatu Hiva (ca. 85 km²) is indicated as an endangered environment, threatened by human activity (deforestation and fire), feral animals (goats), and invasive plant species, thus reducing the extent of the forest.

Specimens examined. Marquesas Islands. Fatu Hiva: Along base of Mt. Natahu, 828 m, 1–3 Aug 1977, Gagné 1266 (BISH); Teavapuhiau Pass, above Ouia Valley, W of pass, 700 m, 1–3 Aug 1977, Gagné 1252 (BISH); Mt. Touaouoho, on NW side of peak, along ridges between Touaouho and Teavapuhiau, 2650 ft [808 m], 8 Sep 1995, Perlman & Wood 14959 (PTBG, US); Crete Ouest du Mt. Mounanui, 810 m, 10°28"S/138°37"W, 26 Jul 1988, Florence & Perlman 9590 (BISH, P, PTBG, US); slopes of Mounanui above Vaieenui Falls, on ridge top, below Mounanui, 2500 ft [760 m], 26 Jul 1988, Perlman & Florence 10166 (AD, BISH, F, MO, NY, OS, P, PAP, PTBG, TEX, UBC, US); on ridges west side of Mounanui, on ridge leading up from Cascade, 2400 ft [732 m], 10 Sep 1995, Perlman 14977 (BISH, P, PAP, PTBG, US); slopes of Mounanui above Vaieenui Falls, on ridge top, below Maunanui, 2780 ft [847 m], 26 Jul 1988, Perlman & Florence 10173 (BISH).

Discussion. *Bidens evapelliana* is distinctive in its nearly exclusive prostrate habit and relatively small elliptic to ovate leaves. One specimen, Perlman 14959, is somewhat atypical to other collections of *B. evapelliana* in that it has larger leaf blades 4.3–5.6 × 2.0–3.5 cm, petioles up to 2 cm long, and slightly longer involucral bracts (ca. 6 mm).

7. ***Bidens wichmanii*** **W.L. Wagner, J.R. Clark & Lorence, sp. nov.**

urn:lsid:ipni.org:names:77139680-1
http://species-id.net/wiki/Bidens_wichmanii
Figure 9

Type. Marquesas Islands. Fatu Hiva: Tevaiua, southern summit region, 870 m, 15 Feb 2003, K. R. Wood 10140 (holotype: PTBG-043994; isotypes: AD, BISH, K, MO, MPU, NY, P, PAP, US).

Description. Scandent to ascending suffrutescent perennial herbs 0.5–2 m tall. Leaves simple, 3.5–13.5 cm long including petiole, blades lanceolate to elliptic-lanceolate, 2.3–9.5 × 1.2–4.5 cm, glabrous, margins serrate, apex acute. Heads 1–3, in diffuse

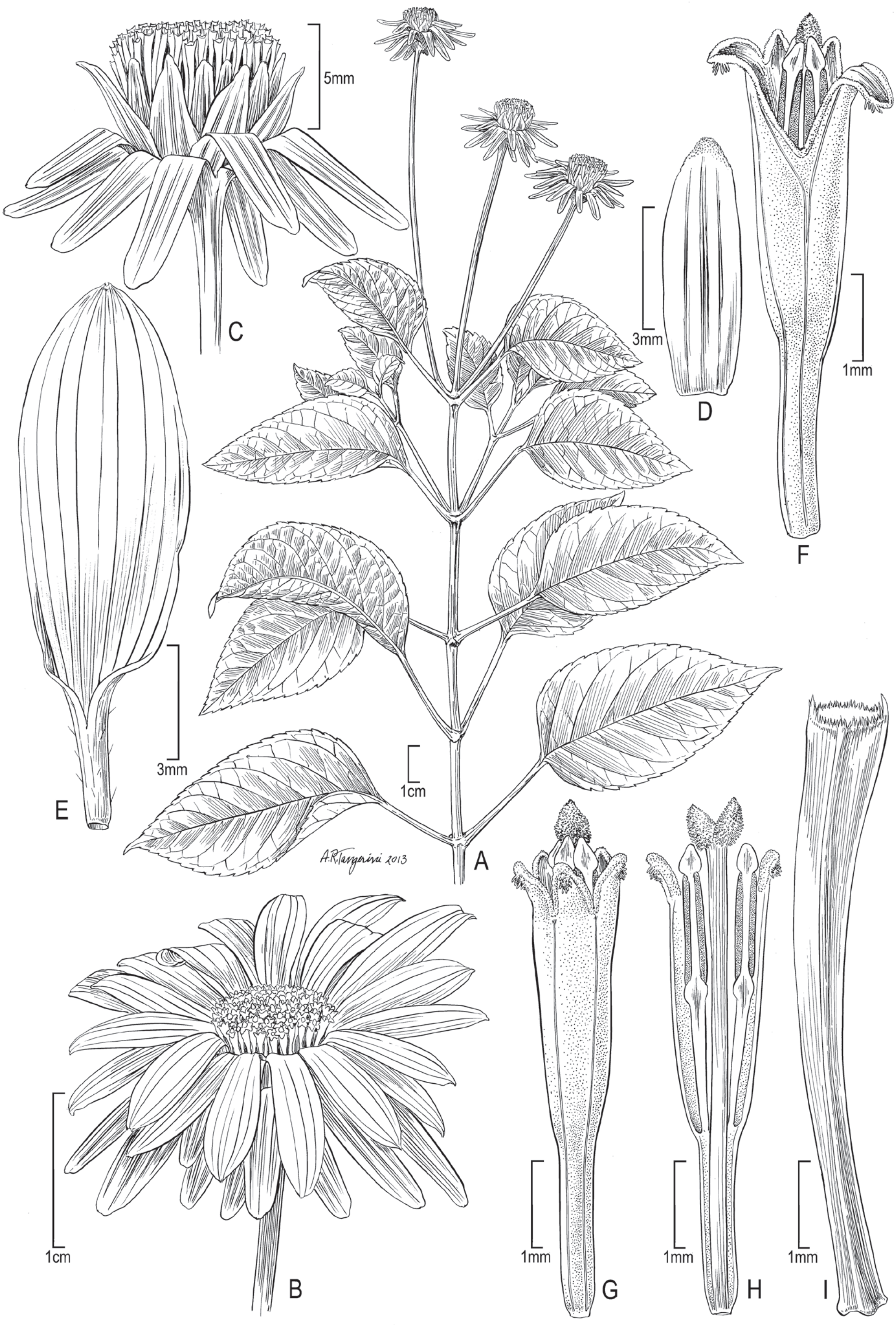

Figure 9. *Bidens wichmanii* W.L. Wagner, J.R. Clark & Lorence **A** Distal part of plant **B** Head showing rays and involucral bracts (outer series) **C** Head post-flowering showing involucral bract **D** Inner involucral bract **E** Ray corolla **F–G** Disk corolla **H** Disk corolla longitudinal section **I** Achene. Drawn from Wood 10140 (isotype, US) [**A, C, I**], and Perlman 10152 (US) [**B, D–G, H**].

cymes terminating main stem and lateral branches, 8–15 mm in diameter excluding rays, peduncles (2–)3.5–14 cm long, glabrous; outer involucral bracts 8–12 mm long, broad, well differentiated from inner bracts; ray florets 14–20+ per head, sterile, rays yellow, 10–18 × 3–4 mm; disk florets ca. 50, perfect, corollas yellow. Achenes black, straight, 7–10 × 1–2 mm, slightly keeled, glabrous; pappus of 2 irregular antrorse barbed awns.

Distribution. Marquesas Islands, known only from the central summit region of Fatu Hiva (Tevaiua, Hanativa, and Tekau), 670–870 m.

Habitat. Occurs in shrubland of *Metrosideros collina* with *Freycinetia impavida, Crossostylis biflora*, and *Dicranopteris linearis*, on the windswept summit or near-summit areas.

Etymology. This new species is named for Charles R. "Chipper" Wichman, Jr., Chief Executive Officer and Director of the National Tropical Botanical Garden since 2005, and previously Director of NTBG's Limahuli Garden on Kaua`i since 1994.

Conservation status. Proposed IUCN Red List Category **Critically Endangered** (CR), criteria B1ab, B2a,b (i–iii): B1, total extent of occurrence less than 100 km^2 (less than 10 km^2); a,b, known from a single location; B2a, area of occupancy estimated to be less than 10 km^2; B2b (i–iii), habitat continuing decline inferred. The estimated area of occupancy for *B. wichmanii* on Fatu Hiva (ca. 85 km^2) is indicated as an endangered environment, threatened by human activity (deforestation and fire), feral animals, and invasive plant species, thus reducing the extent of the suitable habitat.

Specimens examined. Marquesas Islands. Fatu Hiva: Along trail between Omo'a and Uia within 1 km from pass over central ridge, 750 m, 12 Oct 1974, Decker 2397 (BISH, P, NSW, US); Sentier d'Ouia vers Omoa, crête au-dessus de la vallée d'Ouia, S du col de Teava, 680 m, 23 Sep 1975, Schäfer 5843 (MPU[7], PTBG, US); Omoa Valley, past Hoopu to ridge near Tevaiua, top of ridge, 2200 ft [671 m], 22 Jul 1988, Perlman 10152 (BISH, PAP, US); north of Hanativa Valley along ridge crest approaching summit area, 800–900 m, 23 Oct 1974, Decker 2626 (BISH, MO, PTBG, US); along summit crest of ridge above Omoa valley, south of Tekau peak, north of Tevaiua, 760 m, 10°31"10.6'S/138°38"8'W, 15 Feb 2003, Perlman 18453 (PTBG, US); Tevaiua, southern summit region, 870 m, 15 Feb 2003, Wood 10138 (PTBG, US), Wood 10139 (PTBG) [used in molecular study, Funk et al.].

Discussion. *Bidens wichmanii* has the largest heads among the Marquesan species. The glabrous achenes are also distinctive in being keeled along the long axis.

8. *Bidens bipontina* Sherff, Bot. Gaz. (Crawfordsville) 85: 10. 1928.

http://species-id.net/wiki/Bidens_bipontina
Figure 2A–C

Bidens serrulata Sch. Bip., Flora 39: 361. 1856, non (Poir.) Desf. 1815.
Coreopsis serrulata (Sch. Bip.) Drake, Ill. Fl. Ins. Mar. Pac.: 210. 1890, non Poiret 1811.
Campylotheca serrulata (Sch. Bip.) F. Br., Bernice P. Bishop Mus. Bull. 130: 356. 1935.

Type. Marquesas Islands. Nuku Hiva, D.E.S.A. Jardin 132 (holotype: P).

Description. Erect, suffrutescent perennial herbs 1–1.3 m tall. Leaves membranous, simple or compound and trifoliolate, 4.3–15 cm long including petiole, blades elliptic-lanceolate to narrowly elliptic, 3–10.5 × 1–3 cm, glabrous, margins serrate, apex long-acuminate to caudate. Heads 6–15, often with two or three heads in tight clusters, in cymes terminating main stem and lateral branches, 2–5 mm in diameter excluding rays, peduncles 2–25 mm long, glabrous; outer involucral bracts ca. 5 mm long, linear, well differentiated from inner bracts, glabrous; ray florets usually 7–9 per head, sterile, rays yellow, 13–20 × 3–4 mm, apex often minutely bi- or tri-lobed or rounded; disk florets ca. 30–32, perfect. Achenes black, 6–7 mm long, margin setose; pappus usually of 2 minute awns.

Distribution. Marquesas Islands, Nuku Hiva, endemic to the Toovii Plateau area, especially Tapueahu Valley, 500–1165 m.

Habitat. *Bidens bipontina* is known only in montane wet shrubland with *Freycinetia impavida* and *Hibiscus tiliaceus* dominant.

Conservation status. Proposed IUCN Red List Category **Endangered** (EN), criteria B2b i–iii): B2, total area of occupancy less than 500 km^2 (ca. 50 km^2); b (i–iii), habitat continuing decline inferred. The suitable habitat for *Bidens bipontina* on Nuku Huka (ca. 340 km^2) is indicated as an endangered environment, threatened by human activity (deforestation), feral animals, and invasive plants, thus reducing the extent of the suitable habitat.

Specimens examined. Marquesas Islands. Nuku Hiva: Terre Deserte, crête W du Mt. Akaupe, 1165 m, 8°52"S/140°10"W, 10 Aug 1987, Florence 8539 (BISH [2]); Route plateau de Toovii–Terre Deserte, 2 km après le col, 930 m, 8°52"S/140°9"W, 9 Dec 1982, Florence 4348 (BISH, P, PAP, US); Toovii, Ooumu area, top of Tapueahu Valley off new hwy, 1067–1128 m, 8°51"S/140°19"W, 20-22 Sep 1995, Wood & Perlman 4601, (BISH, P, PAP, PTBG, UBC, US); Along old Airport road, across summit crest from Toovii, back drainages of Tapueahu Valley, 1085 m, 21 Sep 1995, Perlman & Wood 15028 (AD, BISH, F, MO, P, PAP, PTBG, US); Ridge crest 2 valleys S of Airport road, back of Tapueahu gulch, to NW of Toovii over summit crest, 1024 m, 21 Sep 1995, Perlman & Wood 15021 (AD, BISH, MO, P, PAP, PTBG) [apparently mixed collection with US sheet, a hybrid]; 500 m, 15 Oct 1922, Quayle 1235 (BISH).

Discussion. *Bidens bipontina* is distinctive in its conspicuously caudate leaves and erect linear involucral bracts.

9. ***Bidens cordifolia*** **Sch. Bip., Flora 39: 36. 1856.**

http://species-id.net/wiki/Bidens_cordifolia
Figure 3C–D

Coreopsis cordifolia (Sch. Bip.) Drake, Ill. Fl. Ins. Mar. Pac.: 208. 1890.
Campylotheca cordifolia (Sch. Bip.) F. Br., Bernice P. Bishop Mus. Bull. 130: 357. 1935.

Type. Marquesas Islands. Nuku Hiva, D.E.S.A. Jardin 199 (holotype: P).

Description. Erect subshrubs 0.4–1 m tall; young stems and leaves moderately to densely pubescent. Leaves simple or compound and trifoliolate, 6–16 cm long including petiole, blade elliptic to elliptic-lanceolate, 4–9 × 2–4.8 cm, moderately pubescent, especially on lower surface, midrib, veins, and in a line along the petiole, margins serrate, apex acuminate to caudate. Heads usually 5, in cymes terminating main stem and lateral branches, 5–10 mm in diameter excluding rays, peduncles 1.5–4 cm long, sparsely pubescent, hair becoming denser near the heads; outer involucral bracts 5–9 mm long, oblong-elliptic, spreading, well differentiated from inner bracts, moderately to sparsely ciliate; ray florets usually 6–13 per head, sterile, rays yellow, ca. 15 × 4 mm; disk florets ca. 30, perfect. Achenes black, straight, ca. 3 × 0.5 mm, margins setose; pappus usually of 2–3 irregular antrorse barbed awns.

Distribution. Marquesas Islands, occurring only in a relative small area of the Toovii Plateau on Nuku Hiva, from 750–1130 m.

Habitat. *Bidens cordifolia* is known from montane wet shrubland or low forest with *Metrosideros collina* and *Weinmannia marquesan*a with fern understory along with other shrubs and trees such as species of *Coprosma, Crossostylis, Cyrtandra, Dicranopteris, Geniostoma,* and *Myrsine*.

Conservation status. Proposed IUCN Red List Category **Critically Endangered** (CR), criteria B1ab, B2a,b (i–iii): B1, total extent of occurrence less than 100 km^2 (less than 10 km^2); a,b, known from a single location; B2a, area of occupancy estimated to be less than 10 km^2; B2b (i–iii), habitat continuing decline inferred. The suitable habitat for *Bidens cordifolia* on Nuku Huka (ca. 340 km^2) is indicated as an endangered environment, threatened by human activity (deforestation, fire), feral animals (goats), and invasive plants, thus reducing the extent of the forest.

Specimens examined. Marquesas Islands. Nuku Hiva: Toovii and road from Taiohae Bay to Toovii, 750 m, 3 Aug 1988, Wagner & Lorence 6258 (BISH, US); Toovii, Ooumu area, top of Tapueahu Valley off new hwy, 1067–1128 m, 8°51"S/140°19"W, 20–22 Sep 1995, Wood & Perlman 4600 (BISH, P, PAP, PTBG, US).

Discussion. *Bidens cordifolia* is one of the least known species of *Bidens* in the Marquesas Islands. We have seen only two collections we refer to this species as well as images taken by Jean-François Butaud in 2008 and 2009 of additional populations. In addition to these collections and observations this species was only known from the type and a collection made in 1840 (Barclay 3213, BM) as cited by Sherff (1937).

10. *Bidens beckiana* (F. Br.) Sherff, Publ. Field Mus. Nat. Hist., Bot. Ser. 16: 80. 1937.

http://species-id.net/wiki/Bidens_beckiana
Figure 3A–B

Campylotheca beckiana F. Br., Bernice P. Bishop Mus. Bull. 130: 359, fig. 66. 1935.

Type. Marquesas Islands. Eiao, 20 September 1922, R.H. Beck 1529 (holotype: BISH-723228!; isotype: BISH).

Description. Erect subshrubs 0.7–1.3 m tall. Leaves simple, 1.5–9.5 cm long including petiole, blades narrowly ovate or lanceolate, 1–7 × 0.8–4 cm, glabrous or pubescent toward the base and in a line along the petiole, margins serrulate, apex acuminate. Heads (1–)3(–4), in diffuse cymes terminating main stem and lateral branches, 5–15 mm in diameter excluding rays, peduncles 1.5–11.8 cm long, glabrous; outer involucral bracts 4–9 mm long, broad and tapering somewhat at the base, apex sometimes erose, inner bracts sometimes erose at apex; ray florets 5–11, sterile, rays yellow, 9–15 × 2–3 mm wide, apex entire or divided into 2–3 acute to rounded lobes; disk florets ca. 30–34, perfect, corollas yellow. Achenes gray, straight or slightly curved, 8–10 × 1 mm, conspicuously setose; pappus of 2 antrorse barbed awns.

Distribution. Marquesas Islands, occurring on Eiao and Hatutaa, 150–500 m.

Habitat. *Bidens beckiana* is scattered to locally common on steep slopes and ridges, ravines, or cliffs, from mesic to xeric shrublands and grasslands with *Dinebra xerophila*, *Waltheria indica* L., *Cordia lutea* Lam., *Dodonaea viscosa*, and *Thespesia populnea* (L.) Sol. ex Corrêa. Judging from the number of collections *B. beckiana* appears to be more common on Hatutaa than Eiao, which has populations of feral sheep, pigs, cats, and rats.

