

### Zurich Open Repository and Archive

University of Zurich University Library Strickhofstrasse 39 CH-8057 Zurich www.zora.uzh.ch

Year: 2011

## Underestimated endemic species diversity in the dry inter-Andean valley of the Río Marañón, northern Peru: An example from Mimosa(Leguminosae, Mimosoideae)

Särkinen, T E; Marcelo-Peña, J L; Yomona, A D; Simon, M F; Pennington, T P; Hughes, C E

Abstract: Molecular phylogenies which include multiple accessions of species and near complete taxon sampling can be an important tool for estimating species diversity when used in combination with traditional morphology-based taxonomy. Here we use a densely sampled plastid gene tree for a morphologically complex group within the legume genus Mimosa (sect. Batocaulon ser. Andinae) to improve estimates of species limits and diversity in the poorly known dry inter-Andean valley of the Río Marañón, northern Peru. Based on the plastid gene tree, Mimosa ser. Andinae, which previously comprised four species, is re-circumscribed to include six Andean dry-forest species from northern Peru, Ecuador and southern Colombia, including the new species, M. jaenensis, described here. A further three candidate species are identified within the section based on high levels of sequence variation among accessions. With the additional species, the Marañón valley is now known to harbour nine narrowly restricted endemic species of Mimosa, a pattern of multiple congeneric endemics mirrored in many other plant genera as well as several animal groups. Our results, in combination with other published studies, suggest that overall species diversity in the Marañón has been significantly under-estimated. Further work is needed to identify conservation priority areas in the Marañón in order to protect its unique flora.

DOI: https://doi.org/10.1002/tax.601012

Posted at the Zurich Open Repository and Archive, University of Zurich ZORA URL: https://doi.org/10.5167/uzh-51346 Journal Article Published Version

#### Originally published at:

Särkinen, T E; Marcelo-Peña, J L; Yomona, A D; Simon, M F; Pennington, T P; Hughes, C E (2011). Underestimated endemic species diversity in the dry inter-Andean valley of the Río Marañón, northern Peru: An example from Mimosa(Leguminosae, Mimosoideae). Taxon, 60(1):139-150.

DOI: https://doi.org/10.1002/tax.601012

# Underestimated endemic species diversity in the dry inter-Andean valley of the Río Marañón, northern Peru: An example from *Mimosa* (Leguminosae, Mimosoideae)

Tiina E. Särkinen,<sup>1,4</sup> José Luis Marcelo-Peña,<sup>2</sup> A. Daza Yomona,<sup>2</sup> Marcelo F. Simon,<sup>1,3</sup> R. Toby Pennington<sup>4</sup> & Colin E. Hughes<sup>1,5</sup>

- 1 Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, U.K.
- 2 Herbario MOL, Departamento de Manejo Forestal, Facultad de Ciencias Forestales, Universidad Nacional Agraria La Molina, Apartado 456, La Molina, Lima, Peru
- 3 Embrapa Recursos Genéticos e Biotechnologia, PqEB, Caixa Postal 02372, Brasilia-DF, 70770-917, Brazil
- 4 Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH5 3LR, U.K.
- 5 Present address: Institute for Systematic Botany, University of Zurich, Zollikerstrasse 107, 8008 Zurich, Switzerland Author for correspondence: Tiina Särkinen, tiinasarkinen@yahoo.com

**Abstract** Molecular phylogenies which include multiple accessions of species and near complete taxon sampling can be an important tool for estimating species diversity when used in combination with traditional morphology-based taxonomy. Here we use a densely sampled plastid gene tree for a morphologically complex group within the legume genus *Mimosa* (sect. *Batocaulon* ser. *Andinae*) to improve estimates of species limits and diversity in the poorly known dry inter-Andean valley of the Río Marañón, northern Peru. Based on the plastid gene tree, *Mimosa* ser. *Andinae*, which previously comprised four species, is re-circumscribed to include six Andean dry-forest species from northern Peru, Ecuador and southern Colombia, including the new species, *M. jaenensis*, described here. A further three candidate species are identified within the section based on high levels of sequence variation among accessions. With the additional species, the Marañón valley is now known to harbour nine narrowly restricted endemic species of *Mimosa*, a pattern of multiple congeneric endemics mirrored in many other plant genera as well as several animal groups. Our results, in combination with other published studies, suggest that overall species diversity in the Marañón has been significantly under-estimated. Further work is needed to identify conservation priority areas in the Marañón in order to protect its unique flora.