Conservation status. Endangered (EN), criteria B2b (i–iii): B2, total area of occupancy less than 500 km^2 (ca. 47 km^2); b (i–iii), habitat quality continuing decline inferred. The suitable habitat for *Bidens beckiana* on Eiao (40 km^2) and Hatutaa (7 km^2) is indicated as an endangered environment, threatened by feral animals, and invasive plants, thus reducing the extent of the suitable habitat.

Specimens examined. Marquesas Islands. Eiao: North side of large valley which is south of Vaituha Valley, Opituha Valley, 320 m, 7 Jul 1988, Perlman & Florence 10051 (BISH, E, F, K, LE, MO, P, PAP, PTBG, OS, UBC, US); NW side of island, Vaituha Bay and summit ridge of island, 400 m, 1 Aug 1977, Gagné 1294 (BISH, US); Tohuanui, secteur est, 480 m, 8°0"S/140°41"W, 8 Jul 1988, Florence & Teikiteetini 9368 (BISH, CHR, K, P, PAP, PTBG, US); Tetuaenui, falaise de la crete, 500 m, 5 Aug 1987, Thibault 1083 (PAP). **Hatutaa:** Plateau, secteur centrale, 320 m, 7°55"S/140°34"W, 11 Jul 1988, Florence & Teikiteetini 9419 (BISH, P, PAP, US), 9426 (BISH, P, PAP, US); Plateau centrale, 150-200 m, 19 Aug 1975, Thibault 148 (BISH, US); Plateau, secteur Ouest, 280 m, 7°56"S/140°35"W, 10 Jul 1988, Florence & Perlman 9408 (BISH, CHR, P, PAP, PTBG, US); Plateau, secteur Ouest, 280 m, 7°56"S/140°35"W, 11 Jul 1988, Florence & Teikiteetini 9410 (BISH, OS, P, PAP, PTBG, US); Main ridge, top, 400 m, 23 Mar 1960, Decker 349 (BISH, US); On top, summit plateau, 320 m, 10 Jul 1988, Perlman 10064 (BISH, F, HAW, MO, P, PAP, PTBG, UBC, US); Plateau, secteur E, 320 m, 7°55"S/140°34"W, 11 Jul 1988, Florence & Teikiteetini 9427 (BISH, CHR, P, PAP, PTBG, US); Tres commun au-dessus de 200 m, 200 m, 9 Aug 1987, Thibault 1102 (PAP).

Discussion. *Bidens beckiana* is characterized by having outer and inner involucral bracts that are scarcely differentiated from the pales, and very broad outer bracts that are usually somewhat constricted at the base.

Putative hybrid *Bidens bipontina* × *Bidens polycephala*

We have examined two gatherings from Nuku Hiva in Tapueahu Valley NW of Toovii that may represent hybrids. One of them (Butaud 2587) was collected in a small population of ca. 10 similar individuals (Butaud, pers. comm.), and could represent either hybrid individuals or less likely an undescribed taxon. A second gathering (Perlman & Wood 15021) seems to represent a mixed collection of one parent (*B. bipontina,* all but one of the specimens) and a putative hybrid (one specimen at US). These plants were growing with or fairly close to populations of *B. bipontina*, which occurs in the valley, and *B. polycephala*, which occurs in nearby areas, but has not been collected specifically near these putative hybrids. More information is needed to make an informed interpretation. These collections differ from both putative parents in having almost exclusively trifoliolate leaves, relatively small heads 1–3 mm in diameter excluding rays, glabrate, but with scattered hairs on margins of bracts, upper surfaces and in axils, outer involucral bracts ca. 2 mm long, linear, sparsely ciliate, ray florets 2–4 per head, rays 4–8 mm long, and achenes ca. 3 mm. The Butaud collection was included in a recent molecular phylogenetic study of Pacific *Bidens* (Funk et al. unpubl.), and it is placed in a small clade consisting of *B. bipontina* and *B. cordifolia*, but is not identical to either.

Specimens examined. Marquesas Islands. Nuku Hiva. Ridge crest 2 valleys S of Airport road, back of Tapueahu gulch, to NW of Toovii over summit crest, 1024 m, 21 Sep 1995, Perlman & Wood 15021 (US); Vaiteheii, flanc nord de Tapueahu, 600 m, 27 Jan 2010, Butaud 2587 (PTBG).

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We are grateful to the Bishop Museum Herbarium (BISH) for access to and loans of their collections. Ray Fosberg made his notes for a revision he preparing of Marquesas *Bidens* available to Wagner that were useful in our analyses leading the revision presented here. In addition to the collections, images and observations made by two of the authors (W.L. Wagner and D.H. Lorence), the observations and descriptions were made possible by field observations, photos, and specimens provided by Ken Wood and Steve Perlman (National Tropical Botanical Garden) as part of the "Vascular Flora of the Marquesas Islands" project, which was supported by a generous private donation to the National Tropical Botanical Garden. We are grateful to the Délégation à la Recherche (Papeete, Tahiti), the Musée de Tahiti et des Iles, and the Service du Développement Rural for logistic support, the Délégation for permission to collect in the Marquesas, and the Délégation and the Haut-Commissariat de la République en Polynésie française for permission to conduct research. The illustrations were skillfully drawn by Alice Tangerini (Smithsonian Institution). We appreciate the download and edits by Nancy Khan of the specimens examined from the Marquesas database as well as an overall edit of the manuscript. We also appreciate the helpful comments, images, and insights on Marquesas *Bidens* by Jean-François Butaud and helpful comments from Jacques Florence. P. Lowrey provided images of the Paris types of the names described by Schultz. We appreciate the useful review comments by Mesfin Tadesse. The contribution by W.L. Wagner to this study was partially supported by the Smithsonian Research Opportunities Fund and the National Tropical Botanical Garden McBryde Endowment for Hawaiian and Pacific Botany.

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Three new species of *Solanum* (Brevantherum Clade) endemic to the Brazilian Atlantic Forest

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Abstract

Three new Brazilian species of the Brevantherum clade of *Solanum* (Solanaceae) are described, all closely related to the poorly known *Solanum inornatum* Witasek. *Solanum bradei* Giacomin & Stehmann, **sp. nov.,** and *Solanum kriegeri* Giacomin & Stehmann, **sp. nov.,** differ from *S. inornatum* in having very small deltate calyx lobes that are not accrescent in fruit. *Solanum bradei* is a shrub up to 1.8 m with generally pedunculate inflorescences and tiny translucent fruits, whereas *Solanum kriegeri* is a dwarf glabrescent plant growing on sandy soils in cloud forests, with larger fruits and sessile to subsessile inflorescence. *Solanum friburgense* Giacomin & Stehmann, **sp. nov.,** has linear calyx lobes like *S. inornatum,* and is characterized by its 2-foliate sympodia and leaf pubescence, with trichomes concentrated on leaf veins. The species here described and illustrated are restricted to the mountain ranges of Mantiqueira and Serra do Mar in the Atlantic forests of southeastern Brazil and are all of considerable conservation concern.

Resumo

Três novas espécies pertencentes ao clado Brevantherum do gênero *Solanum* (Solanaceae) são descritas, todas proximamente relacionadas a *Solanum inornatum* Witasek. *Solanum bradei* Giacomin & Stehmann, **sp. nov.,** e *Solanum kriegeri* Giacomin & Stehmann, **sp. nov.,** diferem de *S. inornatum* por apresentarem lobos do cálice deltoides, muito pequenos, não acrescentes no fruto, mas a primeira se destaca por apresentar um porte marcadamente maior, chegando a formar arbustos de até 1.8 m, com inflorescências geralmente pedunculadas e frutos diminutos translúcidos, enquanto *Solanum kriegeri* é uma forma anã e glabrescente que habita matas nebulares associadas a solos arenosos. *Solanum friburgense* Giacomin & Stehmann, **sp. nov.,** apresenta lobos do cálice lineares, como em *S. inornatum*, mas se diferencia pelo simpódio 2-foliado e indumento das folhas, com tricomas concentrados nas nervuras. As espécies aqui descritas e ilustradas são restritas às Serras da Mantiqueira e do Mar no domínio Atlântico do sudeste brasileiro e são indicadas como ameaçadas de extinção.

Keywords
Atlantic Forest, Brazil, Brevantherum Clade, IUCN conservation status, *Solanum*

Introduction

The phytogeographic domain of the Atlantic Forest in South America is a complex of ecosystems and is recognized as one of the most biodiverse regions on earth (Mittermeier et al. 2004). Most of its extent lies in Brazilian territory (up to 95%), but it also reaches Argentina and Paraguay and is estimated to originally comprise an area between 1,300,000 and 1,500,000 square kilometers (about 15% of Brazilian territory; Morellato and Haddad 2000). The main urban centers in Brazil are within the Atlantic Forest domain, and their cycles of expansion and occupation have led to critical levels of reduction in these originally forested environments (Dean 1996). It is estimated that only 12 to 16% of the original forest cover remains, mostly in small fragments (Ribeiro et al. 2009). Despite this reduction, discovery of new species in the Atlantic forests is still ongoing and reflects a still insufficiently known diversity. For example, 42% of the newly described angiosperm species for Brazil between 1990–2006 were based on collections from this phytogeographic domain (Sobral and Stehmann 2009).

Brazil contains more than a fifth of the species of Solanaceae, mainly due to the richness found in the Atlantic Forest (Stehmann et al. 2009, Stehmann et al. 2013), making this one of the centers of diversity of the family (Knapp 2002a). More than half of Solanaceae species are members of the giant genus *Solanum* L., a proportion also observed in the Brazilian flora. This genus includes globally important crops such as the potato (*Solanum tuberosum* L.) and the tomato (*Solanum lycopersicum* L.). Of the 266 species of *Solanum* listed in Brazil, 68% (181) of them are known to occur in the Atlantic Forest and 46% (124) are restricted to the domain (Stehmann et al. 2013). Ongoing inventories of the Atlantic Forest and work on a preliminary Solanaceae flora of the country has revealed many new species and new distributional records for poorly known taxa; here we describe three of these new species.

The species here described are all closely related to *Solanum inornatum* Witasek, a narrowly distributed and poorly known species from São Paulo state. It has not yet been assigned to any formal infrageneric division of *Solanum*, but was thought in the past to be related to section *Gonatotrichum* Bitter due to a similar habit and hair morphology (L.A. Mentz, pers. comm.). Recent phylogenetic studies using molecular characters (Giacomin 2010, L.L. Giacomin et al. in prep.) showed the *S. inornatum* species group (defined here as including *S. inornatum* and the three species described here) is part of the larger Brevantherum Clade (*sensu* Weese and Bohs 2007, Särkinen et al. 2013), one of the 12 to 15 main lineages of *Solanum*. The *S. inornatum* group is part of a well-supported monophyletic group, together with all other species of the Brevantherum clade, that is sister to a clade formed by members of section *Gonatotrichum* (Giacomin 2010, L.L. Giacomin et al. in prep.).

Species of the Brevantherum Clade are native to the New World, occurring from southern United States through Argentina, with a center of diversity in the Brazilian Atlantic Forest. A few species are widespread and invasive in tropical regions in the Old World (e.g., *S. erianthum* D. Don, *S. mauritianum* Scop.). Morphologically, members of the Brevantherum Clade are unarmed herbs to shrubs or small trees with unbranched (section *Gonatotrichum* and members of *S. inornatum* species group) to variously branched or stellate trichomes (all other species), and small oblong-ellipsoid poricidal anthers with introrsely opening pores. The species of the *S. inornatum* group are herbs to small shrubs with exclusively unbranched trichomes and are all restricted to southeastern Brazil. Although they share unbranched (and rarely geniculate; see Giacomin 2010, Stern et al. 2013) trichomes with section *Gonatotrichum*, members of *S. inornatum* group are morphologically and phylogenetically distinct from those species. They can be readily distinguished from the species of section *Gonatotrichum* in that they lack the characteristic explosive fruit dehiscence (Stern et al. 2013) and have more deeply lobed corollas. All the other species of Brevantherum clade except the *S. inornatum* group and section *Gonatotrichum* are shrubs to trees with stellate or lepidote trichomes (Giacomin 2010). A revision of the morphological delimitation of the *S. inornatum* species group as well as a discussion of its phylogenetic position will be subject of another manuscript that is in preparation (L.L. Giacomin et al. in prep.).

Materials and methods

Material from the following herbaria were studied (acronyms from *Index Herbariorum*, http://sweetgum.nybg.org/ih/): BHCB, BM, CESJ, ESA, FUEL, MBM, MBML, R, RB, SP, SPF, SPSF, UEC, UPCB, VIC, W and WU. Cited material is ordered geographically. Barcodes of type specimens, when present, are noted in square brackets after the herbarium citation. Plants obtained in the field were cultivated in a greenhouse in Belo Horizonte and fresh flowers were fixed in alcohol to permit detailed descriptions and illustrations. We assessed the conservation status using IUCN Red List Categories and Criteria (IUCN 2013). For the estimation of the extent of occurrence (EOO) and area of occupancy (AOO) we used the CAT tool described in Bachman et al. (2011) and available at http://geocat.kew.org/. For the AOO estimation was used the standard IUCN cell size of 4 km^2.

Taxonomic treatment

***Solanum bradei* Giacomin & Stehmann, sp. nov.**
urn:lsid:ipni.org:names:77139681-1
http://species-id.net/wiki/Solanum_bradei
Figs 1–2A, B

Diagnosis. Differs from all other species of the *S. inornatum* group in its shrub-like, woody habit and long-pedunculate inflorescences (peduncles up to 1 cm). Unlike *S.*

inornatum Witasek it has deltate, rather than linear-lanceolate, calyx lobes that are not accrescent in fruit.

Type. BRAZIL. Rio de Janeiro: Mun. Itatiaia. Parque Nacional do Itatiaia, continuação da BR após posto de vigilância, margens da estrada próximo a casa, 1171 m, 22°26'11.15"S, 44°37'27.55"W, 3 Nov 2008 (fl), *L.L. Giacomin, L.H.Y. Kamino & T.E. Almeida 359* (holotype: BHCB [BHCB-012523]; isotypes: BM, NY, RB).

Description. Herbs to shrubs, woody at base, erect, to 1.8 m tall, usually much-branched, the upper branches decumbent, flexuous on young plants. Stems moderate to densely pubescent with simple uniseriate 2–3(4)-celled trichomes up to 2.8 mm long, these appressed, arcuate, or erect along stems, or sometimes geniculate and antrorse. Bark of older stems turning brownish-green, glabrescent, not exfoliating, normally matte brown on new growth. Sympodial units 3-plurifoliate, mostly geminate, when so markedly anisophyllous, differing in shape and size, with the smaller leaves highly reduced. Leaves simple, the major ones 2–11.5 × 0.9–3 cm, lanceolate to narrowly-elliptic, chartaceous, slightly discolorous, drying light green beneath, dark green above, not shiny, moderate to densely pubescent in both surfaces with unbranched antrorse, appressed, or erect hairs, with up to 3 cells; base attenuate to rounded, sometimes slightly asymmetric, not decurrent onto the petiole; margins entire, sometimes slightly revolute, ciliate, with the trichomes lying antrorsely parallel to the margin; apex acute to acuminate; petioles 2–13 mm long, with pubescence similar to the stems; minor ones 0.35–2.6 × 0.2–1.3 cm, broadly elliptic to circular; the base obtuse to rounded, margins like those of the major leaves; the apex rounded to acute, the petioles absent to 3 mm; venation brochidodromous; midrib and secondary veins visible to the naked eye, prominent abaxially, with only the midrib slightly prominent to impressed adaxially. Inflorescences pedunculate, terminal, lateral or sub-opposite the leaves, unbranched cymes with 3–7 flowers, the axis with pubescence like that of the stems; peduncle 2.2–10 mm long; pedicels 2–8 mm in the flower, 6–14 mm in fruit, articulated at base, spaced up to 8 mm apart. Calyx up to 3 mm long, the lobes 1–2 mm long in flower and fruit, about 1 mm wide, the lobes ovate-deltate, with an acuminate apex, abaxially moderately to densely pubescent with antrorse trichomes like those of the stem abaxially, adaxially densely pubescent with capitate glandular trichomes less than 1 mm long, with single-celled stalks and a multicellular head; calyx not accrescent in fruit. Corolla 6–10 mm in diameter, white, stellate, membranaceous, the lobes 3–5 × 2–3 mm, ovate-lanceolate, glabrous abaxially and adaxially. Stamens 2–3 mm long, equal in length, the filaments ca. 1 mm long; anthers 1–2 mm long, ca. 1 mm wide, oblong-ellipsoid, slightly connivent, yellow, the base cordate, the apex emarginate and poricidal, the subapical pores directed introrsely, not opening into longitudinal slits. Ovary glabrous; style white, 4–6 mm long, exserted beyond stamens, straight, cylindrical, glabrous, the stigma light green, capitate. Fruit a globose berry 4–7.8 mm in diameter, slightly translucent green to dull green when ripe, drying dark, glabrous. Seeds 2–4 per berry, 2–4.5 × 2–3.3 mm, flattened, ovate-reniform, with a small hollow at hilum region; the seed surface undulate; margins flattened.

Figure 1. *Solanum bradei* Giacomin & Stehmann. **A** Habit **B** Inflorescence detail, showing the long peduncle **C** Corolla cross section showing stamens **D** Fruit, note the small, deltate calyx lobes. All from *Giacomin et al. 359* (BHCB). Scale bars **A**= 5 cm; **B** and **D** = 5 mm; **C** = 2 mm. Drawings by B. Raddichi.

Distribution. Restricted to the Brazilian states of Minas Gerais, Rio de Janeiro and São Paulo (Fig. 3). The known specimens are mainly from the Mantiqueira mountain range in the border area between those states, with one disjunct collection from Serra do Mar, in the Bocaina region of northeastern São Paulo State.

Ecology. Occasional in the understory or shaded forest edges of well-preserved or secondary fragments of the Brazilian Atlantic coastal rainforest (*Floresta Ombrófila Densa* of Veloso et al. 1991), normally close to water courses, in elevations ranging from 1,000 to 2,000 m. In cultivation in Belo Horizonte, *S. bradei* flowered year round. Preliminary crossing studies suggested it was self-incompatible as no fruits were produced in selfed plants, but more individuals should be used for a definitive conclusion.

Phenology. *Solanum bradei* seems to produce flowers year round but a flowering peak is observed in the rainy season, as most of the collections are from between the months of October and March. None of the examined collections are from December or January. Most of the specimens flowering in October and November and fruiting from February through May. The only well developed fruit was found in a collection from May.