**Keywords** Amotape-Huancabamba Zone; candidate species; chloroplast DNA; cryptic diversity; new species; sectional re-circumscription

#### **■** INTRODUCTION

Conservation planning and priorities should ideally be based on measures of species diversity and endemism, but for many tropical areas, factors such as collecting deficit and incomplete taxonomic knowledge can lead to serious underestimates of diversity. While increased field collecting in poorly known areas is critical for understanding how biodiversity is distributed both locally and more regionally (Knapp, 2002), the tasks of identifying species and delimiting and describing new taxa can be challenging, especially for large and morphologically complex taxonomic groups.

The availability of relatively inexpensive and rapid DNA sequencing has provided taxonomists with an additional tool for detecting and delimiting species and estimating species diversity. Recent studies using these approaches have suggested that many species that have remained undetected in traditional taxonomic revisionary work can be delimited based on deep genealogical lineages that correspond to morphological and ecological variants (e.g., amphibians: Vieites & al., 2009; butterflies: Hebert & al., 2004; fig-wasps: Molbo & al., 2003; flies: Condon & al., 2008; and parsitoid wasps: Smith & al., 2008). These so called 'cryptic species' may be defined as two

or more distinct species that were previously classified as a single species due to morphological similarity (Bickford & al., 2006; Trontelj & Fišer, 2009; Vieites & al., 2009). The depth of the lineage split, coupled with morphological differences not noted or used in previous taxonomies, is often used to justify the recognition of these clades as species, or candidate species (as in many animal studies, e.g., Vieites & al., 2009).

Studies aiming to identify and explore the presence of cryptic diversity rely on densely sampled phylogenies including multiple accessions (populations, and individuals within populations) sampled per species, combined with complete or near-complete sampling of known species, and in-depth taxonomic knowledge of the study group (e.g., Vieites & al., 2009). Once a robust and densely sampled phylogeny is available, cryptic species can be detected based on topology. Monophyletic clades of accessions comprising distinct morphological and/or geographical lineages, subtended by long branches and deep lineage splits, are the simplest case of cryptic species. These have been referred to as monophyletic 'cryptic species' clades (Bickford & al., 2006; Vieites & al., 2009). Para- or polyphyletic cryptic species clades are more problematic, however. These terms refer to taxa that have been previously recognised as a single species, but are resolved as para- or polyphyletic on

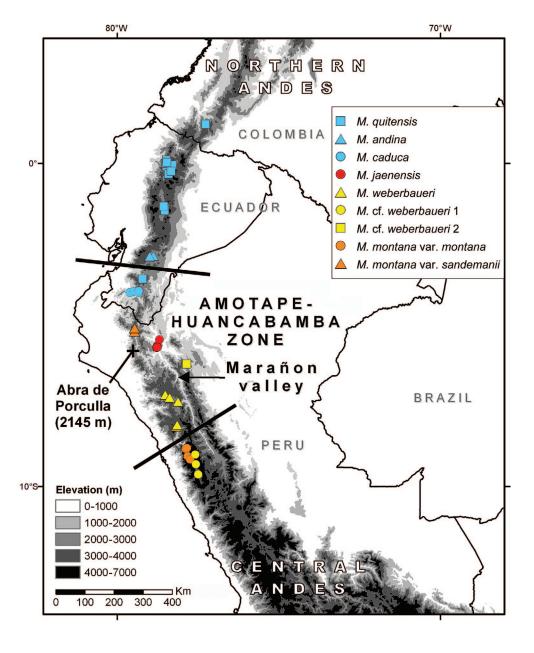
a gene tree. There can be many causes why taxa are resolved para- or polyphyletic, including hybridization, introgression and incomplete lineage sorting, but where the para- or polyphyletic entities are correlated with morphology, ecology and/or geography, these lineages can represent previously undetected cryptic species (Funk & Omland, 2003).

So far, there are only a few examples of densely sampled phylogenetic studies for tropical plants (e.g., Lavin & al., 2003; Sotuyo & al., 2007). This is mainly due to the general failure of phylogeographic studies in plants, in which plastid DNA (cpDNA) yields generally low levels of sequence variation (Bickford & al., 2006). The availability of markers with adequate levels of sequence variation has not been a problem in many animal groups, where mitochondrial DNA (mtDNA), unlike in plants, evolves rapidly enough to provide resolution at shallow taxonomic levels (Bickford & al., 2006). More densely sampled phylogenies of tropical plant groups are likely

to rapidly increase as more variable DNA sequence loci become available (Bickford & al., 2006). The few densely sampled species-level phylogenies that have been published thus far indicate that taxa endemic to particular tropical biomes, such as the Neotropical seasonally dry tropical forests (SDTF), might show generally higher levels of sequence divergence compared to other biomes (e.g., Lavin & al., 2003; Lavin, 2006; Sotuyo & al., 2007; Simon & al., 2009; Pennington & al., 2010). This is thought to be due to the long evolutionary history of the SDTF flora in South America (Lavin & al., 2003; Lavin, 2006; Sotuyo & al., 2007; Pennington & al., 2009).

In this study we use a densely sampled plastid gene tree to re-examine species delimitation and diversity in the morphologically complex series *Andinae* Barneby (sect. *Batocaulon* Barneby) of the legume genus *Mimosa* L. (Mimosoideae, Leguminosae) as part of work to estimate species diversity and endemism in the dry inter-Andean valley of the Río

Fig. 1. Map of northern Peru and Ecuador, showing the location of the Marañón valley within the Amotape-Huancabamba Zone between the Central and Northern Andes, and the distribution of species of Mimosa ser. Andinae. The new species, including the three candidate species, are labelled M. jaenensis, M. cf. weberbaueri 1, M. cf. weberbaueri 2, and M. montana var. sandemanii. The Marañón valley lies between the Cordillera Occidental to the west, and Cordillera Central to the east. The Huancabamba Depression where the Andean cordilleras descend to their lowest elevation is just west of the Marañón valley at Abra de Porculla (2145 m elevation), Dept. Piura, northern Peru.



Marañón, northern Peru. The ca. 250 km long Marañón valley is situated within the biogeographically interesting Amotape-Huancabamba Zone at the meeting point of the Northern and Central Andes close to where the Andean cordilleras reach their lowest elevation at Abra de Porculla (2145 m) (Fig. 1; Weigend, 2002). The Marañón dry forests extend north from Pataz (Dpto. La Libertad) along the deep, narrow and geographically isolated trench of the Río Marañón to the Bagua Grande area and the lower flanks of the Rio Chinchipe and Utcubamba tributaries (Dptos. Cajamarca and Amazonas) (Fig. 1). These Marañón dry forests have long been known to harbour significant numbers of endemic plants (Hensold, 1999; Weigend, 2002; Young & al., 2002; Bridgewater & al., 2003; Linares-Palomino, 2006) and animals (e.g., birds, Stattersfield & al., 1998), and a recently assembled preliminary checklist of woody dry-forest plants in Peru lists 69 species endemic to the Maranón amounting to 38% of the woody flora (Linares-Palomino & Pennington, 2007). However, there is evidence that species diversity and endemism in these forests may have been significantly underestimated.

The genus *Mimosa* comprises ca. 530 species, distributed mainly in the Neotropics with ca. 40 species in the Old World (Barneby, 1991). Mimosa is well-known for its sensitive, bipinnate leaves and the weedy habits of some of its species (e.g., M. pudica L. and M. pigra L.) which can be aggressive invasives. However, the majority of species of *Mimosa* are narrowly distributed endemics restricted to savannas or SDTFs, such as the Marañón valley, which is known to harbour eight endemic Mimosa species. Despite a relatively recent monographic account of Neotropical Mimosa (Barneby, 1991), many new species continue to be described (e.g., Barneby, 1992, 1993; Grether & Martinez-Bernal, 1996; Fortunato & Palese, 1999; Queiroz & Lewis, 2000; Atahuachi & Hughes, 2006; Lewis & al., 2010; Simon & al., 2010). Mimosa ser. Andinae, which is the focus of this study, currently comprises four species, M. andina Benth., M. weberbaueri Harms, M. montana Kunth and M. quitensis Benth., all of them restricted to the dry forests of northern Peru, Ecuador and southern Colombia. The series has previously been defined by the combination of pentamerous flowers, microphyllidious leaves, and pseudofollicular or follicular pod dehiscence (Barneby, 1991).

#### ■ MATERIALS AND METHODS

**Taxon sampling.** — Multiple accessions of all four species of *Mimosa* ser. *Andinae*, as well as a near-complete sampling of all other Andean *Mimosa* species were used in this study, making a total of 76 Andean *Mimosa* accessions (29 of the 30 Andean endemics, plus four of the five widespread Neotropical species found in the Andes; Barneby, 1991, 1993; Atahuachi & Hughes, 2006; Lewis & al., 2010) (Appendix). Sequences were analysed as part of a much larger sample that included 259 (49%) of the 530 species representing the morphological, geographic and ecological diversity of *Mimosa* (Simon & al., 2009) in order to properly assess the relationships of the Andean species in the context of the genus as a whole.