Etymology. The epithet honors the German botanist Alexander C. Brade [1881–1971] who greatly contributed to the growth of botany in Brazil in the middle 1900s. His efforts to better understand the flora of Itatiaia led to the earliest known collections of *S. bradei.*

Preliminary conservation status (IUCN, 2013). Endangered (EN) B1; B2 ab (ii,iii,iv). The EOO and AOO calculated were 4,076.04 km^2 and 48 km^2 respectively resulting in the assessment of the Endangered category. The species is known from eight localities only, most of which are subject to urban expansion and deforestation due to tourism and agriculture. Although the species is known to occur in three protected areas [Área de Preservação Ambiental Serra da Mantiqueira (APA Mantiqueira), Parque Estadual de Campos do Jordão and Parque Nacional de Itatiaia] we suggest to maintain it as Endangered due to: the effectiveness of APAs in protecting the species is doubtful, the Parque Estadual de Campos do Jordão have considerable areas with exotic species, and both it and Parque Nacional do Itatiaia have considerable areas with habitats not suitable to *S. bradei* (such as outcrops and highland grassfields). Although *S. bradei* is known to grow on secondary fragments and in a wide elevation range, threats to it are clear, considering that the southern Mantiqueira range, where most collections are from, is situated between the two main urban centers in Brazil and has become a tourism hub. In addition, over the past few decades the montane forests and the highland fields of Mantiqueira have been increasingly converted to pastures, monocultures or urban centers.

Discussion. *Solanum bradei* is the most widely distributed and morphologically variable species of the *Solanum inornatum* species group. It is the only species of the group not necessarily associated with well-preserved sites, although always found in shaded environments, and is also the one that has the broadest elevational range. Despite the usual shrubby, robust habit of the species, specimens as small as 20–25 cm tall were found flowering, these mainly from the municipalities of Camanducaia and Gonçalves, in southern Minas Gerais State. The species has distinctive geminate sympodia,

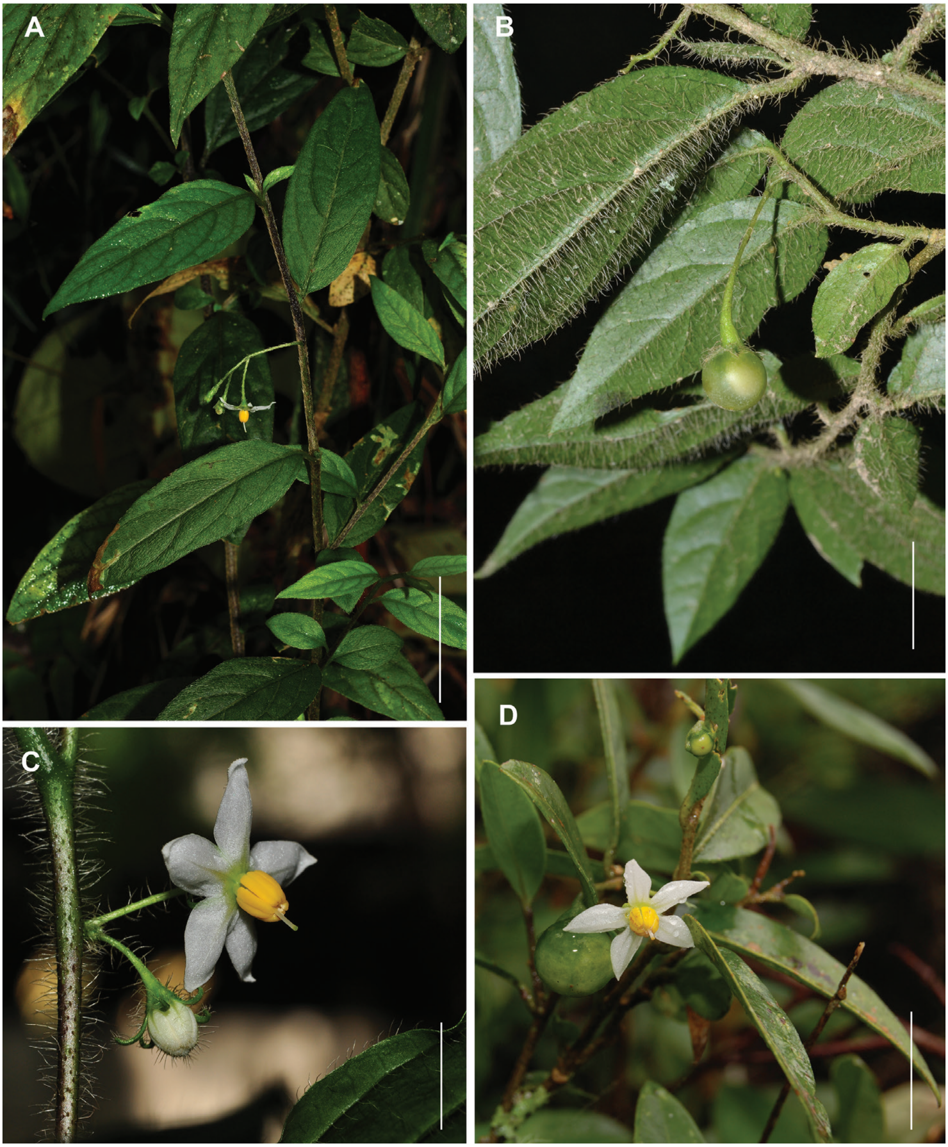

Figure 2. Photographs of the species in the field. **A–B** *Solanum bradei* Giacomin & Stehmann **A** Shoot showing the anisophyllous sympodia and lateral emergence of the inflorescence [from *Hattori et al. 914* (BHCB)] **B** Translucent fruit [from *Agra et al. 7398* (BHCB, JPB)] **C** Inflorescence of *S. friburgense* Giacomin & Stehmann in cultivation showing its hispid indumentum [from *Giacomin 940* (BHCB)] **D** Inflorescence of *S. kriegeri* Giacomin & Stehmann [from *Giacomin et al.* 770 (BHCB); photo by F.D. Gontijo] . Scale bars **A**= 2 cm; **B–D**= 1 cm.

with leaves differing in shape and size to a degree not observed in any other species of the group. Although this character was observed in all specimens in the field, some branches preserved on herbarium sheets do not retain well-developed minor leaves.

Due to this, anisophylly was not used as a diagnostic character to separate the species, but it is certainly a useful character in the field.

Some plants seem to develop diseased flowers, possibly the result of fungal or viral infection, as has been previously reported in other species of *Solanum* (see Hernández and Hennen 2003). In these cases an unusual form of calyx growth is observed where the expanded calyx covers the entire flower, making it resemble a fruit. This has resulted in misleading annotations on some labels [e.g. *Polisel et al. 228* (SPSF) has "Fruto imaturo verde" written on the label but the specimen is actually flowering]. When dissected, the diseased flowers show an opened and lobed corolla, retained in the expanded calyx, and purplish blue anthers (in dried material) that produce less pollen than normal. These putatively infertile flowers are more common in young plants from disturbed areas.

Solanum bradei can be easily distinguished from *S. inornatum* by its tiny deltate calyx lobes (1–2 mm long) that are not accrescent in fruit and its long-pedunculate inflorescence (peduncles up to 1 cm). *Solanum inornatum* has linear, 3–5 mm long calyx lobes and inflorescences with peduncles 1–4 mm long. The characters that separate it from the other species described in this paper are discussed further below, on each species discussion.

In the past, sheets of *S. bradei* have been determined as *S. apiahyense* Witasek by various *Solanum* taxonomists, another poorly known species of uncertain affinities from secondary formations in São Paulo, Paraná and Santa Catarina states. More recently, *S. apiahyense* was found to be closely related to *S. trachytrichium* Bitter, a species previously assigned to the Geminata clade (Knapp 2002b, L.L. Giacomin in prep.). Among species that could be confused with members of *S. inornatum* group and that are not considered part of the Brevantherum clade, these two (*S. apiahyense* and *S. trachytrichium*) are the only ones that we judge should be mentioned here. They can be distinguished from all species of the *S. inornatum* group by having inflorescences with fruiting peduncle longer than 1 cm and pedicels apically expanded with a constriction at the receptacle. The pubescence of the species are also distinctive: while *S. apiahyense* has very long, multicellular (up to 7 cells) unbranched trichomes, *S. trachytrichium* has unicellular trichomes that are hooked on a mound-like base, giving the leaves an scabrous aspect, rough to the touch (Knapp 2002b).

Specimens examined. BRAZIL. **Minas Gerais**: **Mun. Camanducaia**. Próximo a Gonçalves, Na mata do Sr. Altair, 1900 m, 23 Oct 2001 (fl), *J.R. Stehmann & I.B. Castro 3022* (BHCB, RB); Mun. Camanducaia. Divisa com Gonçalves, Próximo a Pedra de São Domingos, 1727 m, 22°42'27.1"S, 45°56'1.39"W, 12 Mar 2003 (fl, fr), *J.R. Stehmann & G.S. França 3415* (BHCB); same locality, 12 Mar 2003 (fl, fr), *J.R. Stehmann & G.S. França 3416* (BHCB); same locality 12 Mar 2003 (fl, fr), *J.R. Stehmann & G.S. França 3417* (BHCB). **Mun. Delfim Moreira**. Margens da estrada que liga Delfim Moreira a Campos do Jordão, 1781 m, 22°34'40.84"S, 45°15'49.07"W, 1 Nov 2008 (fl), *L.L. Giacomin et al. 319* (BHCB); same locality, 1673 m, 22°35'40.93"S, 45°19'19.81"W, 1 Nov 2008 (fl), *L.L. Giacomin et al. 346* (BHCB); Fazenda da Onça (área mantida pelo Exército Brasileiro), próximo ao pórtico de entrada da fazenda, 1674

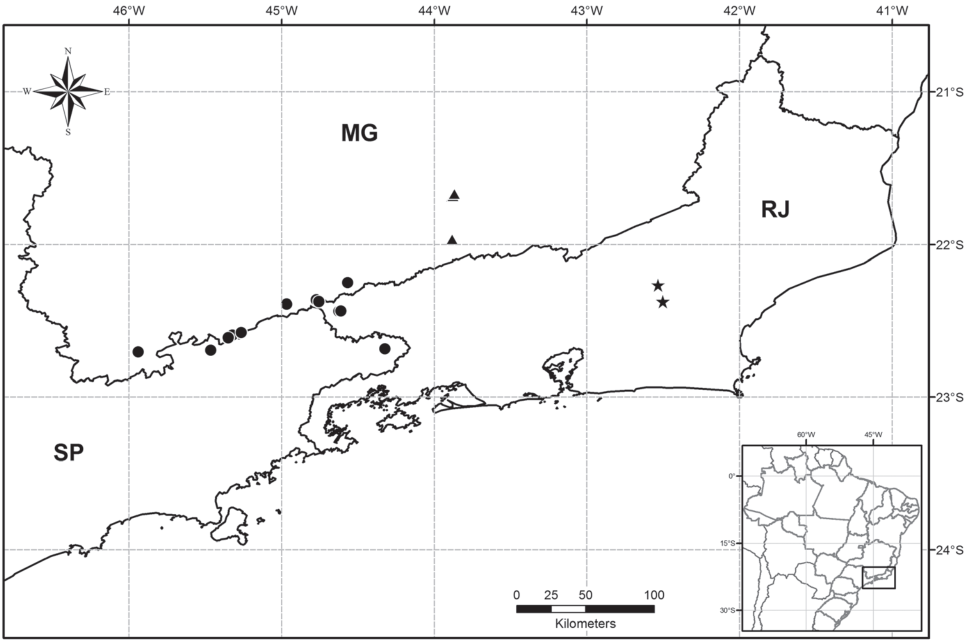

Figure 3. Known distribution of *Solanum bradei* Giacomin & Stehmann (circles), *S. friburgense* Giacomin & Stehmann (stars) and *S. kriegeri* Giacomin & Stehmann (triangles) in the states of Minas Gerais (**MG**), Rio de Janeiro (**RJ**) and São Paulo (**SP**) in southeastern Brazil.

m, 22°36'41"S, 45°20'56"W, 15 Mar 2011 (fl), *L.L. Giacomin et al. 1372* (BHCB). **Mun. Gonçalves.** Às margens da estrada de terra que liga Gonçalves a BR-381, Próximo a mata do Altair, 1786 m, 22°42'15.33"S, 45°56'20.16"W, 13 Jul 2008 (bs), *L.L. Giacomin & J.R. Stehmann 180* (BHCB); same locality, 1786 m, 22°42'13,57"S, 45°56'18,59"W, 28 Oct 2008 (fl), *L.L. Giacomin et al. 257* (BHCB). **Mun. Itamonte.** [close to] Parque Nacional de Itatiaia, Outskirts of park on road toward Agulhas Negras, 1728 m, 22°22'25", 44°45'17", 6 May 2011 (fr), *M.F. Agra et al. 7398* (BHCB, JPB); Margens da BR-354, 1558 m, 22°21'47.10"S, 44°46'23.05"W, 12 Jul 2008 (fl), *L.L. Giacomin & J.R. Stehmann 171* (BHCB); same locality, 1558 m, 22°21'45.17"S, 44°46'21.52"W, 5 Nov 2008 (fl), *L.L. Giacomin et al. 372* (BHCB); Margens da rodovia não pavimentada que leva para o Pico das Agulhas Negras e parte alta do Parque Nacional do Itatiaia (BR-485); ca. 1 km após a entrada, 1711 m, 22°22'24"S, 44°45'19"W, 20 Nov 2013 (fl), *L.L. Giacomin et al. 2028* (BHCB, BM, UT); Estrada para Rio de Janeiro, 1576 m, 22°21'49.13"S, 44°46'26.67"W, 22 Nov 2006 (fl, fr), *J.R. Stehmann et al. 4503* (BHCB; ESA). **Mun. Passa Quatro**. Serra da Mantiqueira, Fazenda São Bento, 1700 m, Nov 1948 (bs, fr), *J. Vidal s.n.* (R 209896). **Rio de Janeiro**: **Mun. Itatiaia**. Maromba, Arbusto nas pedras, 3 Feb 1945 (fl), *A.C. Brade 17391* (BHCB, RB); Caminho Rio Bonito, 2 Feb 1948 (fl, fr), *A.C. Brade 18802* (RB); Parque Nacional do Itatiaia, Trilha do Hotel Simon para o Três Picos, 1500 m, 22°15'S, 44°34'W, 23 Nov 1994 (fl), *J.M.A. Braga 1629* (RB); Parque Nacional do

Itatiaia, próximo a cachoeira da Maromba, 1186 m, 22°26'10.43"S, 44°37'29.14"W, 3 Nov 2008 (fl, fr), *L.L. Giacomin et al. 357* (BHCB); Parque Nacional do Itatiaia, Trilha do Hotel Simon para o Três Picos, 1087 m, 22°26'7.5"S, 44°36'38.14"W, 3 Nov 2008 (fl), *L.L. Giacomin et al. 361* (BHCB); Parque Nacional do Itatiaia, Trilha do Véu da Noiva, 1163 m, 22°26'4"S, 44°37'24"W, 16 Oct 2009 (fl), *E.K.O. Hattori et al. 914* (BHCB); Parque Nacional do Itatiaia, Trilha para o Rebouças, 16 Oct 2009 (fl), *E.K.O. Hattori et al.* 927 (BHCB). **São Paulo**: **Mun. Bananal.** Serra da Bocaina, Sertão do Rio Vermelho, 1200 m, 6 Oct 1949 (fl), *A.C. Brade & A.Duarte 20106* (RB). **Mun. Campos do Jordão.** Parque Estadual de Campos do Jordão, Trilha da cachoeira, 22°41'30"S, 45°27'52"W, 27 Apr 2007 (bs, fl), *R.T. Polisel et al. 228* (SPSF).

Solanum friburgense Giacomin & Stehmann, sp. nov.

urn:lsid:ipni.org:names:77139689-1
http://species-id.net/wiki/Solanum_friburgense
Figs 2C, 4

Diagnosis. Differs from *S. inornatum* Witasek in its elliptic leaves with attenuate bases and cuspidate apices, its leaf pubescence of upright spreading trichomes denser along the veins, its 2-foliate sympodial units, and its strongly recurved calyx lobes at anthesis. Also differs from *S. bradei* Giacomin & Stehmann by its conspicuous, linear-lanceolate calyx lobes.

Type. BRAZIL. Rio de Janeiro: Mun. Nova Friburgo. Reserva Ecológica de Macaé de Cima, trilha para o Vale dos xaxins. 27 Oct 1990 (fl), *A. Amorim, B.C. Kurtz & L. Sylvestre 276* (holotype: RB [RB–00413518]; isotype: BHCB).