Molecular methods. — Total genomic DNA from silicadried leaves or herbarium material was isolated using the DNeasy Plant Mini Kit (Qiagen). The trnD-trnT non-coding chloroplast region (Shaw & al., 2005) was used as it is variable at species level, and because of the large number of sequences already available for Mimosa (Simon & al., 2009). For most samples the trnD-trnT locus was amplified in a single PCR reaction using the Shaw & al. (2005) primers plus an additional forward primer trnD2 (GTG TAC AGC ATG CAT ATT CTT ACG) designed by Simon & al. (2009). For highly degraded DNA templates, amplifications were performed using internal primers trnE and trnY, and sometimes the primer trnT2 (GAC GTA TCG CCG AGT AAT TCC; Simon & al., 2009). Reactions were carried out in a total volume of 25 µl containing ~5– 20 ng of DNA template, 1× Buffer, 0.5 M of betaine, 1.5 mM of MgCl<sub>2</sub>, 0.1 mM of each dNTP, 0.5 µM of each primer, and 0.6 U of Taq polymerase (Yorkshire Bioscience). PCR conditions were 94°C for 45 s, 30 cycles of 45 s at 94°C, 1 min at 55°C and 1 min at 72°C, followed by a final extension of 5 min at 72°C. PCR products were purified using exonuclease I and shrimp alkaline phosphatase (Exo/SAP) and sequenced in four reactions using the two PCR primers and two internal primers, following Big Dye chemistry. Consensus sequences from the four strands were assembled using Sequencher software (GeneCodes Corp., Ann Arbor, Michigan), and aligned using ClustalW with default settings as implemented in BioEdit Sequence Alignment Editor v.7.0.9 (Hall, 1999-2007) with manual adjustments.

**Phylogenetic analyses.** — The final alignment (2337 base pairs) included a number of informative indels, but these were not used in the Bayesian analysis. GenBank accession numbers and voucher information for newly published sequences are in the Appendix. Bayesian analyses were conducted using MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2003; Ronquist & Huelsenbeck, 2005) on the free online Bioportal (www.bioportal.uio.no). The GTR+G+I nucleotide substitution model was chosen based on the Akaike Information Criterion as implemented in Modeltest (Posada & Crandall, 1998). Each Markov chain was started from a random tree and ran for up to 10 million generations, with a sampling frequency of 1000. Two independent runs of four chains were run simultaneously with default priors. The initial one million generations were discarded as burn-in samples.

**Morphological evaluation.** — The molecular analysis was coupled with a re-assessment of the morphological characters and variation used by Barneby (1991) to delimit species (Table 1) by examining ca. 60 herbarium sheets from key herbaria (AAU, E, FHO, K, MOL, NY, OXF).

#### **■ RESULTS**

**Sequence divergence.** — There are 654 variable characters in the *trnD-trnT* dataset within *Mimosa*, and 423 (18.1% of total characters) parsimony-informative (PI) characters, of which 28 (1.9% of total characters) are informative within clade C where all members of *Mimosa* ser. *Andinae* are placed

**Table 1.** Morphological differences between species of Mimosa sect. Batocaulon ser. Andinae, including the new species M. jaenensis and the three candidate species here designated as M. cf. weberbaueri 1, M. cf. weberbaueri 2, and M. montana var. sandemanii. See text for details on the fruit dehiscence types.

	M. cf. w M. weberbaueri baueri 1	M. cf. weber-baueri 1	M. cf. weber-baueri 2	M. montana var. sandemanii	M. montana var. montana	M. jaenensis	M. caduca	M. andina	M. quitensis
Number of pairs of pinnae	5-7	4-6(-7)	6-9	1–2	1–2	3–5	4-6	2–3	(5-)6-13
Leaflet pairs per pinna	9–15	8–13	14–18	5–6	4-8	9–17	6-10	7–10	11–20
Leaflet size (mm)	$3-5 \times 0.8 - 1.8$	$2-3 \times 0.7 - 1.3$	$4-5 \times 0.8 - 1.5$	$2-4 \times 0.6 - 2.0$	$2-4 \times 0.6 - 2.0$	$1.5-3.5\times0.8-1.0$ $8-13\times3.0-6.5$	$8-13 \times 3.0-6.5$	$4.5 - 7.5 \times 1.6 - 2.7$	$4.5-7.5 \times 1.6-2.7$ $1.6-3.0 \times 0.5-0.8$
Leaf rachis including petiole (mm) 20–70	20–70	30–35	20–70	3.5–15(–18)	3.5–15(–18)	(15-)19-30	40–100	20–45	(15–)20–65
Peduncle (mm)	15–25	10–20	18–25	8–21	8–21	8-10(-11)	9–20	5–25	10–26
Capitula diameter (mm)	5-7	5-7	5-7	5-7	4-5	5-5.5	5-7	6-7.5	6.5-8
Capitula length (mm)	7–15	7–12	23–35	5-8	3-4	4-5	6-10	9–11	5–6
Calyx length (mm)	0.5-1	1–1.5	ż	1.5–2	0.5-1	0.5	1–1.5	1–2	1–1.5
Corolla length (mm)	2–3	3-4	ż	3–3.5	2–3	2–3	2–3.5	2.5–3.5	3-4
Stamen length (mm)	7–10	7–9	ن	2-9	2-9	2-9	4–5	4–6	7–8
Mode of fruit dehiscence	Pseudo-follicular	Pseudo-follicular Pseudo-follicular Unknown	Unknown	Pseudo-follicular	Pseudo-follicular Pseudo-follicular Craspedium	Craspedium	Craspedium	Follicular	Follicular
Fruit size (cm)	$5-7 \times 0.8 - 1.0$	$5-7 \times 0.8 - 1.0$	Unknown	$2.0 - 4.5 \times 0.5 - 0.7$	$2.0 - 4.5 \times 0.5 - 0.7  2.0 - 4.5 \times 0.5 - 0.7  2.5 - 4.0 \times 0.6 - 0.9  4 - 5 \times 0.5 - 0.8$	$2.5 - 4.0 \times 0.6 - 0.9$	$4-5 \times 0.5 - 0.8$	$4.5-6.0\times0.9-1.4$ $3-7\times0.6-0.8$	$3-7 \times 0.6 - 0.8$
Replum armed with aculei	Yes	Yes	Unknown	Occasionally	Occasionally	No	No	No	No

(Fig. 2). Within clade C, the highest sequence divergence is between *M. jaenensis* and *M. caduca* (1.1%, uncorrected and corrected pairwise distance with GTR+G+I model), with lower (0.5%–0.6%) sequence divergences (uncorrected distances) found between *M. jaenensis* and *M. weberbaueri*, and *M.* cf. weberbaueri 1 and *M.* cf. weberbaueri 2.

**Mimosa ser. Andinae.** — All four species of ser. Andinae are placed within a robustly supported monophyletic group (clade C, Fig. 2), which is nested within a larger clade which includes ca. 60 Mesoamerican dry-forest species with pentamerous or tetramerous flowers from various series of *Mimosa* sect. Batocaulon (clade B, Fig. 2). Within clade C, the plastid gene tree strongly suggests re-circumscription of ser. Andinae to include the two additional Andean dry-forest species M. jaenensis sp. nov. (see below) and M. caduca (Humb. & Bonpl. ex Willd.) Poir. (Fig. 2).

The morphological, ecological and geographic affinities of M. caduca to ser. Andinae were noted by Barneby (1991), despite his placement of the species in M. ser. Bimucronatae Barneby. Mimosa caduca is a narrowly restricted Andean dry-forest endemic from southern Ecuador, with pentamerous flowers like other members of ser. Andinae (Barneby, 1991). However, M. caduca differs in having pods that readily break up into indehiscent one-seeded articles leaving a persistent replum (i.e., craspedial pod dehiscence sensu Barneby, 1991), whilst other species of ser. Andinae have pods where the valves break away entire from the replum (i.e., follicular dehiscence sensu Barneby, 1991) or only tardily disjointing into articles (i.e., pseudofollicular pods sensu Barneby, 1991). With the addition of the new species M. jaenensis (see below), which also has pods with craspedial pod dehiscence similar to M. caduca, it is clear that ser. Andinae needs to be expanded to include species with different modes of dehiscence.

While inclusion of *M. caduca* and *M. jaenensis* within ser. Andinae is justified based on the plastid gene tree, morphology, ecology and geography, further work is needed to resolve the placement of the two lowland South American species placed in clade C, M. detinens and M. hexandra. These two taxa differ from ser. Andinae in terms of morphology, distribution and ecology, and were placed in M. ser. Farinosae Barneby and ser. Bimucronatae, respectively, in sect. Batocaulon by Barneby (1991). Denser taxon sampling is needed to fully explore the re-delimitation of these two series as they are polyphyletic on the plastid gene tree (Simon & al., 2009). It is clear, however, that all members of ser. Farinosae and ser. Bimucronatae including species likely to be phylogenetically closely related to M. detinens and M. hexandra, such as M. exalbescens and M. ostenii currently not sampled – are distributed outside the Andes in different biomes such as Chaco and seasonally inundated scrublands, and differ further from ser. Andinae in having 3-4-merous flowers.