Description. Herbs to shrubs, woody at base, few-branched, rhizomatous, up to 50 cm high, the branches on new growth ascending, becoming prostrate. Stems densely hispid-pubescent with uniseriate simple upright, spreading trichomes ca. 2.6 mm long, with up to 3 cells. Bark of older stems becoming light brown, glabrescent; new growth greenish brown, shiny. Sympodial units 2–foliate, not geminate. Leaves simple, solitary, the blades 3–11 × 1–5 cm, elliptic, chartaceous, slightly discolorous, drying darker above, not shiny, sparsely pubescent on both surfaces with simple trichomes like those of the stems, the trichomes denser along the veins (of any order); base attenuate, slightly decurrent onto the petiole; margins entire, ciliate, with spreading trichomes like those of the blade; apex acute to acuminate; petioles 6–12 mm long, with as pubescence like that of the stems; venation brochidodromous; midrib and secondary veins visible to the naked eye, prominent on both surfaces. Inflorescences sessile, lateral, unbranched cymes of 1–4 flowers; pedicels 4–12 mm long in flower, unknown in fruit, nearly contiguous. Calyx 3–5 mm long, deeply lobed, the tube ca. 1 mm long, the lobes 3–4 mm long, ca. 1mm wide, linear-lanceolate, densely pubescent abaxially with trichomes like those of the stem, glabrous adaxially, strongly recurved at anthesis. Corolla 1.4–1.8 cm in diameter, white, stellate, membranaceous, the lobes 5–7 × 2–3 mm, ovate-lanceolate, sparsely pubescent abaxially mainly along the midrib with trichomes like those of the calyx but shorter, up

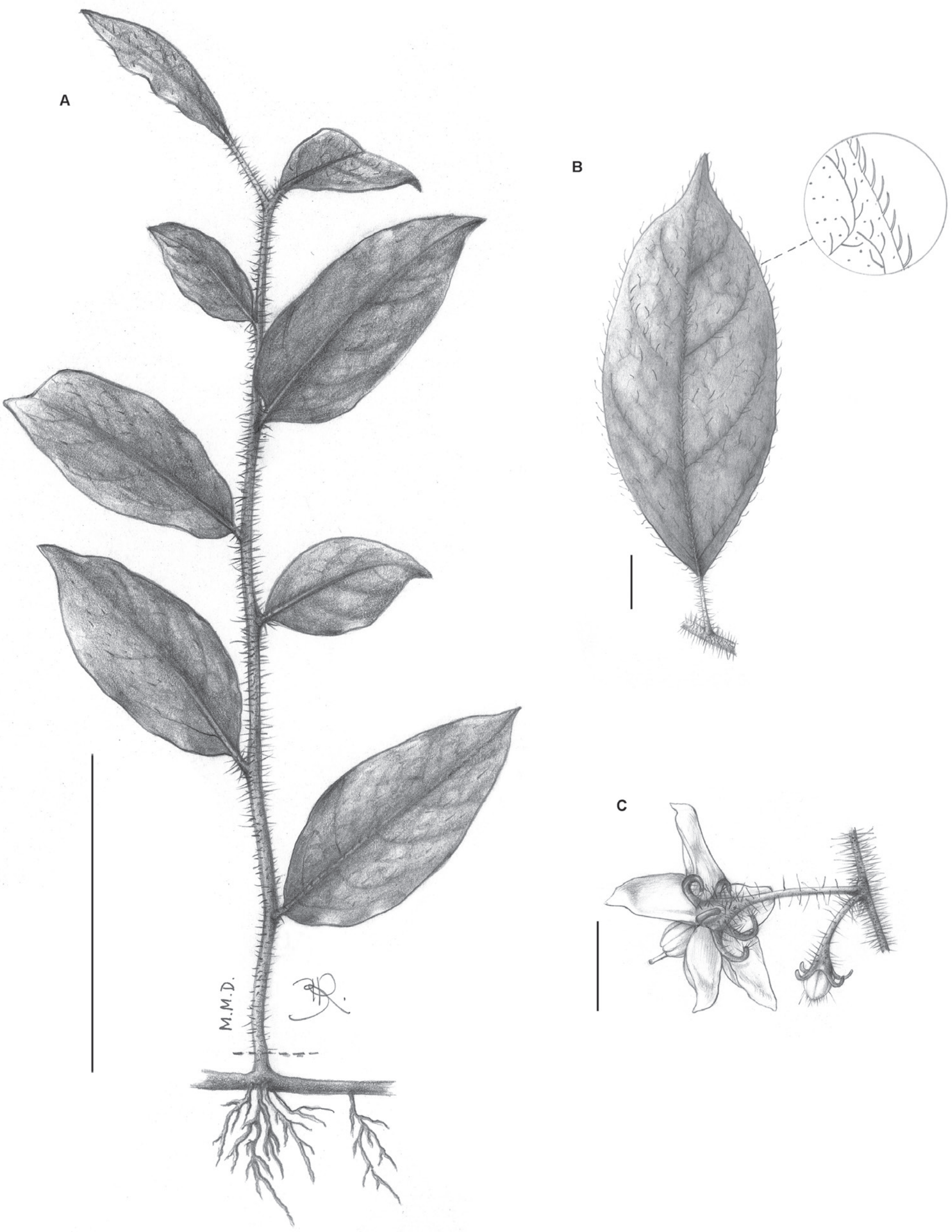

Figure 4. *Solanum friburgense* Giacomin & Stehmann. **A** Rhizomatous habit **B** Detail of the typical leaf shape and indumentum **C** Inflorescence detail, showing the diagnostic recurved calyx at anthesis. All from *Giacomin 940* (BHCB). Scale bars **A**= 10 cm; **B** = 1 cm; **C** = 5 mm. Drawings by M.M. Duarte and B. Raddichi.

to 1.5 mm long, glabrous adaxially. Stamens 3–5 mm long, equal in length, the filaments ca. 1 mm long; anthers 2–4 mm long, ca. 1 mm wide, oblong, slightly connivent, yellow, the base cordate, the apex emarginate and poricidal, the subapical pores directed introrsely, not opening into longitudinal slits. Ovary glabrous; style white, 4–5 mm long, straight, cylindrical, the stigma light green, capitate. Fruit unknown.

Distribution. Narrowly endemic, known from only two localities in the municipality of Nova Friburgo in the state of Rio de Janeiro, Brazil (Fig. 3). Both localities are within conservation units, one public (Reserva Ecológica de Macaé de Cima) and one private (RPPN Bacchus).

Ecology. Rare in the understory of well-preserved fragments of the Brazilian Atlantic coastal rainforest, at elevations of about 1,500 m. The species always shows a well-developed rhizome system. This suggests the plant invests heavily in vegetative propagation, which is consistent with the few flowering specimens found in the field. In cultivation, so few flowers were produced that no crossing studies were performed.

Phenology. The flowering material studied was collected in October and November but one of these is from cultivation. The fruits are unknown.

Etymology. The species is named after the municipality where all known collections are from, Nova Friburgo, in the state of Rio de Janeiro.

Preliminary conservation status (IUCN, 2013). Critically Endangered (CR) B1; B2 ab (iii, iv). *Solanum friburgense* is known from two localities closely situated to each other within the same municipality, that represents an AOO of 8 km^2. The type specimen was collected in 1990 and despite an intensive inventory that was recently carried out in the area (Lima and Guedes-Bruni 1997), no additional collections were made until 2009. Although the EOO could not be calculated because only two points are available, if the species is actually endemic to Nova Friburgo and surroundings it would probably fit the Critically Endangered category (less than 100 km^2). Even considering the occurrence within two conservation units and the paucity of material available for analysis, we provisionally suggest it to be assessed as Critically Endangered, regarding it seems to have a reproductive system based on vegetative propagation (see Discussion below). Within RPPN Bacchus two large populations are known (about 50 individuals), but no flowering specimens were observed in the field over three consecutive years (2009, 2010 and 2011).

Discussion. *Solanum friburgense* is the only species of the *S. inornatum* group that has 2-foliate non-geminate sympodial units. It shares the linear-lanceolate calyx lobes with *S. inornatum* but can be distinguished from it by having the calyx lobes strongly recurved at anthesis, and the leaf pubescence concentrated along the veins and only sparsely present on the mesophyll of the leaf lamina, while *S. inornatum* has straight to slightly curved calyx lobes and trichomes evenly distributed on veins and mesophyll. The leaf shape is also a good character to separate the species: *S. friburgense* has elliptic leaves with attenuate bases and cuspidate apices and *S. inornatum* ovate leaves with rounded bases and attenuate apices. *Solanum friburgense* can be readily distinguished from *S. bradei* in its conspicuous linear-lanceolate calyx lobes versus tiny deltate calyx lobes of the former.

As for all species of the *S. inornatum* group, *S. friburgense* has very discrete and almost hidden inflorescences, that are covered by the leaves if seen from above. This cryptic flowering could be the reason why the oldest known collection of the species is very recent, from the 1990s.

The species has an intriguing reproductive system, apparently based mainly on vegetative propagation. Although two large populations were found at RPPN Bacchus, no flowering specimens were seen in three consecutive years of field work encompassing almost three months of the rainy season, when the two only flowering specimens were collected. No fruit was seen in the field or produced in cultivation, and we believe that the few known specimens are the result of a very restricted distribution and not a lack of collecting effort. *Solanum friburgense* inhabits the understory of primary cloud forest fragments, which are not uncommon in the mountain ranges surrounding Nova Friburgo, suggesting that its restricted distribution is due to its vegetative reproductive strategy and not habitat specificity. Future efforts should be made to locate this species at nearby reserves in Rio de Janeiro state such as Parque Estadual dos Três Picos, in Nova Friburgo and Parque Nacional da Serra dos Orgãos, in Teresópolis, in order to search for additional populations.

Specimens examined. BRASIL. Rio de Janeiro: Mun. Nova Friburgo. Macaé de Cima, Sítio do Srs. David e Isabel Muller, Trilha que leva para topo da serra, passando pela antena; espécime floresceu em casa de vegetação na Fundação Zoo-Botânica de Belo Horizonte, 1577 m, 22°22'24.64", 42°30'17.5", 20 Oct 2009 (fl), *L.L. Giacomin 940* (BHCB); RPPN Bacchus, Macaé da Cima, owned by David and Isabel Miller, Trilha do Telefone, 1555 m, 22°22'27"S, 42°30'04"W, 29 Apr 2010 (veg), *M.F. Agra et al. 7293* (BHCB, JPB).

Solanum kriegeri **Giacomin & Stehmann, sp. nov.**

urn:lsid:ipni.org:names:77139691-1
http://species-id.net/wiki/Solanum_kriegeri
Figs 2D, 5

Diagnosis. Differs from *S. bradei* Giacomin & Stehmann in its small shrub-like habit, its shiny leaves with extremely sparse pubescence, its sessile to subsessile inflorescences sometimes with a very short peduncle of up to 2 mm, and by its larger opaque fruit with more numerous seeds. Also differs from *S. inornatum* Witasek by having deltate, up to 2 mm calyx lobes.

Type. BRAZIL. Minas Gerais: Parque Estadual da Serra do Ibitipoca, Proximidades da Lombada, 1650 m, 21°41'S, 43°53'W, 20 Jan 2005 (fl, fr), *R.C. Forzza, L.C. Assis, L.M. Bezerra, M.F. Calió & L.G. Temponi 3959* (holotype: RB; isotypes: BHCB, BM).

Description. Herbs to small shrubs up to 50 cm tall, woody at base, often with a single stem or few branches, these primarily erect, ascending, becoming arched and pendant. Stems sparsely to moderately pubescent with simple uniseriate trichomes up to 1 mm long, with 2–3 cells, normally curved and antrorse, rarely spreading, sometimes geniculate. Bark of older stems becoming whitish, exfoliating, almost completely glabrous, that of new growth greenish brown. Sympodial units plurifoliate, normally not geminate, but if so, with leaves differing in size and shape. Leaves simple, 1.5–7 × 0.5–2 cm, narrowly elliptic, chartaceous to slightly coriaceous, concolorous, drying notably shiny on both surfaces, glabrous to glabrescent on both surfaces with sparse simple trichomes up to 0.6 mm long, with up to 2 cells, these most common along the midrib; base attenuate, not decurrent onto petiole; margins entire, sparsely ciliate, with trichomes like those of the leaf veins, lying antrorsely parallel to the margin; apex acute; petioles 2–5 mm long, with pubescence similar to the stems; minor leaves, if present, 0.4–1.2 × 0.3–0.6 cm, elliptic-ovate to circular, the base rounded to obtuse, the apex rounded to acuminate, the petioles absent to 2 mm long; venation brochidodromous; midribs and secondary veins visible to the naked eye, the midrib prominent on both blade surfaces, the secondary veins prominent abaxially and impressed adaxially. Inflorescences sessile to subsessile, lateral or subopposite the leaves, unbranched cymes with 1–6 flowers, the axis with the same pubescence as that of the stems; peduncle 1–2 mm long; rachis normally absent or rarely up to 6 mm long; pedicels 4–6 mm long in flower, 6–12 mm in fruit, articulated at the base, spaced up to 2 mm apart. Calyx to 5 mm long, the lobes 1–2 mm long in flower, up to 4 mm long in fruit, ca. 1 mm wide, deltate, glabrous to glabrescent abaxially, with trichomes if present like those of the stems, adaxially densely pubescent with capitate glandular trichomes less than 1 mm long, with single-celled stalks and a multicellular head; calyx not accrescent in fruit. Corolla 6–10 mm in diameter, white, stellate, membranaceous, the lobes 3–5 × 2–3 mm, ovate-lanceolate, glabrous on both surfaces. Stamens 2–3 mm long, equal in length, the filaments ca. 1mm long; anthers 1–2 mm long, ca. 1mm wide, oblong, slightly connivent, yellow, the base rounded, the apex emarginate and poricidal, the subapical pores directed introrsely, not opening into longitudinal slits. Ovary glabrous; style white, 3–5 mm long, straight, cylindrical, the stigma light yellow to greenish, capitate. Fruit a globose berry 6–12 mm in diameter, dull green when ripe, drying dark, glabrous. Seeds 6–12 per fruit, 3–5 × 2–3 mm, slightly swollen, reniform, with a small hollow at hilum region; the seed surface undulate, the margins flattened.

Distribution. Endemic to Brazil in southern Minas Gerais state, close to the border with Rio de Janeiro State, where it is known from two adjacent mountain ranges within the Mantiqueira region, Serra do Ibitipoca and Serra Negra (Fig. 3). All known collections are from two conservation units, APA Serra da Mantiqueira and Parque Estadual do Ibitipoca.

Ecology. Occasional to rare in the understory of well preserved dwarf cloud forests (*Floresta Ombrófila Densa Altomontana*; Veloso et al. 1991) and normally associated with sandy soils or quartzite outcrops, in elevations of about 1,500 to 1,900 meters above sea level. Although few flowers were produced in cultivation, crossing studies suggested this species is self-incompatible, like *S. bradei.*

Phenology. Fertile specimens were collected between September and March. A flowering peak was observed between November and January and fully developed fruits were observed in January and March.

Etymology. The epithet honors the Father Leopoldo Krieger, a Brazilian naturalist and founder of the CESJ herbarium (Juiz de Fora, Brazil), one of the most important collections in Minas Gerais state. In 1969, Dr. Krieger was hired as a Professor at Univer-

Figure 5. *Solanum kriegeri* Giacomin & Stehmann. **A** Habit with detail of the typical indumentum **B** Subsessile inflorescence detail showing the very short peduncle **C** Corolla cross section showing stamens **D** Fruit with small calyx lobes **E** Seed. All from *Giacomin et al. 770* (BHCB). Scale bars **A**= 10 cm; **B** and **D** = 1 cm; **C** = 5 mm; **E** = 2 mm. Drawings by B. Raddichi.

sidade Federal de Juiz de Fora, when he started collecting in the surrounding areas. His efforts at Serra do Ibitipoca led to the first collections of *S. kriegeri*. In herbarium sheets and in most databases, is common to find Krieger's collections wrongly cited as "P.L. Krieger"; the "P" corresponds to the Portuguese word for Father (*Padre*) and not to a forename. Nevertheless we decided here to maintain the orthography used on individual labels in the cited material, noting with square brackets the common misuse of the "P.".

Preliminary conservation status (IUCN, 2013). Endangered (EN) B2 ab (iii, iv). The species is known from two localities that are about 30 km away from each other with six points available. The calculated EOO was of 34.3 km^2 what would led to the Critically Endangered category while the AOO of 20 km^2 led to Endangered. We have chosen here to assign it to Endangered, a less severe category for three reasons: the species occurs in more than one location, it is known from within a effectively protected area (Parque Estadual do Ibitipoca), and the other location where it is found is somewhat remote. Nevertheless, *Solanum kriegeri* is from a very specific habitat in well-preserved forest fragments and monitoring its populations is strongly recommended. In light of the deforestation pressure surrounding the areas where it is found, we surmise that it might be restricted to its few known localities.

Discussion. *Solanum kriegeri* is most similar to *S. bradei*; both have small, deltate calyx lobes (1–2 mm long). It is, however, a much smaller plant than *S. bradei* with glabrous or glabrescent leaves, with sparse trichomes normally restricted to the midrib and a sessile to subsessile inflorescence. *Solanum kriegeri* occasionally has geminate leaves, but not as frequently as in *S. bradei* and, when present, the minor leaves are very reduced and look like stipules. The fruits of *S. kriegeri* are also distinctive; they are larger than those of *S. bradei* (6–12 versus 4–7.8 mm) due to the seed size and number (6–12 versus 2–4 seeds per fruit respectively). Another good field character is the fruit aspect at maturity: dull green in *S. kriegeri* and shiny, and translucent (watery) in *S. bradei.* Besides the calyx morphology *S. kriegeri* can be readily distinguished from *S. inornatum* and *S. friburgense* by the glabrescent indument of its shiny chartaceous leaves, the only species of the group that presents such feature.

Solanum kriegeri inhabits a very specific vegetation type and was thought to be endemic to Serra do Ibitipoca until recently when it was found in a neighboring mountain range. It is associated with dwarf cloud forests that grow as islands in highland grassy areas on sandy soils, normally within quartzite matrices. These formations are normally not as shaded as the habitats in which other species of the group are found, and although the soil is more well-drained, the atmospheric humidity is quite similar. It is common to find *S. kriegeri* growing in *Sphagnum* L. (Sphagnaceae) mats in these environments.

Specimens examined. BRAZIL. Minas Gerais: Mun. Lima Duarte. Parque Estadual do Ibitipoca, Lombada, 8 Mar 2006 (fl, fr), *F.M. Ferreira et al. 1009* (CESJ); Parque Estadual da Serra do Ibitipoca, Mata próxima a Lagoa Seca, 1870 m, 21°40'S, 43°52'W, 24 Nov 2004 (fl), *R.C. Forzza et al. 3710* (RB); Parque Estadual do Ibitipoca, Mata e campo ao lado do alojamento, 21 Nov 2006 (fl, fr), *R.C. Forzza et al. 4322* (RB; BHCB); Conceição de Ibitipoca, Parque Florestal Estadual de Ibitipoca, Na mata, 29 Nov 1970 (fl), *[P.]L. Krieger & C.C. Urbano 9355* (CESJ, RB); Serra de Ibitipoca, perto de mata de galeria, 1500 m, 2 Nov 1973 (fl), *L. Krieger 13179* (CESJ); Parque Estadual do Ibitipoca, Na trilha de subida para a Lombada, 1623 m, 21°41'1"S, 43°52'24"W, 17 Mar 2009 (fl, fr), *L.L. Giacomin et al. 770* (BHCB); Parque Estadual do Ibitipoca, Mata nebular entre Lombada e Lagoa Seca, 1650 m, 21°40'57"S, 43°52'34"W, 27 Oct 2004 (fl), *B.R. Silva et al. 1369* (RB); Parque Estadual do Ibitipoca, Mata pluvial montana, 12 Nov 1987 (fl), *H.C. Sousa s.n.* (BHCB 14650; RB). **Mun. Rio Preto**. Serra Negra, Burro de Ouro, 1525 m, 21°58'09"S, 43°53'13"W, 17 Oct 2011 (fl), *L.L. Giacomin et al. 1642* (BHCB, BM, RB, UT); Serra Negra, Fragmento de floresta ombrófila altomontana anexa ao Pico das Três Divisas, 1601 m, 21°57'54"S, 43°52'57"W, 17 Oct 2011 (fl), *L.L. Giacomin et al. 1643* (BHCB, BM, UT).