**Species delimitation and cryptic species within Mimosa ser. Andinae.** — The six species placed in the expanded ser. *Andinae* can be distinguished morphologically based on quantitative leaf traits, armature, arrangement of flowering shoots, and pod dehiscence (Table 1). Multiple accessions of four of these species, *M. caduca*, *M. quitensis*, *M. andina*, and *M. jaenensis*,



**Fig. 2.** Position of ser. *Andinae* within *Mimosa* and species relationships within ser. *Andinae*. **A,** Phylogeny of *Mimosa* and outgroups based on Simon & al. (2009) with the addition of 52 accessions from the Andes. Bayesian majority-rule consensus tree based on analysis of 339 non-coding plastid *trnD-trnT* DNA sequences. Posterior probability (PP) values are shown above branches, while branches with less than 0.8 PP are marked with asterisks. Major clades are drawn in proportion to expected species numbers. **B,** Species relationships within ser. *Andinae*. Posterior probability (PP) values are shown above branches, while branches with less than 0.8 PP are marked with asterisks. The new species, including the three candidate species, are labelled *M. jaenensis*, *M.* cf. *weberbaueri* 1, *M.* cf. *weberbaueri* 2, and *M. montana* var. *sandemanii*.

form robustly supported monophyletic species clades (Fig. 2), with high levels of sequence divergence (0.5%–1.1% uncorrected pairwise distances). Results regarding the new taxon, *M. jaenensis*, and the two species which are resolved polyphyletic on the plastid gene tree (*M. montana* and *M. weberbaueri*), are discussed in more detail below.

The robustly supported *M. jaenensis* clade, which is made up of four accessions from a narrowly restricted area around Jaén (Dpto. Cajamarca, northern Peru) (Fig. 2), shows high sequence divergence (1.1%) compared to morphologically wellestablished species such as *M. quitensis* and *M. caduca* (0.7%). Material from these populations was first identified as *M.* aff. weberbaueri based on flowering material alone, but the plastid gene tree topology and subsequent collection of fruiting specimens confirms that these populations from Jaén should be recognised as a distinct species. These individuals differ from *M. weberbaueri* in quantitative leaf traits, armature, inflorescence characters and fruit morphology (Table 1).

Accessions of two species, *M. weberbaueri* and *M. montana*, are resolved polyphyletic on the plastid gene tree (Fig. 2). In both species, the polyphyly corresponds to morphological variants, some of which have been previously recognized as distinct species or infraspecific varieties, suggesting the presence of additional cryptic species within ser. *Andinae*. The first of these, *M. montana*, is straightforward in that the polyphyletic lineages correspond to the two morphological varieties are geographically restricted: typical *M. montana* var. *montana* occurs from Dpto. Cajamarca south to the Santa valley in Dpto. Ancash, whilst *M. montana* var. *sandemanii* Barneby, which is represented by a single accession in the plastid gene tree, is restricted to the Huancabamba valley in Dpto. Piura (Fig. 1) (Barneby, 1991).

The second polyphyletic species, M. weberbaueri, presents a more complex and poorly studied pattern of morphological variation. Within M. weberbaueri, there are three distinct morphological units: M. weberbaueri itself, M. cf. weberbaueri 1, and M. cf. weberbaueri 2 (Fig. 2). One of these, M. cf. weberbaueri 1, is a morphologically distinct higher-elevation variant from Dpto. Ancash which corresponds to the previously described taxon, M. dichoneuta Macbride (Macbride, 1930, 1943), which was treated as conspecific with M. weberbaueri by Barneby (1991). The placement of M. cf. weberbaueri 1 apart from other M. weberbaueri accessions in the plastid gene tree suggests that the Ancash populations could indeed represent a distinct species as proposed by Macbride (1930, 1943). The isolated Ancash populations differ from specimens of M. weberbaueri from further north in Dptos. Cajamarca and La Libertad in the size of leaflets and flowers, as well as in their calyx indumentum (Table 1).

A third cryptic species is represented by two accessions labelled as *M.* cf. *weberbauri* 2, which are nested together with accessions of *M. weberbaueri* in the plastid gene tree (Fig. 2). Despite the lack of sequence divergence, these accessions represent another case of cryptic species based on morphology alone. The main morphological difference between the two taxa is in the size and shape of the inflorescence. The

accessions of *M.* cf. *weberbaueri* 2 from Dpto. Amazonas have distinctly spicate inflorescences not observed in any other Andean species of *Mimosa*, and differ from those of typical *M. weberbaueri* from Dptos. Cajamarca and La Libertad which have ellipsoid capitate inflorescences (Table 1; Figs. 2–3). The morphological differences are striking, but as all the available specimens of *M.* cf. *weberbaueri* 2 lack fruits, further material is needed to confirm the distinctions of this candidate new species.

#### DISCUSSION

**Mimosa ser. Andinae.** — With the addition of *M. jaenensis* and *M. caduca*, ser. *Andinae* now includes a set of six ecologically similar species endemic to the seasonally dry tropical forests from northern Peru, Ecuador and adjacent southern Colombia. Although ecologically and morphologically similar to other members of ser. *Andinae*, the two additional species differ from rest of the series in their mode of pod dehiscence, and the concept of the series is here broadened to include species with diverse fruit dehiscence, including craspedial, follicular, and pseudofollicular pods.

The discovery of well-resolved lineages in the plastid gene tree, which correspond to previously recognised taxa or, in some cases, unrecognised morphological variants, reflects cryptic diversity within ser. Andinae in northern Peru. Four cryptic species were identified based on morphological differences, which in most cases were coupled with sequence divergence in the plastid gene tree: M. jaenensis sp. nov., M. cf. weberbaueri 1 (i.e., M. dichoneuta), M. cf. weberbaueri 2, and M. montana var. sandemanii. One of these cryptic species, M. jaenensis, is described as new (below), but the formal recognition of the three other taxa must await denser sampling of accessions and genes. Two of the taxa, M. dichoneuta and M. montana var. sandemannii, are represented by single sequences in the plastid gene tree, and more accessions are needed to test the monophyly of these taxa. The need for dense sampling within species has been highlighted by other recent studies (e.g., Sotuyo & al., 2007; Queiroz & Lavin, in press; Duno de Stefano & al., 2010). A biparentally inherited nuclear gene tree would also be valuable to look for evidence of potential reticulation. Furthermore, the important node grouping M. montana var. sandemannii with the Weberbaueri clade is unsupported, and there are lingering gaps in the morphological data (e.g., lack of pods to compare M. dichoneuta with M. weberbaueri, etc.). Confirmation of the status of these three taxa as distinct species must await more intensive field collecting, but meanwhile, they can be considered candidate species sensu Vieites & al. (2009).

**Cryptic species diversity.** — The results presented here illustrate the use of densely sampled gene trees, in combination with traditional morphology-based taxonomy, as a valuable approach in discovering new and often cryptic taxa for large and morphologically complex genera like *Mimosa*. The value of this approach, where multiple accessions per species are sequenced and analysed, has also been demonstrated by other

recent studies (Queiroz & Lavin, in press; Duno de Stefano & al., 2010; Pennington & al., 2010 and in press). These studies highlight the need for dense sampling in species-level phylogenetic studies in plants in order to fully explore the depth of sequence divergence.

**Species diversity in the Marañón valley.** — Even without a complete checklist of vascular plants, it is clear that levels of endemism are extremely high in the Marañón, and that overall species diversity in the valley has been underestimated. Many

new endemic species to the Marañón have been described just in the last decade alone (e.g., Leguminosae: Hughes & al., 2003, 2004; Hughes, 2005; Lewis & al., 2010; Polygonaceae: Pendry, 2004; Clusiaceae: Mats Gustafsson, unpub. data; Malpighiaceae: William Anderson, unpub. data; geckos: Koch & al., 2006; Venegas & al., 2008; scaled lizards: Reeder, 1996; harlequin frogs: Lötters & al., 2004; land snails: Thompson, 1982). This suggests that the Marañón dry forests remain undercollected and poorly known.