Key to the species of the *Solanum inornatum* group

1 Herbs to shrubs, up to 1.8 m; stems glabrescent to densely pubescent, if pubescent most of the trichomes antrorse or apressed; calyx lobes deltate, up to 2 mm long, not accrescent in fruit **2**

– Herbs to small shrubs, up to 50 cm; stems hirsute, the trichomes spreading to patent (sometimes hispid) or unordered (pointing in several directions, never completely antrorse); calyx lobes linear-lanceolate, 3-5 mm long, accrescent in fruit **3**

2 Leaves matte when dried, conspicuously pubescent; inflorescences always pedunculate, peduncles 2.2–10 mm long; abaxial calyx surface conspicuously pubescent; fruits translucent green at maturity, 4–7.8 mm in diameter .... ***S. bradei*** **Giacomin & Stehmann**

– Leaves shiny when dried, glabrescent, with sparse trichomes mainly along midrib; inflorescences sessile to subsessile, with peduncles up to 2 mm long; abaxial calyx surface glabrescent; fruits dull green at maturity, 6–12 mm in diameter .... ***S. kriegeri*** **Giacomin & Stehmann**

3 Sympodial units 2-foliate; leaves elliptic with attenuate bases and cuspidate apices; leaves with trichomes concentrated on veins of any order; calyx lobes strongly recurved at anthesis .... ***S. friburgense*** **Giacomin & Stehmann**

– Sympodial units 3-plurifoliate; leaves ovate-elliptic with rounded to subcordate bases and attenuate apices; trichomes evenly distributed on veins and mesophyll; calyx lobes straight, not strongly recurved at anthesis .... ***S. inornatum*** **Witasek**

Acknowledgments

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A new species of *Cissampelos* (Menispermaceae) from Bolivia and Paraguay

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Abstract

The new species *Cissampelos arenicola* M. Nee & R. Ortiz, from the Bolivian and Paraguayan Chaco is described, its affinities are discussed, and its preliminary conservation status is evaluated. The species is at present known from 13 collections from sand dunes or dry forests. *Cissampelos arenicola* is distinguished from all other American species in the genus by its ovate- to subreniform-trilobed leaves, 8-locular synandria, and relatively large, and scarcely ornamented endocarps. The most common perianth condition in the pistillate flowers of *Cissampelos* is one sepal and one antesepalous petal, and while these may vary in number, they are always found adaxial to the carpel, and although the southern African taxon called *Cissampelos capensis*, whose generic position is uncertain, superficially resembles *Cissampelos arenicola*, its sepals and petals are consistently lateral to the carpel and not adaxial.

Keywords

Bolivia, *Cissampelos*, conservation status, IUCN, Menispermaceae, Paraguay, sand dunes

Introduction

The pantropical genus *Cissampelos* L., together with African *Antizoma* Miers and the mostly Asian *Cyclea* Arn. ex Wight, were placed in subtribe Cissampelinae, one of the three subtribes in tribe Menispermeae, which together with seven other tribes were recognized by Diels (1910) in the family Menispermaceae. In studies based on *ndhF*, *matK*, *trnL-F*, *ITS*, *rbcL*, and *atpB* sequence data, subtribe Cissampelinae has been consistently recovered as monophyletic (Ortiz et al. 2007, Wang et al. 2007, Hoot et al. 2009, Jacques et al. 2011, Wang et al. 2012), although relationships within the subtribe remain unresolved (Jacques et al. 2011). The sampled species of *Cissampelos* form a clade that is sister to *Cyclea* (Ortiz et al. 2007, Wang et al. 2012, Ortiz et al. in prep.), but studies including the southern African *Cissampelos capensis* L. f. recovered a polyphyletic *Cissampelos*, with *Cyclea* (Hoot et al. 2009, Jacques et al. 2011), and *Antizoma* (Jacques et al. 2011) nested within. While *Cissampelos capensis* is recognized in *Cissampelos* (Botha 1980), at times it has been placed in *Antizoma* (Diels 1910), which is characterized by a shrubby habit, a spur borne along the stem [abaxial to the petiole], pistillate flowers with two sepals on opposite sides of the carpel, and two antesepalous petals (Miers 1851). The most common perianth condition in the pistillate flowers of *Cissampelos* is one sepal and one antesepalous petal, occasionally, more than one sepal and petal are found in some of the species (Diels 1910). Based on the fact that some species of *Cissampelos* display variation in sepal and petal number, the shrubby *C. capensis* was removed from *Antizoma* and included in the genus *Cissampelos* (Botha 1980). However, commonly overlooked is that while the pistillate flowers of *Cissampelos* may show variation in the number of sepals and petals, these are consistently located facing the adaxial slit of the carpel (Fig. 1A). On the other hand, the sepals and the antesepalous petals of *Antizoma* are usually located at both sides of the adaxial slit of the carpel (i.e., on the lateral sides of the carpel) (Fig. 1B), or around the carpel when more than two sepals/petals are present. The pistillate flowers of *C. capensis* have not only two sepals and two antesepalous petals but these are located in a similar manner as in *Antizoma angustifolia* Miers ex Harv. and in *A. miersiana* Harv.

At present, the taxonomic status and phylogenetic affinities of *Cissampelos capensis* are unclear, similarly, the generic boundaries and relationships between *Cissampelos*, *Antizoma*, and *Cyclea* remain unresolved, and a re-assessment of all the genera in subtribe Cissampelinae is warranted, but is beyond the scope of this paper. Until further studies clarify the taxonomy and affinities of *Cissampelos capensis*, here it is still provisionally referred to as *Cissampelos* and we compare it to the new species *C. arenicola* as they both share superficial morphological resemblance in habit and foliage.

The last comprehensive revision of the genus *Cissampelos* recognized 20 species, nine of them distributed in the Americas, nine in Africa, one in Asia, and the pantropical *Cissampelos pareira* L. (Rhodes 1975). Species of *Cissampelos* are often found growing in open, disturbed habitats, and with a few exceptions, are morphologically variable, such that species limits are frequently difficult to discern. As new collections have accumulated since Rhodes's (1975) revision, it has become evident that a number of collections from similar habitats in Bolivia and adjacent Paraguay, are conspecific but differ from all other described American species of Menispermaceae. Still, placing this material generically has been challenging. Because of the general similarity in leaf shape with the North American *Cocculus carolinus* (L.) DC., the specimens were initially identified as belonging to *Cocculus* DC. However, the Old World- cen-

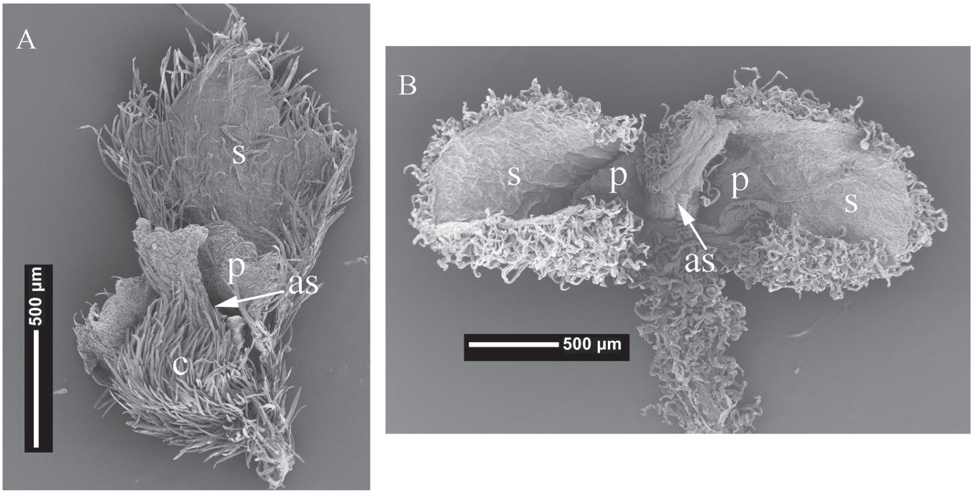

Figure 1. Pistillate flowers of **A** *Cissampelos arenicola* M. Nee & R. Ortiz, (*M. Nee 49044*, MO) **B** *Cissampelos capensis* L. f., (*S.L. Williams 295*, MO) showing locations of sepals and petals; s = sepal; p = petal; c = carpel; as = adaxial suture.

tered *Cocculus* (Diels 1910, Troupin 1962), has only a few species in temperate and subtropical North America and Mexico, but none in South America. Examination of the minute staminate flowers of these Bolivian and Paraguayan plants allowed for the specimens to be confidently placed in *Cissampelos*, and the new species is described here as *Cissampelos arenicola*.

Materials and methods

We studied all 13 herbarium collections of the new species housed at MO and at NY. Most of the collections have duplicates in several other herbaria but these were not available during this study. The specimens studied include male, female, and fruiting individuals, an infrequent situation in dioecious plants, such as Menispermaceae. Additionally, for comparison, we examined specimens for two other species that share some morphological similarities with the new species. These included: the Paleotropical *C. mucronata* A. Rich. (five specimens) and the southern African *C. capensis* (seven specimens). Measurements given in the species description refer to ranges of the mean values stemming from two to three replicate measurements of each structure and organ per individual voucher specimen. Before measuring, floral parts were first rehydrated, and endocarps were first boiled in water for a few minutes and the fleshy part of the fruit removed. Menispermaceae fruits develop asymmetrically so that the long axis do not necessary correspond with fruit length; endocarp measurement follow the convention of Ortiz (2012).

Taxonomy

Cissampelos arenicola M. Nee & R. Ortiz, sp. nov.

urn:lsid:ipni.org:names:77139692-1
http://species-id.net/wiki/Cissampelos_arenicola
Fig. 2

Diagnosis. *Cissampelos arenicola* is distinguished from the remaining American species by its small, ovate- to subreniform-trilobed leaves and by its (6)8(10)-locular synandria. Its small leaves and viny habit superficially resemble the southern African *Cissampelos capensis* but differs by its (6)8(10)-locular synandria (vs. 4) and by sepals and petals located adaxial to the ventral slit of the carpel. The (6)8(10)-locular synandria of *C. arenicola* resembles that of African *C. mucronata*, from which it differs by its smaller (0.8–3 × 1.3–4 cm vs. 3.3–4.3 × 4.5–6.6 cm) leaves and its larger endocarp (6 × 7 mm vs. 4.3 × 4.7 mm).

Type. BOLIVIA. Dpto. **Santa Cruz**. **Prov. Andrés Ibáñez**: along hwy from Santa Cruz to Abapó, 3 km S of crossing of railroad and 2 km S of bridge over Quebrada Peji, 17°58'00"S, 63°11'18"W, 450 m, 1 May 2001 (♂ fl), *M. Nee, S. Knapp & J. M. Mendoza 51717* (holotype USZ; isotypes LPB, MO-6393940, NY, and to be distributed to K).

Description. *Twining*, perennial; stems striate, the older ones woody and glabrous, the younger ones subherbaceous and sparsely silvery-pilose, unarmed, growing in tangled viny masses to at least 5 m high in shrubs and small trees, to 5 mm in diameter; plants dioecious or infrequently monoecious. *Leaves* spiral, ovate- to subreniform-trilobed, usually broader than long, 0.8–3 × 1.3–4 cm, leaves associated with the inflorescences usually much smaller, lateral lobes divergent, rounded at apex, terminal lobe rounded and apiculate to aristate at the apex, chartaceous to subcoriaceous, glaucous, sparsely silvery-sericeous on both surfaces to nearly glabrous, palmately 6-nerved, basifixed or subpeltate with petiole inserted to 0.1–0.4 mm from the margin; petiole 5–17 mm long, pulvinulate at both ends. *Staminate* inflorescences: dichasium or monochasium, 1-2 from axils on adult or young leaves along the main stem or on young leaves of secondary axillary branches, silvery-pilose, peduncle 1.3–4.9 mm long, main axis of monochasium 1.2–3.2 mm long, bracts linear, 0.4–1.5 mm long; staminate flowers 5–6(–17); pedicels 0.5–1.6 mm long; sepals 4–6, 1.0–1.5 × 0.7–1.2 mm, obovate, shortly connate at base, concave, slightly spreading at anthesis, light cream-colored throughout, silvery-pilose abaxially, glabrous adaxially; petals usually 1, patelliform to barely cupuliform, 0.9–1.1 mm in diameter, or less frequently 3–4 and obovate, 0.7 × 1.1 mm, free, light cream-colored throughout, sparsely silvery-pilose abaxially, glabrous adaxially; synandrium 0.1–0.2 mm high, (6–)8(–10)-locular, loculi connate, transversely dehiscent, and radiating from a peltiform connective; carpellode absent. *Pistillate* inflorescences: 3–5 flowers fasciculate in the axils of adult or young leaves, sparsely silvery-pilose; pistillate flowers with pedicels 1.3–1.8 mm long; sepals and petals adaxial to the carpel; sepal 1(2), 1.2–1.5 × 0.9–1.2 mm, obovate, light cream-colored throughout, moderate

The New York Botanical Garden
Plants of **BOLIVIA**

Menispermaceae *Cocculus*

Cissampelos sp nov...
Det. R. Ortiz (MO),2013

Depto. Santa Cruz, Prov. Ibáñez, grassy, sandy dune fields with patches of shrubs and low forest, grazed but still quite natural, along hwy. from Santa Cruz to Abapó, 3 km S of crossing of railroad and 2 km S of bridge over Quebrada Pejí. 17°58'S, 63°11'30'W. alt. 450 m.

18"

Twining in shrubs. Male; flowers yellow-green. This is the same area (but not the same plants collected by *Nee et al. 48487* of 27 Feb. 1998).

Coll.: M. Nee, S. Knapp & J. M. Mendoza F. 51717
1 May 2001

Figure 2. Isotype of *Cissampelos arenicola* M. Nee & R. Ortiz (*Nee et al. 51717*, MO).

silvery-pilose abaxially, less densely so adaxially; petals 1 (–3), subreniform, when 2 or 3, the petals free or partly to fully connate, opposite to the sepal, 0.7–0.9 × 0.9–1.4 mm, light cream-colored throughout, silvery-pilose abaxially, glabrous adaxially; sepal and petal soon deciduous, staminodes absent; carpel 1, gibbous, obliquely borne on pedicel, silvery-pilose, style 0.2–0.3 mm long, stigma 3–5-lobed, erect to spreading. *Drupe* globose, ca. 8 mm in diameter, glabrous, turning orange then red at maturity; mesocarp juicy; endocarp 6 × 7 mm, suborbicular-bilaterally compressed, with one tiny circular perforation on the lateral faces, ornamentation obscure, consisting of a very low medial ridge and obscurely transverse ridges (Fig. 3A); condyle bilaterally compressed, septiform (sensu Ortiz 2012).

Distribution and ecology. The species is at present known from southern Bolivia and northwestern Paraguay (Fig. 4). All Bolivian collections are from similar habitats of the sandy dune systems southwest of the city of Santa Cruz on the main highway which runs south to Abapó and on to Camiri and to Yacuiba on the Argentinian border. In Paraguay the species was collected along ruta Transchaco and also near the border with Bolivia in the proposed National Park Médanos del Chaco, where it has been found in seasonal forests and in dunes. In Bolivia there are extensive sandy savannas and large active dunes, the most well-known being the "Lomas de Arena" recreation area 15–20 km SSE of the center of Santa Cruz de la Sierra. The area where the species has been collected is on the western edge of this dune field. Plants were collected from 300–470 m elevation.

Pollination. No observations of pollinators are available, nor notes on any possible odor. The extremely small size of the flowers suggests that a very small insect must be involved in pollination. Label note of *Nee 51401*: "It is difficult to separate the sparse and inconspicuous flowering and immature fruiting material from the vegetative mass".

Phenology. Male flowers were collected in February, May, November, and in December, pistillate flowers and mature fruits in February, April, June, and in December.

Etymology. From the Latin, *arenicola*, dweller in sand, as the species seems to be restricted to sandy savanna soils and edges of dunes.

Preliminary conservation status. *Cissampelos arenicola* is at present known from 13 collections at nine localities from southern Bolivia and northwestern Paraguay. The sandy savannas in the area surrounding Santa Cruz de la Sierra are frequently burnt and heavily grazed by cattle. This appears to have little effect on the native vegetation, but development of the land for subdivisions and chicken ranches is a greater threat and is destroying much of the original vegetation. Although the Viru-Viru pampa surrounding the international airport north of the city of Santa Cruz is maintained as a natural savanna, *C. arenicola* has never been collected there. In Paraguay, *C. arenicola* has been collected in habitats described as seasonal forest, but also in areas with nomadic sand dunes. Thus, the "ephemeral" condition described on the labels may refer to its dynamic and transient habitat and not to the plant per se. Because of the fragmented and threatened habitat in Bolivia, its reported ephemeral condition of its habitat in Paraguay, and its usually small population sizes, *C. arenicola* may be considered as vulnerable.

Figure 3. Endocarp ornamentation of **A** *Cissampelos arenicola* M. Nee & R. Ortiz (*F. Mereles & R. Degen 5075*, MO) **B** *Cissampelos capensis* L. f., (*W. Giess et al. 5247*, MO) **C** *Cissampelos mucronata* A. Rich., (*Muller & Biegel* 2281 MO). Scale bars = 3 mm.

On the other hand, by applying the IUCN Red List Criteria (IUCN 2012), *C. arenicola* falls in the category of Endangered (EN) and meets the following criteria: A2c, as much as 50% decline of the population during the next 50 years inferred by the decline in habitat quality in the area of occupancy; B2c(ii,iii,iv), at present the area of occupancy is estimated as less than 500 km^2, moreover, there are likely to be extreme fluctuations in the area of occupancy because of its unstable habitat.

Paratypes. Bolivia. Santa Cruz: Prov. Andrés Ibáñez, along Quebrada Peji, vic. bridge of new hwy from Santa Cruz to Camiri and railroad bridge, 17°57'30"S, 63°11'00"W, 440 m, 11 Dec 1994 (imm & mat fr), *Nee 45861* (LPB, NY!, USZ); along hwy from Santa Cruz to Abapó, 3 km S of crossing of railroad and 2 km S of bridge over Quebrada Peji, 17°58'S, 63°11.3'W, 450 m, 27 Feb 1998 (♂ fl, imm fr), *Nee et al. 48487* (LPB, NY!, USZ); 15 Nov 2000 (♂ fl, imm fr), *Nee 51401* (NY); along hwy from Santa Cruz to Abapó, 5.4 km S of turnoff at "km 13", 17°55'S, 63°15'W, 470 m, 18 Apr 1998 (imm fr), *Nee 49044* (LPB, NY!, USZ); Prov. Cordillera, a 3–4 km al S de Puerto Guaraní, al norte de la frontera Paraguaya, sabanas planas, partes húmedas, 20°30'S, 62°15'W, 400 m, 19 Jun 1992 (♀ fl & mat fr), *Mostacedo et al. 385* (MO!, USZ). **Paraguay.** Alto Paraguay: Fortín Teniente Montania, seasonal forests and swamps on clay soils, 22°03'15"S, 59°57'14"W, 5 Feb 2002 (♂ fl), *Zardini & Guerrero 57845* (MO!). Boquerón: Ruta Transchaco, a partir del km 702, entre PN Tte. Enciso y PN Médanos del Chaco, ambiente ruderal, 20°36'19"S, 62°02'54"W, 22 Feb 2006 (♂ fl), *De Egea et al. 923* (FCQ, BM, CTES, G, MO!, PY, SI, UNR); proposed National Park Médanos del Chaco, ephemerals on dunes, 20°41'03"S, 61°57'37"W, 300 m, 12 Dec 1998 (♂ fl), *Zardini & Duarte 49600* (AS, MO!); (mat fr), *Zardini & Duarte 49630* (AS, MO!); 13 Dec 1998 (♀ fl & imm fr), *Zardini & Duarte 49829* (AS, MO!). Nueva Asunción: 5 km después del Destacamento, sobre vegetación, 19 Mayo 1993 (♂fl), *Degen & Mereles 2969* (MO!). Presidente Hayes: Tyto Villazón, Fortín Guaraní, en espatillar arenoso, [22°44'S, 59°30'W], 2 Feb 1993 (♀ fl & mat fr), *Mereles & Degen 5075* (FCQ, MO!).

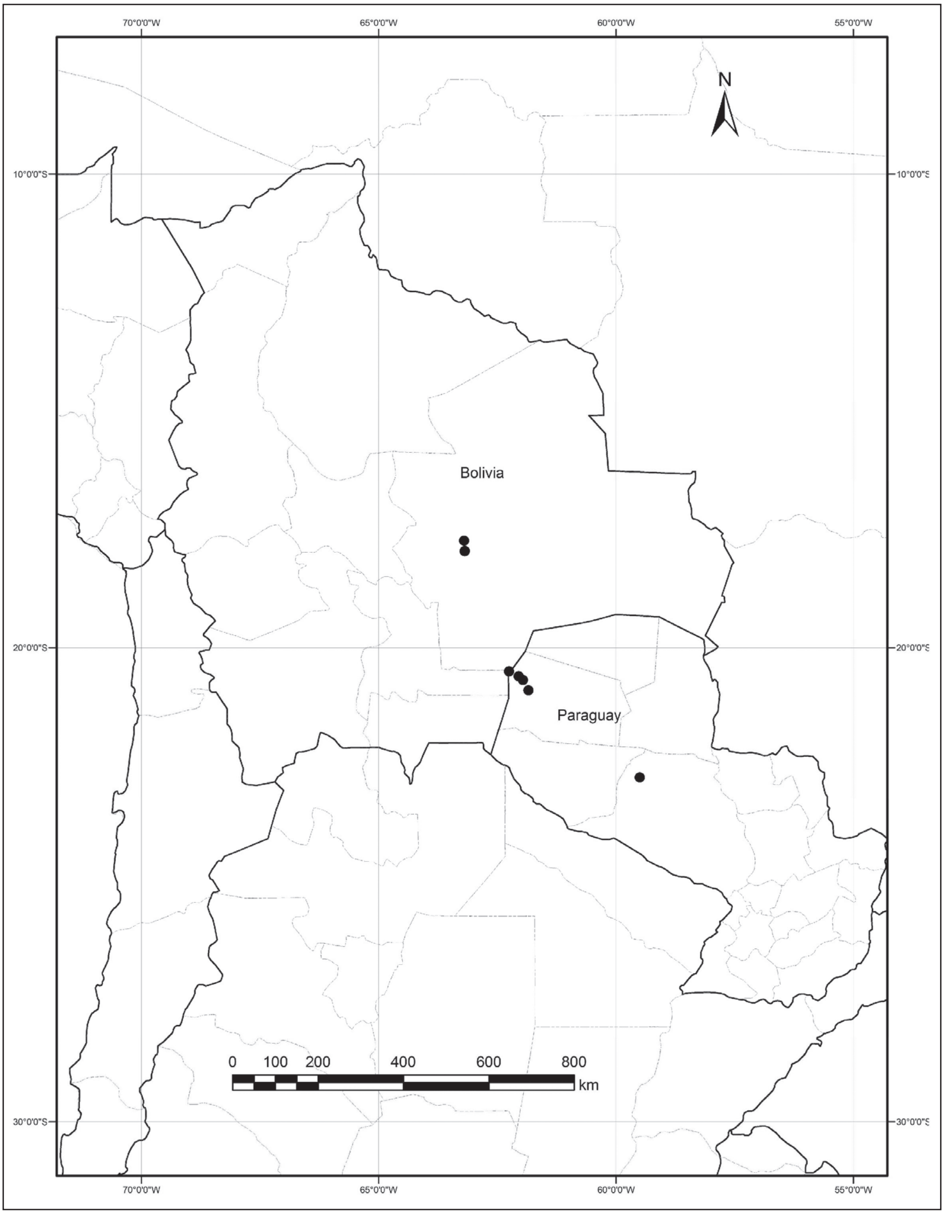

Figure 4. Distribution of *Cissampelos arenicola* M. Nee & R. Ortiz, based on examined collections with coordinates.

Discussion

Although, the phylogenetic relationships of *Cissampelos* and the other genera in the Cissampelinae are still unresolved, *Cissampelos* is the oldest name in the clade and will therefore stand any future generic reassessment. While *Cissampelos arenicola* has not yet been included in any DNA based studies and as a result its phylogenetic affinities are not known, and despite the fact that the sepals and petals are variable in number, they are consistently located on the adaxial side of the carpel, a feature that is shared by all other studied species of *Cissampelos* with exception of *C. capensis*. Hence, we are confident that our new species belongs to *Cissampelos* s. str.

The genus *Cissampelos* is characterized by its dioecy, as are nearly all Menispermaceae. However, rare instances of monoecy have been reported by Miers (1871), and we observed monoecy in two collections (*Nee 48487*; *51401*) both from Bolivia, in which a few pistillate flowers and immature fruits were observed in the same inflorescence that is predominantly staminate. Petals of pistillate flowers in this inflorescence resemble these of staminate flowers in being cupuliform. There are reports of sex switching in Menispermaceae such as Asian *Tinospora cordifolia* (Willd.) Miers, where complete switching in a plant from staminate to hermaphrodite and back to staminate flowers have been observed (Geetha et al. 2007). Only plants with staminate flowers exhibit this labile sex expression, while plants with pistillate flowers show consistency in their expression (Geetha et al. 2007, Malpotra et al. 2009). The report of monoecy in the American species *Disciphania spadicea* Barneby is based on observations of a single collection from Jalisco (Mexico) (Carrillo-Reyes et al. 2013) which had both staminate and pistillate inflorescences on the same plant. Our case is similar to that of *Tinospora* where inflorescences with mostly staminate flowers may have a few pistillate flowers.

Anther cells in *C. arenicola* vary from 6–10 (Table 1), with about 45% of the sampled 24 staminate flowers having an 8-locular synandrium. This condition is also rarely observed in *Cissampelos grandifolia* Triana & Planch., but is unknown in the remaining American species of *Cissampelos* recognized by Rhodes (1975), which all have a 4-, rarely 6-locular synandrium. Similar 8-locular synandria are most commonly found in the vining *C. mucronata* A. Rich. from tropical Africa. *Cissampelos mucronata* differs from *C. arenicola*, however, in several characters, most obviously, larger leaves that are densely light golden hispidulous-tomentose on both surfaces. Vegetatively, *Cissampelos arenicola* superficially resembles the southern African *Cissampelos capensis*, from which it can be distinguished by the staminate flowers with a 6–10-locular (vs. 4-locular) synandrium, and pistillate flowers having sepals and petals located at the adaxial side of the carpel only. The larger and scarcely ornamented endocarp of *C. arenicola* (Fig. 3A) is readily distinguished from both, *C. capensis* (4.2 × 5.5 mm), and *C. mucronata* (Fig. 3B–C), (4.3 × 4.7 mm), respectively (Table 1).

Table 1. Main quantitative and qualitative variables that distinguish *Cissampelos arenicola* M. Nee & R. Ortiz from African species that are vegetatively similar and/or with 8-locular synandria.

Species	Habit	Leaf shape	Leaf size (cm)	Synandria locule #	Sepals & petals position regarding the carpel vs	Endocarp size (mm)
C. arenicola	vine	ovate-subreniform-trilobed	0.8–3 × 1.3–4	(6)8(10)	adaxially	6 × 7
C. capensis	shrub	ovate-triangular	1.1–3.9 × 0.8–2.8	4	laterally	4.2 × 5.5
C. mucronata	vine	ovate	3.3–4.3 × 4.5–6.6	(6)8(10)	adaxially	4.3 × 4.7

Key to *Cissampelos arenicola* and African species vegetatively similar and/or with 8-locular synandria

1 Inflorescences and flowers of both sexes densely to sparsely silvery-tomentose; staminate flowers with 4-locular synandria; pistillate flowers with sepals and petals located lateral to the adaxial slit of the carpel, often with staminodes .... ***C. capensis***
1’ Inflorescences and flowers of both sexes moderately silvery-pilose; staminate flowers with 6–10-locular synandria; pistillate flowers with sepals and petals located opposite to the adaxial slit of the carpel, lacking staminodes **2**
2 Inflorescences of both sexes with well-developed, foliaceous bracts; perianth conspicuously brownish-speckled .... ***C. mucronata***
2’ Inflorescences of both sexes with small, ovate bracts; perianth pale cream-colored through .... ***C. arenicola***

Key emphasizing endocarps of *C. arenicola* and African species vegetatively similar and/or with 8-locular synandria

1 Endocarp 6 × 7 mm, lateral faces perforated .... ***C. arenicola***
1’ Endocarp 4.2 × 5.5 mm, lateral faces not perforated **2**
2 Endocarp pyriform, surface ornamented with ridges and tubercles ... ***C. capensis***
2’ Endocarp subglobose, surface ornamented with well-developed transverse ridges .... ***C. mucronata***

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RESEARCH ARTICLE

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Morphological analyses suggest a new taxonomic circumscription for *Hymenaea courbaril* L. (Leguminosae, Caesalpinioideae)

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Abstract

Hymenaea is a genus of the Resin-producing Clade of the tribe Detarieae (Leguminosae: Caesalpinioideae) with 14 species. *Hymenaea courbaril* is the most widespread species of the genus, ranging from southern Mexico to southeastern Brazil. As currently circumscribed, *H. courbaril* is a polytypic species with six varieties: var. *altissima*, var. *courbaril*, var. *longifolia*, var. *stilbocarpa*, var. *subsessilis*, and var. *villosa*. These varieties are distinguishable mostly by traits related to leaflet shape and indumentation, and calyx indumentation. We carried out morphometric analyses of 14 quantitative (continuous) leaf characters in order to assess the taxonomy of *H. courbaril* under the Unified Species Concept framework. Cluster analysis used the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) based on Bray-Curtis dissimilarity matrices. Principal Component Analyses (PCA) were carried out based on the same morphometric matrix. Two sets of Analyses of Similarity and Non Parametric Multivariate Analysis of Variance were carried out to evaluate statistical support (1) for the major groups recovered using UPGMA and PCA, and (2) for the varieties. All analyses recovered three major groups coincident with (1) var. *altissima*, (2) var. *longifolia*, and (3) all other varieties. These results, together with geographical and habitat information, were taken as evidence of three separate metapopulation lineages recognized here as three distinct species. Nomenclatural adjustments, including reclassifying formerly misapplied types, are proposed.

Keywords

Fabaceae, Detarieae, integrative taxonomy, nomenclatural changes

Introduction

Hymenaea L. is a genus of caesalpinioid legumes with 14 species (Lee and Langenheim 1975). The genus is distributed throughout tropical America, from Mexico to Paraguay, with one species in coastal East Africa (Mackinder 2005). *Hymenaea* is included in the Resin-producing Clade of the tribe Detarieae, and is most closely related to the genera *Guibourtia* Benn. and *Peltogyne* Vogel (Bruneau et al. 2001, 2008; Fougère-Danezan et al. 2007), all presenting similar leaf morphologies, with two asymmetrical pellucid-punctate leaflets. *Hymenaea* can be differentiated from these related genera by its rather larger and more massive bat-pollinated flowers with a robust hypanthium, and indehiscent, pulpy and woody pods with very large seeds.

The current taxonomy of the genus is largely based on Lee and Langenheim's (1975) revision. In addition to recognizing the 14 currently accepted species, they reduced several species to varietal rank. These polytypic species were viewed by Lee and Langenheim (1975) as showing complex relationships with other species of *Hymenaea*. They hypothesized, for example, that *H. oblongifolia* Huber var. *oblongifolia* is more closely related to *H. aurea* Lee and Lang. and *H. eriogyne* Benth., while *H. oblongifolia* var. *davisii* (Sandwith) Lee and Lang. is probably more closely related to *H. parvifolia* Huber, *H. rubriflora* Ducke, and *H. reticulata* Ducke. According to their concepts, *H. oblongifolia* should be regarded as a polyphyletic species. Another example of a putative polyphyletic species, according to Lee and Langenheim's (1975) conceptual framework, is *H. courbaril*, with var. *villosa* Lee and Andrade-Lima hypothesized as being more closely related to *H. martiana* Hayne, and var. *longifolia* (Benth.) Lee and Andrade-Lima to *H. velutina* Ducke and *H. stigonocarpa* Mart. ex Hayne.

Hymenaea courbaril is the most widely distributed species of the genus, almost matching the geographic range of *Hymenaea* in the New World. It also has the greatest economic importance in the genus, due to the high quality of its wood and its resin, the latter being used by native populations as incense, cement, in the manufacture of varnishes, and for medicinal purposes. Its nutritive fruits are sought after by mammals and birds (Rizzini 1971; Langenheim 1967; Lee and Langenheim 1975). *Hymenaea courbaril* is the most taxonomically complex species, with six varieties: var. *altissima* (Ducke) Lee and Lang., var. *courbaril*, var. *longifolia*, var. *stilbocarpa* (Hayne) Lee and Lang., var. *subsessilis* Ducke, and var. *villosa*. These varieties are differentiated by their leaflet sizes, shapes, and indumentation, calyx indumentation, petal shapes, ovary stipe sizes, and pod sizes and shapes. These variations in several diagnostic features make the boundaries of putatively related taxa rather imprecise. The widely circumscribed *H. courbaril*, as defined by Lee and Langenheim (1975), is hereafter referred to as the *H. courbaril* complex.

The species and varietal limits of *H. courbaril*, *H. stigonocarpa,* and *H. martiana* were investigated by Pestana (2010). This author did not employ objective analytical methods and used the same classical taxonomic approach as Lee and Langenheim (1975), thus coming to similar conclusions as the latter authors in keeping *H. courbaril* as a polytypic species with six varieties.

Delineating precise species boundaries is a key task in plant taxonomy. This process has direct impacts on society, as there is a growing demand for credible taxonomic information that allows us to conserve, manage, and understand natural biodiversity (Wheeler et al. 2004). However, questions of species recognition can be affected by several theoretical, methodological, and practical issues. De Queiroz (2005, 2007) defined species as separately evolving metapopulation lineages (the Unified Species Concept–USC), and proposed that all other previously considered properties of species should be reinterpreted as contingent rather than critical. These additional contingent properties, such as phenetic distinctiveness, reciprocal monophyly, genetic coalescence, or ecological distinctiveness, are acquired during speciation and should be considered as different lines of evidence relevant to assessing lineage separation. The USC, by treating species conceptualization and species delimitation as clearly separate issues, allows the use of properties formerly treated as secondary criteria in species delimitations. More importantly, it allows for currently accepted species limits to be considered as hypotheses to be tested using the presence of any one of those secondary properties as evidence for the existence of a species.

Analyses of morphometric data can be useful in objectively demonstrating species limits, especially when combined with molecular markers (Andrés-Sánchez et al. 2009; Newmaster and Ragupathy 2009). Additionally, the use of morphological information represents the fastest and least expensive manner of assessing taxonomic complexes– and has been used to solve problems of species limits in many different plant groups, especially when molecular data was not easily available (Handerson 2006; Estrella et al. 2009; Pedersen 2010; Ceolin and Miotto 2012; Rahman and Rahman 2012; Castello and Galeto 2013; Scrivanti et al. 2013), as was the case of the group studied here.

The problem of defining species limits in the polytypic *H. courbaril* complex is revisited here under the USC conceptual framework by exploring morphometric, geographical, and ecological patterns as lines of evidence for the existence of separate metapopulation lineages. Specifically, we sought to test Lee and Langenheim's (1975) hypothesis that *H. courbaril* should be treated as a polytypic species with six varieties.

Materials and methods

A total of 96 specimens of the *H. courbaril* complex were examined in this study (vouchers listed in Appendix 1). All analyzed materials were sheets from the following herbaria: B, CEN, CEPEC, HRB, HUEFS, IBGE, IPA, LAGU, M, MBM, NY, RB, SP, SPF, U, UB, and UC. We selected specimens that displayed branch ends with fully-developed (mature) leaves. This criterion avoided considering young leaves from the tips of the branches or leaves at the bases of the branches that are often much larger. Each specimen analyzed was considered an individual, and identifications strictly followed Lee and Langenheim (1975), although these names were only used as nomenclatural references in this study.

The leaves in the group studied here are bifoliolate; the leaflets range from oblong to ovate or obovate, with rounded, acute or obtuse apices; the main vein is displaced

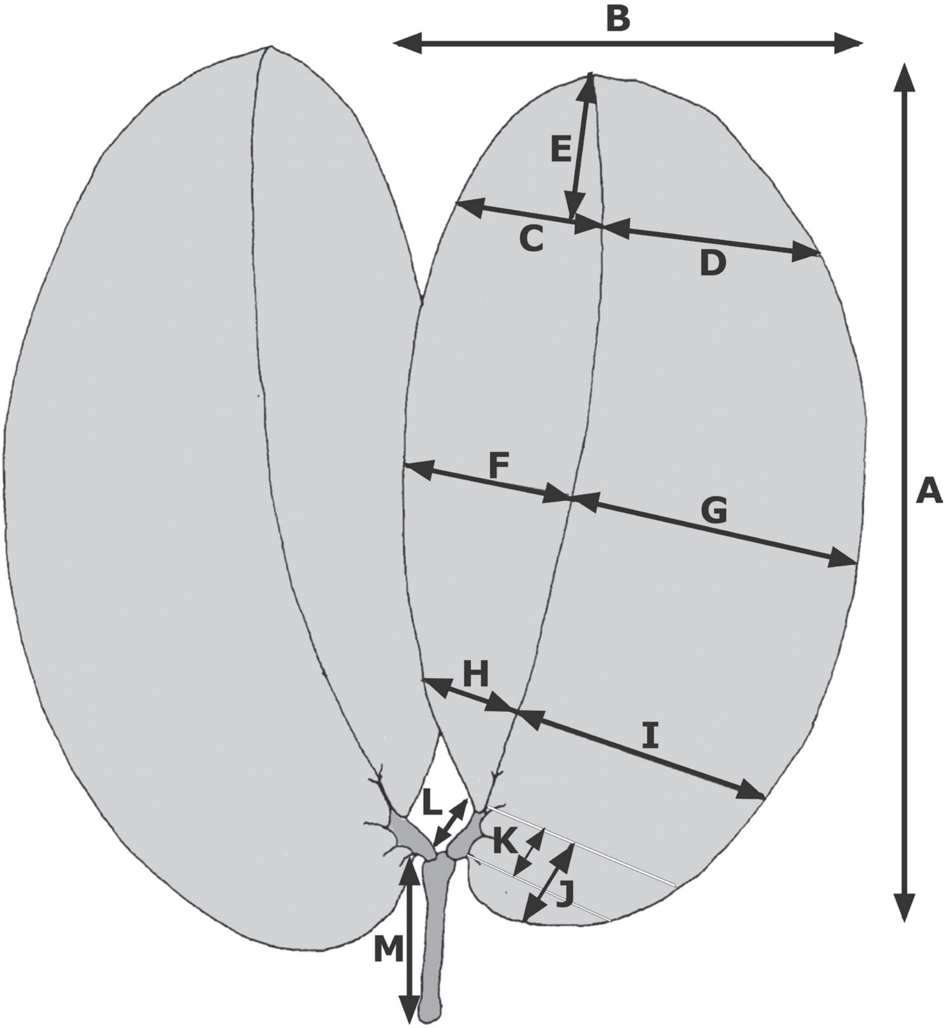

Figure 1. Quantitative leaf characters of specimens of the *Hymenaea courbaril* complex. Letters refer to the measurements described in Table 1.

towards the inner margin resulting in an asymmetrical base, the outer portion being wider than the inner and extending beyond the attachment to the petiolule (Figure 1). Fourteen quantitative (continuous) characters were examined (Table 1; Figure 1). Only leaf traits were measured and quantified, as most herbarium sheets lacked flowers and/or fruits. In any case, flower morphology is much conserved in the species studied and the herbarium material examined usually contained only incomplete or damaged flowers. Measurements were taken of two fully developed leaves per dried herbarium sheet, using a graduated ruler (precision 1 mm).

All multivariate analyses were carried out using Past software (Hammer et al. 2001). Cluster analyses used the Unweighted Pair Group Method with Arithmetic Mean (UP-

Table 1. List of the quantitative leaf characters in specimens of the *Hymenaea courbaril* complex. Letters in the second column refer to measurements depicted in Figure 1.

Leaf characters (cm)	Measurements in Figure 1
1 - Total length of the leaflet	A
2 - Leaflet length /width ratio	A / B
3 - Length of the distal sixth	E
4 - Inner width in distal third	C
5 - Outer width in distal third	D
6 - Inner width in middle third	F
7 - Outer width in middle third	G
8 - Inner width in basal third	H
9 - Outer width in basal third	I
10 - Main vein displacement	(G–F) / (I–H)
11 - Base extension (length of the base from the inner attachment of the petiolule)	J
12 - Petiole length	M
13 - Petiolule length	L
14 - Distance between inner and outer attachment of the petiolule	K

GMA) based on Bray-Curtis dissimilarity matrices. Principal Component Analyses (PCA) were carried out based on the same morphometric matrix. Two sets of Analyses of Similarity (ANOSIM; Warwick, Clarke and Suharsono 1990) and Non Parametric Multivariate Analysis of Variance (NPMANOVA; Anderson 2001) were carried out to evaluate statistical support for: (1) the major groups recovered in the UPGMA and PCA; and (2) the varieties as defined by Lee and Langenheim (1975). *Hymenaea courbaril* var. *villosa* was not included in the second analysis because it is known from only two specimens (Lee and Langenheim 1975) and only one was located during this study. Both ANOSIM and NPMANOVA used Bonferroni corrections, 10,000 permutations, and Bray-Curtis distances. As *H. courbaril* var. *villosa* was represented by only a single specimen, we carried out a second set of UPGMA, PCA, and similarity analyses for the major groups without including this variety in order to test its influence on the results.

Distribution maps of the specimens studied were prepared using DIVA-GIS software (Hijmanns et al. 2005), based on the geographic coordinates recorded on the herbarium sheet labels. For material lacking original coordinates, a central coordinate for the municipality was used as provided by the Species Link website (available at http://specieslink.org.br).

Species limits were tested following the USC framework (de Queiroz 2005, 2007). Species ranks were ascribed to groups that showed morphological and habitat distinctiveness and geographical consistency. We considered as morphologically distinct groups those that were recovered in UPGMA and PCA and that exhibited statistical significance in both ANOSIM and NPMANOVA tests. Habitat distinctiveness was assessed from the vegetation type where the taxon occurs, following the UNESCO (1973) classification. Species diagnoses were prepared based on vegetative and reproductive characters.

Results and discussion

Both UPGMA and PCA recovered three major groups (Figure 2): Group 1 included all specimens of var. *altissima*; Group 2 all specimens of varieties *courbaril*, *stilbocarpa*, *subsessilis*, and the single specimen of *villosa*; and Group 3 all specimens of var. *longifolia*. Within Group 2, individuals of the different varieties did not cluster together and appeared intermixed in UPGMA, or formed highly overlapping groups in two first axes of PCA. The first PCA axis accumulated 88.3% of the total variance, with the two first axes summing 93% of the observed variation. Leaflet length was the trait that explained most of the variation found in first axis, and the three major groups were sorted mostly by leaflet size. These results indicate that Group 3 includes specimens with largest leaflets, and Group 1 the smallest leaflets (Figure 3).

The results of the UPGMA and PCA were consistent with both ANOSIM and NPMANOVA. Comparisons of the varieties of *H. courbaril* showed significant differences ($p < 0.05$) between the varieties *altissima* and *longifolia* and all other varieties, but no significant differences between the varieties *courbaril*, *silbocarpa*, and *subsessilis* that clustered in Group 2 (Table 2). The same analyses comparing the three groups recovered in UPGMA and PCA found significant morphological differences between them (Table 3).

The complex morphological variations found in Group 2 appear to reflect its wide geographic range and large genetic variability (Ramos et al. 2009). Phylogeographic studies in part of the geographic range of *H. courbaril* var. *stilbocarpa* clearly demonstrated the wide genetic base and geographic structure of this genetic variation (Ramos et al. 2009). The morphological distinctions among the varieties clustered in Group 2 are made by rather continuous characters, such as the color of the calyx lobes (ochraceous to golden or rusty brown), leaflet shape (broadly to narrowly falcate), and the shapes of the outer sides of the leaflet base (straight to nearly straight or rounded). The var. *subsessilis* presents a short ovary stipe (c. 2 mm long) that grades to a medium-sized stipe in var. *stilbocarpa* (3–4 mm) and then large in var. *courbaril* (4–6 mm).

Leaflet indument distinguishes var. *villosa* from the remaining varieties of Group 2 (Lee and Andrade-Lima 1974, 1975). The ovary is also described as slightly pilose on one side, a condition not observed in other varieties of *H. courbaril*. The exclusion of var. *villosa* from the similarity analyses did not alter the results obtained with its inclusion (Table 3). The var. *villosa* is known from only two specimens from the eastern coastal areas of the states of Paraíba and Pernambuco (northeastern Brazil) where the range of var. *stilbocarpa* overlaps with that of *H. martiana*. This species (*H. martiana*) has tomentose leaflets and an ovary with a tuft of trichomes near its base. The rarity of *H. courbaril* var. *villosa*, as well as the transitional nature of the leaflets and ovary indumentation in relation to *H. martiana* and the other varieties of the *H. courbaril* complex clustered in Group 2, all suggest that var. *villosa* could represent a hybrid between *H. martiana* and *H. courbaril*.

The habitats of the taxa of Group 2 include mostly tropical ombrophilous alluvial (gallery) forests in areas subject to seasonally dry climates from Mexico and the

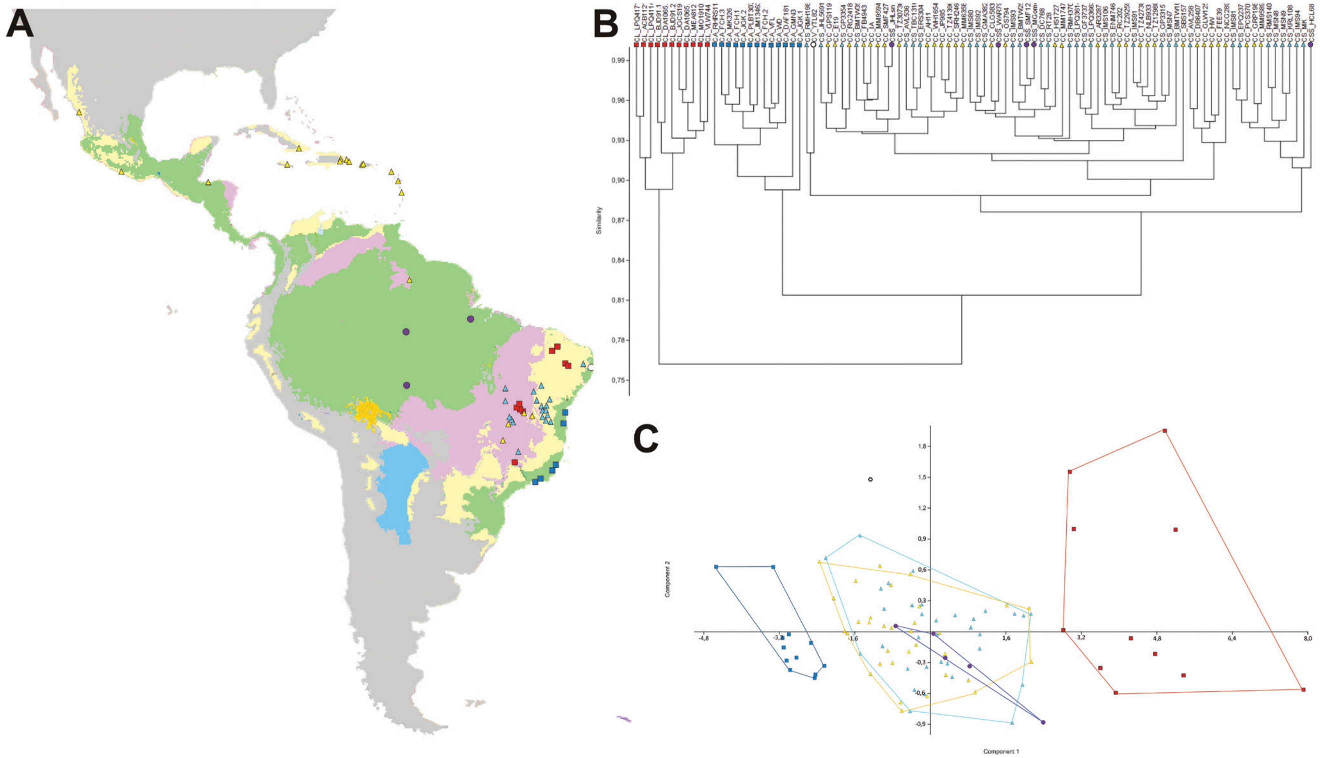

Figure 2. A Distribution of the *Hymenaea courbaril* complex in the Neotropics. The major biomes where this complex occurs are shown in color: wet forests (green), seasonally dry forests and woodlands (yellow), and savannas (purple). The varieties of *H. courbaril* recognized by Lee and Langenheim (1975) are represented by different symbols: var. *altissima* (blue squares), var. *coubaril* (yellow triangles), var. *longifolia* (red squares), var. *stilbocarpa* (blue triangles), var. *subsessilis* (purple circles), and var. *villosa* (white circles) **B** UPGMA analysis of the *H. courbaril* complex based on 14 quantitative leaf measures (see Figure 1 and Table 1 for measurement details and Bray-Curtis distances). Varieties are represented by the same symbols used for the map **C** Scatter diagram showing the first two axes of the PCA using the same data matrix as the UPGMA analysis. Ellipses represent the varieties as recognized by Lee and Langenheim (1975), and they are represented by the same symbols used for the map.

Table 2. Results of ANOSIM and NPMANOVA testing the consistence of the varieties of *Hymenaea courbaril*, using 10,000 permutations and Bray-Curtis distances. ANOSIM R-values are given above the diagonal and NPMANOVA F-values are given below the diagonal. Numbers between brackets are Bonferroni-corrected p-values. Significant differences are indicated by shadowed cells.

	stilbocarpa	**courbaril**	**subsessilis**	**altissima**	**longifolia**
stilbocarpa		0.09933 [0.0195]	-0.1343 [1]	0.9325 [0.0015]	0.8858 [0.0015]
courbaril	5.313 [0.0855]		0.09375 [1]	0.8524 [0.0015]	0.9471 [0.0015]
subsessilis	0.8397 [1]	3.296 [0.489]		0.9972 [0.0045]	0.9329 [0.0075]
altissima	79.79 [0.0015]	57.97 [0.0015]	49.86 [0.003]		1 [0.0015]
longifolia	67.13 [0.0015]	94.08 [0.0015]	30.27 [0.006]	235.5 [0.0015]	

Table 3. ANOSIM and NPMANOVA (10,000 permutations and Bray-Curtis distances) for the groups recovered in UPGMA and PCA analyses of 78 individuals of *Hymenaea courbaril* complex. Group 1 included all specimens of var. *altissima*, Group 2 all specimens of the varieties *courbaril*, *stilbocarpa*, *subsessilis*, and *villosa*, and Group 3 all specimens of var. *longifolia*. Values before the slash resulted from the analyses including var. *villosa* and after one excluding it. ANOSIM R-values are given above the diagonal and NPMANOVA F-values are given below the diagonal. Numbers in brackets are Bonferroni-corrected p-values. Significant differences are indicated by shadowed cells.

	Group 1	**Group 2**	**Group 3**
Group 1		0.8762 / 0.8771 [0.0003 / 0.0003]	1 / 1 [0.0003 / 0.0003]
Group 2	73.65 / 74.35 [0.0003 / 0.0003]		0.9045 / 0.9055 [0.0003 / 0.0003]
Group 3	235.5 / 235.5 [0.0003 / 0.0003]	84.47 / 85.58 [0.0003 / 0.0003]	

Caribbean islands to central Brazil, but not the Amazonian region (var. *courbaril* and *stilbocarpa*), tropical ombrophilous lowland forests in central and eastern Amazon basin (var. *subsessilis*), or tropical ombrophilous submontane forests in the northeastern Brazilian state of Paraíba (var. *villosa*) (Figure 2).

The var. *altissima* (Group 1) constitutes a morphologically, geographically and ecologically consistent taxon. It is distinguished from the other varieties of *H. courbaril* complex by having smaller, falcate and acuminate leaflets, not exceeding 6.5 cm long on the flowering branches (Table 4). The leaflets of this taxon have a thinner texture than the remaining varieties, allowing its tertiary venation to appear as raised and reticulate veins. The flowers of var. *altissima* are also the smallest within the *H. courbaril* complex, measuring less than 15 mm long (Lee and Langenheim 1975, Pestana 2010). This variety is distributed in tropical ombrophilous lowland and submontane forests of the Atlantic Forest phytogeographical domain along the eastern coast of Brazil (Figure 2). It was cited for the southeastern Brazilian states of São Paulo and Rio de Janeiro (Mattos 1968, Lee and Langenheim 1975, Rizzini 1978, Pestana 2010), but we found specimens occurring northwards into Espírito Santo and Bahia states. It was originally described as *H. altissima* Ducke (Ducke 1935). Lee and Langenheim

Table 4. Morphological comparison between *Hymenaea courbaril*, *H. altissima,* and *H. longifolia*.

	H. courbaril	***H. altissima***	***H. longifolia***
Leaflet outline	Elliptic or ovate, not or slightly falcate	Falcately elliptic	Oblong or narrowly elliptic, not falcate
Inner margin of the leaflet	Straight or slightly concave	Strongly concave	Straight
Outer base of the leaflet	Slightly rounded	Truncate	Rounded
Apex	Acute, rarely obtuse	Abruptly acuminate	Obtuse, rarely rounded
Petiole length (cm)	1.1–1.7 (– 2)	1–1.3 (– 1.7)	2.6–3
Petiolule length (mm)	4–5	3–4 (– 5)	7–8
Leaflet size (cm)	6–9 (– 10.2) × 2.8–4 (– 5.1)	4–5.7 (– 6.4) × 2.0–2.5	10.1–12.5 (–15.4) × 4.5–6.5 (– 6.9)
Flower length (cm)	2.2–3.1	2–2.7	2.6–3.8
Fruit shape	Cylindrical, rounded in cross section	Cylindrical, rounded in cross section	Oblongoid, compressed in cross section
Seeds per fruit	Mostly > 4	Mostly 1–2	Mostly > 4

(1974: 448) considered that the foliar characters and relative flower size “do not appear sufficiently significant to warrant specific status for this taxon” and considered it as a variety of *H. courbaril*.

Var. *longifolia* (Group 3) comprises the morphs with largest leaflets. This variety also differs from the remaining groups by having oblong leaflets with an obtuse apex, clawed petals, and fruits compressed and enlarged toward the apex (Table 4). It occupies a very particular habitat in submontane tropical drought-deciduous thorny forests in the Caatinga and Cerrado phytogeographical domains that extend from western Bahia and Piauí states to the Araripe mountain range in the border area between the states of Ceará and Pernambuco (Figure 2). It was first proposed as a variety of *Hymenaea splendida* Vogel. Lee and Langenheim (1974, 1975) considered *H. splendida* var. *splendida* to be synonymous with *H. courbaril* var. *stilbocarpa* and segregated *H. splendida* var. *longifolia* as another variety of *H. courbaril*.

In addition to morphological distinctions, ecological and geographical information can be used for interpreting the three groups recovered by UPGMA and PCA as separately evolving lineages that would be considered different species under the USC framework (see Taxonomy section). With respect to the variation in Group 2, studies of wider samplings, including especially the collections made after Lee and Langenheim’s (1975) work, shows that the diagnostic features used for defining the varieties included in Group 2 have more complex variations. Indumented leaflets, for example, the diagnostic character for var. *villosa*, can be found to varying degrees in var. *stilbocarpa*. A short stipe was used as a diagnostic feature of var. *subsessilis,* but this trait is variable and grades into var. *courbaril*. Finally, the distinctions between vars. *courbaril* and *stilbocarpa* rely on the types and colors of the calyx lobe indumentation, traits that tend to change during the duration of the flower. Thus, a more parsimonious way to treat the taxonomy of Group 2 is to consider it a variable species, without recognizing varieties.

Taxonomic treatment

***Hymenaea courbaril* L., Sp. Pl. 1192. 1753. Lectotype. "Ceratia diphyllos Antegoana, Ricini majoris, fructu osseo, siliqua grandi incluso" in Plukenet, Phytographia, t. 82, f. 3, 1691 (designated by Lee and Langenheim in Univ. Calif. Publ. Bot. 69: 81. 1975).**

= *Hymenaea resinifera* Salisb., Prodr. 327. 1796, *nom. nud.*

= ? *Hymenaea animifera* Stokes, Bot. Mat. Med. 2: 449. 1812, *fide* Lee and Langenheim in Univ. Calif. Publ. Bot. 69: 81. 1975.

= *Hymenaea candolleana* Kunth [spelled '*candolliana*'], Nov. Gen. and Sp. 6: 323, pl 556. 1824. Type: México, Acapulco, *Bonpland 3875* (holotype P!).

= *Hymenaea confertifolia* Hayne, Getreue Darstell. Gew., 11, pl. 9. 1830. Lectotype (designated here): *Sellow* s.n., s.d. (lectotype W 48857!).

= *Hymenaea stilbocarpa* Hayne, Getreue Darstell. Gew., 11, pl. 11. 1830. *Hymenaea courbaril* var. *stilbocarpa* (Hayne) Lee and Lang., J. Arnold Arbor. 55: 449. 1974, syn. nov. Lectotype (designated here): "S. Pauli, sylv. ad Faz. de S. Anna", *Martius* (lectotype M! [barcode n° M-0215314], photo HUEFS!, isolectotype M! [barcode n° M-0215313], photo HUEFS!).

= *Hymenaea retusa* Willd. ex Hayne, Darst. Beschreib. Arzneigew. 11: pl. 12. 1830. Type: México, Acapulco, *Humboldt* (holotype B!), *nom. illegit.*

= *Hymenaea splendida* Vogel, Linnaea 11: 409. 1837. Type: *Sellow 1025* (holotype B†).

= *Hymenaea courbaril* var. *obtusifolia* Ducke, Arch. Jard. Bot. Rio de Janeiro, 4: 47. 1925. Type: Brazil, Pará, Belém (Ilha do Marajó?), *Ducke RB 16906* (holotype RB!, isotypes A!, MG!, P!, U!, US!).

= *Hymenaea courbaril* var. *subsessilis* Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 265. 1925, syn. nov. Neotype (designated by Lee and Langenheim in Univ. Calif. Publ. Bot. 69: 89. 1975): Brasil, Amazonas, Flores, *Ducke MG 11167* (neotype MG!).

= *Hymenaea multiflora* Kleinhoonte, Recueil Trav. Bot. Neerl. 22: 405. 1925. Type: Suriname, Boschreserve, Kaboeri, Coll. by the Forestry Bureau Herb. 4943 (holotype U!).

= *Inga megacarpa* M.E. Jones, Contr. West Bot. 15: 140. 1929. Type: México, Nayarit, *M.E. Jones 23012* (holotype RSA!, isotypes F!, GH!, NY!).

= *Hymenaea courbaril* var. *villosa* Y.T. Lee and Andrade-Lima, J. Arnold Arbor. 55: 446. 1974, syn. nov. Type: Brasil, Paraíba, Paquevira de Natuba, *Lee and Andrade-Lima 83* (holotype UC!).

Description. Large trees, to 30 m tall. Petiole 1.1–1.7 (–2) cm long; petiolule 4–5 mm long; leaflets 6–9 (–10.2) × 2.8–4 (–5.1) cm, elliptic, rarely ovate, straight or slightly falcate due to central vein with an angle c. 10°, apex acute or obtuse, rarely acuminate, base acute along the inner margin and rounded along the outer margin, distance from the inner margin to central vein 7–10 mm in the basal region. Flower buds 2.1–2.5 cm long; flower 2.2–3.1 cm long; hypanthium 7–15 mm long; petals 1.1–2.0 cm long. Fruit cylindrical, of uniform width, apex mostly rounded and apiculate.

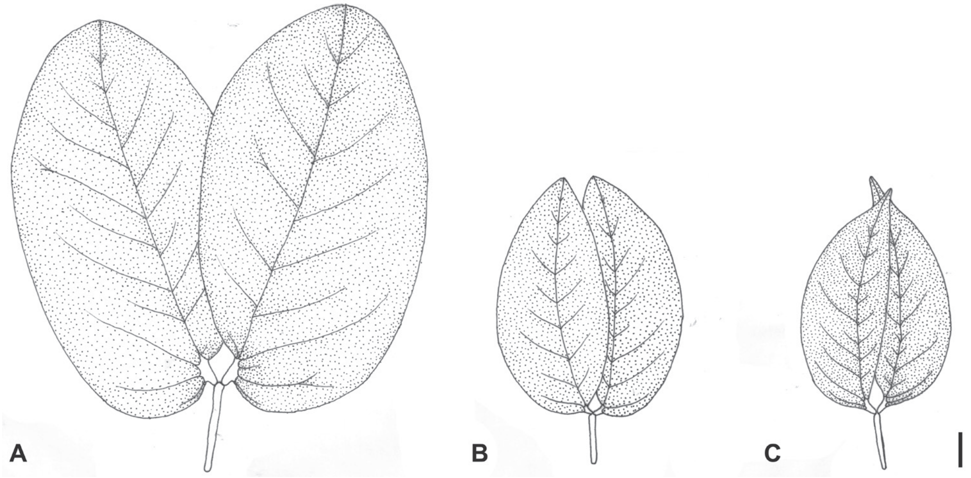

Figure 3. Leaf morphology of the species recognized in the *Hymenaea courbaril* complex: **A** *Hymenaea longifolia* **B** *Hymenaea courbaril* **C** *Hymenaea altissima*. Scale bar = 1 cm.

Hymenaea courbaril is defined here more narrowly than the circumscription adopted by Lee and Langenheim (1975), as we are proposing the exclusion of the varieties *altissima* and *longifolia* and their recognition as distinct species. In this narrower sense, *H. courbaril* is characterized by leaflets with slightly convex inner margins and midrib slightly arched, resulting in an elliptic or ovate outline, not or only slightly falcate, apex mostly acute or obtuse (Figure 3). It presents flowers larger than the other species of the *H. courbaril* complex, and cylindrical fruits mostly with more than five seeds (Table 4). It has a wide geographical range, mostly in different nuclei of Seasonally Dry Forests in Mexico, Central America, Caribbean, northern South America, Bolivia, and Brazil (from the Amazon region to Paraná State in the south).

Nomenclatural problems with several names associated with *H. courbaril* were not amended by Lee and Langenheim (1975) when they undertook their taxonomic revision of the genus. No formal type for *H. stilbocarpa* was cited by Lee and Langenheim (1975), who stated that no specimen was cited in the original description of Hayne (1830). However, Hayne (1830) based *H. stilbocarpa* on material collected by Martius, citing "Wäscht in Brasilien in Wäldern der Provinzen S. Paulo, Minas Geraes und Bahia (Martius)". We found a specimen in the M herbarium collected by Martius in the Brazilian state of São Paulo (Santana farm) with an attached label indicating that this plant was distributed over the "Prov. Rio de J°., S. Paulo, Minas Geraes, Bahia", which probably served as the original material for Hayne's description of *H. stilbocarpa*. Thus, we are lectotypifying this species with Martius' specimen held in M under the barcode number M-0215314.

Hymenaea confertifolia Hayne was based on material collected by Sellow and Olfers in Brazil ("Wächst in Brasilien (Olfers u. Sellow)"; Hayne 1830: table 9). Lee and Langenheim (1975: 88) stated that this name was based on *Sellow 1025* and that the "holotype" in the B herbarium was destroyed. However, as Hayne (1830) did not refer to one particular specimen, all materials collected by Sellow or Olfers that can be linked with *H. confertifolia* should be considered syntypes. No such specimens can be found in the B herbarium, and were probably destroyed. A duplicate from B collected by Sellow was found in W annotated as *Hymenaea confertifolia,* and is designated here as the lectotype of this name.

Hymenaea retusa Willd. ex Hayne was published as a homotypic synonym of *H. candolleana* (Hayne 1830). It is thus illegitimate under the Article 52 of the International Code of Botanical Nomenclature (McNeill et al. 2011).

Hymenaea courbaril var. *obtusifolia* Ducke was published based on a tree cultivated in the Pará Botanical Garden (now Museu Paraense Emílio Goeldi, Belém, state of Pará, Brazil). Lee and Langenheim (1975) misinterpreted this as evidence that the holotype was the specimen in the herbarium of this museum (MG). However, Ducke (1925: 47) explicitly stated that "specimina florifera and fructus in herb. Jard. Bot. Rio n. 16.906", and thus the RB material should be considered as the holotype of this name.

Ducke (1925: 265) did not cite any specimen when describing *H. courbaril* var. *subsessilis* Ducke. Lee and Langenheim (1975) did not explicitly designate a type for this variety, but chose a "representative specimen" collected "in the same general area believed to be the type locality". We are accepting it as an inferential typification, and the status of this material should be a neotype since no other specimen was refereed in the protologue.

Hymenaea altissima **Ducke, Anais Acad. Brasil. Ci. 7: 207. 1935. Lectotype (designated by Egler in Bol. Mus. Emílio Goeldi. Nov. Ser. Botânica. 18: 51. 1963): Brazil, Rio de Janeiro, Avelar, Faz. Pau Grande, Posse,** *G. M. Nunes 3* **(lectotype RB!, isolectotypes MG!, R!).**

≡ *Hymenaea courbaril* var. *altissima* (Ducke) Lee and Lang., J. Arnold Arbor. 55: 448. 1974.

Description. Large trees, up to 38 m tall. Petiole 1–1.3 (–1.7) cm long; petiolule 3–4 (–5) mm long; leaflets 4–5.7 (–6.4) × 2–2.5 cm, oval, narrow-elliptic or elliptic, strongly falcate, due to central vein with an angle c. 35°, apex acuminate, rarely acute, base acute along the inner margin and truncate along the outer margin, distance from the inner margin to central vein 4–5 mm in the basal region. Flower buds 1.5–2.5 cm long; flower 2–2.7 cm long; hypanthium 7–12 mm long; petals 1.2–1.6 cm long. Fruit cylindrical, of uniform width, apex mostly rounded and apiculate.

Hymenaea altissima shows the smallest leaflets and flowers in the species group related to *H. courbaril* (Table 4). Additionally, its leaflets are strongly falcate due to the strongly curved and displaced midvein, with an abruptly acuminate apex. The base of the leaflet is acute along the inner margin and truncate along the outer margin (Figure 3). The fruits are mostly cylindrical, as in *H. courbaril,* but usually shorter than those of this species (4–5 vs. 8–20 cm long) because they have only one or two seeds, while in *H. courbaril* they usually have six or more seeds. This species is restricted to the coastal rain forests of eastern Brazil, from southern Bahia State to São Paulo and Paraná states.

This species was described by Ducke (1935) as *H. altissima*. Lee and Langenheim (1974) treated it as a variety of *H. courbaril*. Later, these latter authors highlighted the differences between this taxon and the other varieties as having smaller and falcate leaflets and smaller flowers (Lee and Langenheim 1975: 86), but kept it as a variety of *H. courbaril*, a position also adopted by Pestana (2010). Our results indicated that the leaf traits of *H. altissima* are clearly distinct of those of *H. courbaril* and *H. longifolia*. These results, together with the distinctive flower and fruit traits and the coherent distribution and habitat data, all give support to the original view of Ducke (1935) in considering it a different species.

Lee and Langenheim (1975: 84) stated that the lectotype of *H. altissima* was designated by Egler (1963) as the specimen "*A. Ducke RB 30306*". However, Egler (1963: 51) simply indicated that the type should be "Type: RB 23.306". We could not track any specimens of *Hymenaea* in the RB herbarium with the numbers RB 30306 or RB 23306. We encountered, however, a specimen annotated by Ducke as *H. altissima* that was collected in the state of "Rio de Janeiro, Avelar" by G. M. Nunes in 1925 and could be linked to the protologue of *H. altissima* (Ducke 1935). This specimen is numbered RB 20306, and we are assuming that both Egler (1963) and Lee and Langenheim (1975) erroneously noted the RB number when referring to the lectotype of *H. altissima*.

***Hymenaea longifolia* (Benth.) I.M. Souza, Funch & L.P. Queiroz, comb. et stat. nov.**
urn:lsid:ipni.org:names:77140226-1

º *Hymenaea splendida* var. *longifolia* Benth., Fl. Bras. (Martius) 15(2): 236. 1870. *Hymenaea courbaril* var. *longifolia* (Benth.) Y.T.Lee and Andrade-Lima, J. Arnold Arbor. 55: 448. 1974. Lectotype (designated here): Brasil, Bahia, Villa de Barra, *Blanchet 3135* (lectotype: R!, isolectotypes K!, P!).

Description. Medium-sized trees c. 5–12 (–18) m tall. Petiole 2.6–3 cm long; petiolule 7–8 mm long; leaflets 10.1–12.5 (–15.4) × 4.5–6.5 (–6.9) cm, elliptic, narrow-elliptic, or oblong, not falcate, due to central vein with an angle c. 24°, apex obtuse or acute, base acute or rounded along the inner margin and rounded or slightly rounded along the outer margin, distance from the inner margin to central vein 10–11 mm in the basal region. Flower buds 2.2–3.3 cm long; flower 2.6–3.8 cm long; hypanthium 9–14 mm long; petals 1.3–2.1 cm long. Fruit oblongoid, compressed, wider at distal region, apex slightly truncate and apiculate.

Hymenaea longifolia, as circumscribed here, is characterized by large leaflets, both longer and wider than those of the related species *H. courbaril* and *H. altissima*, with longer petioles and petiolules (Table 4). The leaflets are elliptic or oblong with obtuse (rarely acute) apices and rounded bases along the outer margin (Figure 3). This species occurs in Seasonally Dry Forests within the Caatinga and Cerrado phytogeographical domains in northeastern Brazil, from Ceará State to the northern portion of Bahia State.

It was first described by Bentham (1870) as *H. splendida* var. *longifolia,* and considered related to *H. courbaril* and *H. stilbocarpa* because of the glabrous leaflets, but differing from them by having larger leaflets. Lee and Langenheim (1975) treated all these taxa under a more widely circumscribed *H. courbaril*, a position not supported by the results presented here. Lee and Langenheim (1975: 86) misinterpreted the specimen *Blanchet 3135* (R) as the holotype of *H. splendida* var. *longifolia*. However, when describing this variety, Bentham (1870: 236) cited two syntypes, *Blanchet 3135* ("ad Villa da Barra prov. Bahia") and *Gardner 1938* ("Serra da Araripé, prov. Ceara"). Thus, the material cited by Lee and Langenheim (1975) as the holotype should be considered as a lectotype.

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Appendix 1

Materials examined for the morphometric study of the *Hymenaea courbaril* complex. Nomenclature follows Lee and Langenheim (1975).

***Hymenaea courbaril* var. *altissima*–BRAZIL, Bahia**, Ilhéus, *R.H.R.Sambuichi 1169* (CEPEC). **Esprírito Santo**, Linhares, *D.A.Folli 181* (RB). **Rio de Janeiro**, Nova Iguaçu, *W.Dias s/n* (HUEFS); Resende, *J.G.Kuhlmann 179* (RB); Rio de Janeiro, *J.G.Kuhlmann s/n* (RB). **São Paulo**, Moji das Cruzes, *P.L.B.Tomasulo 307* (SP); São Paulo, *F.C.Hoehne s/n* (SP, SPF); *J.Mattos 13463* (SP); *M. Kirizawa 326* (SP); *V.F.Lima s/n* (SP).

***Hymenaea courbaril* var. *courbaril*–BRAZIL, Bahia**, Baianópolis, *S.B. da Silva 157* (HRB). Bom Jesus da Lapa, *S.M. de Faria 427* (RB). **Goiás**, Niquelândia, *G.P.Silva 1192* (CEN); Santa Bárbara de Goiás, *A.Raw 3287* (UB). **COLOMBIA**, Santa Maria, *Espina 19* (UC). **CUBA, Santiago de Cuba**, Mella, *I.Arias s/n* (B). **EL SALVADOR**, s/l, *R.Cruz 202* (LAGU); *P.C.Standley 3705* (UC). **HONDURAS, Morazan**, Jicarito, *G.L.Webster 12529* (F). **MEXICO**, Acapulco, *W. Humboldt s/n* (B). **PANAMA**, Barro Colorado, *N.C.Garwood 2891A* (F); *O.Shattuck 794* (UC). **SURINAME**, Boschreserve, *F.Bureau 4943* (U).

***Hymenaea courbaril* var. *longifolia*–BRAZIL, Bahia**, Barreiras, *L.P. de Queiroz 4114* (HUEFS); Formosa do Rio Preto, *D.Alvarenga 1065* (RB); *B.J.Dias 91* (IBGE, SP); *L.P. de Queiroz 4171* (HUEFS). **Ceará**, Brejo Santo, *J.G.Carvalho-Sobrinho 1925* (HUEFS); Missão Velha, *Academia Brasileira de Ciências 1121* (IPA). **Piauí**, Brasileira, *M.E.Alencar 812* (HUEFS); Campo Maior, *M.Oliveira 1910* (IPA). **São Paulo**, Bauru, *V. de L. Weiser 744* (RB).

***Hymenaea courbaril* var. *stilbocarpa*–BRAZIL, Bahia**, Caetité, *L.P. de Queiroz 3614* (HUEFS); Gentio do Ouro, *K.R.B.Leite 108* (HUEFS); *E.R. de Souza 304* (HUEFS); *R.Tourinho 28* (HUEFS); Jaguaripe, *E.N. de Matos 746* (HUEFS); Livramento do Brumado, *R.M.Harley 19889* (IPA); *L.P. de Queiroz 3663* (HUEFS); Miguel Calmon, *E.P.Queiroz 2372* (MBM); Mucugê, *R.M.Harley 3702* (HUEFS); Palmeiras, *M. de S. Nunes 7, 8, 9* (HUEFS); *I.M.Souza 80, 81, 91, 92, 93, 94, 106* (HUEFS); Rui Barbosa, *D.Cardoso 768* (HUEFS); Vitória da Conquista, *J.H.Langenheim 5641* (IPA). **Goiás**, Alto Paraíso de Goiás, *T.B.C. 1310* (HUEFS); Colinas do Sul, *B.M.T.Walter 1038* (HUEFS); Minaçu, *B.M.T.Walter 3570* (HUEFS); Niquelândia, *B.M.T.Walter 2515* (HUEFS). **Minas Gerais**, Araguari, *G.M.Araújo 382* (NY). **Paraíba**, São João do Cariri, *A.V.Lacerda 258, 536* (HUEFS). **Pernambuco**, Chapada do Araripe, *G.Fotius 3737* (HUEFS). **Piauí**, Caracol, *R.M.Santos*

1400 (HUEFS). **São Paulo**, São Paulo, *M.Koscinski s/n* (IPA). **Tocantins**, Colméia, *G.Pedralli 3315* (HUEFS); Santa Rosa do Tocantins, *G.Pedralli 3354* (HUEFS).

***Hymenaea courbaril* var. *subsessilis*–BRAZIL, Amazonas**, Manaus, *W.A.Rodrigues 7906* (INPA). **Mato Grosso**, Aripuanã, *M.Gomes 576* (INPA). **Pará**, Porto Trombetas, *H.C. de Lima 6808* (RB); *S.M. de Faria 1241* (RB).

***Hymenaea courvaril* var. *villosa*–BRAZIL, Paraíba**, Near Paquivera de Netuba, *Y-T.Lee 82* (NY).