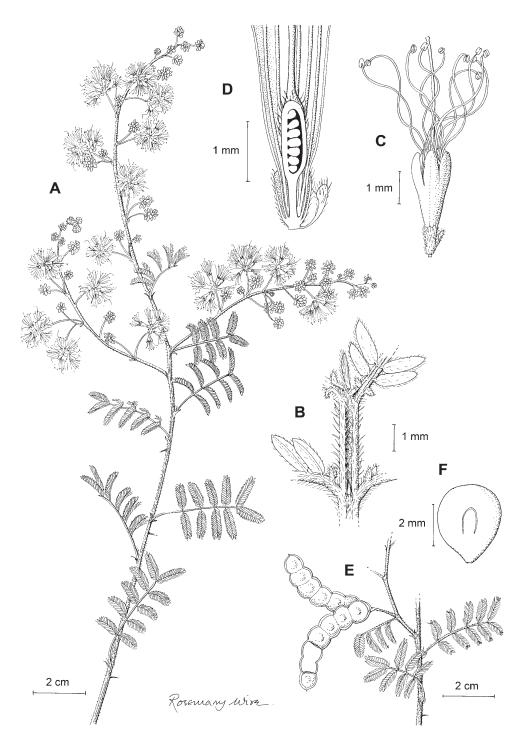


Fig. 3. Mimosa jaenensis. A, Habit; B, leaf rachis showing spicules between pinnae pairs, paraphyllidia at the base of each pinna, and leaflets; C, flower; D, longitudinal section of flower; E, pods; F, seed. A–D, Särkinen & al. 3070; E–F, Särkinen & al. 3062. Illustration by Rosemary Wise.

The discovery of cryptic species in *Mimosa*, and in other Andean dry-forest groups such as in the Andean jay genus *Cyanolyca* (Bonaccorso, 2009), further suggests that diversity and endemism in the Marañón may have been even more substantially underestimated. The illumination of species boundaries and cryptic diversity in ser. *Andinae* provided by the densely sampled plastid gene tree, which resulted in description of one new species and recognition of three additional candidate species, represents a 100% increase in estimates of species diversity within this group.

The Marañón valley is now known to harbour nine endemic Mimosa taxa including the three putative candidate species (M. ctenodes Barneby, M. incarum Barneby, M. montana var. sandemanii, M. pectinatipinna Burkart, M. cf. weberbaueri 2, M. jaenensis, M. polycarpa Kunth var. polycarpa, M. polycarpa var. redundans Barneby, M. lamolina C.E. Hughes & G.P. Lewis), as well as at least three more widespread taxa (M. caduca, M. revoluta (Kunth) Benth., M. albida Kunth var. albida). Many other plant genera also have multiple congeneric Marañón endemics (e.g., Armatocereus Backeb., Browningia Britton & Rose, Espostoa Britton & Rose, Matucana Britton & Rose, Caesalpinia L., Calliandra Benth., Coursetia DC., Senna Miller, Clusia L., Jacquemontia Choisy, Ruprechtia C. Meyer, Onoseris Willd. (Lavin, 1988; Bregman, 1996; Lewis, 1998; Pendry, 2004; Hughes, 2005; Lewis & al., 2010; Mats Gustafsson, unpub. data). The same pattern is observed for many animal groups, such as Inca-finches (Incaspiza: Stattersfield & al., 1998), geckos (Koch & al., 2006; Venegas & al., 2008), scaled lizards (Reeder, 1996), land snails (Thompson, 1982), and harlequin frogs (Lötters & al., 2004).

Patterns of species diversification. — In Mimosa, one of the striking features of the molecular phylogeny of ser. Andinae is the monophyly of the narrowly restricted, geographically isolated species and generally high levels of sequence divergence, suggesting that these Andean SDTF species have been isolated for a relatively long time. Other Andean SDTF legume genera, such as Coursetia, Poissonia, and Cyathostegia, show similar patterns of geographic structure coupled with strikingly deep lineage splits even within morphologically uniform species between isolated populations (Lavin & al., 2003; Lavin, 2006; Pennington & al., 2010 and in press). These results suggest that the fragmented distribution of the Andean SDTF and the strong physical isolation of individual forest nuclei surrounded by the high Andean cordilleras has played a central role in driving species diversification (Pennington & al., 2010). The high local endemism in the area, including the higher-elevation habitats of the wider Amotape-Huancabamba Zone (Weigend, 2002; Weigend & al., 2010), further highlight the effects of topographical complexity and physical isolation in fostering high numbers of narrowly restricted species.

**Conservation implications.** — The unique assemblages of multiple congeneric endemics found in the Marañón are notable among Neotropical floras and faunas. Despite this, the conservation value of the Marañón forests has hardly been recognised. In a recent study by Morawetz & Raedig (2007), the Marañón valley was identified as one of the most important

centres of Neotropical endemism in need of protection. Bird-Life International has assigned the Marañón valley the status of an Endemic Bird Area, as the region hosts 16 endemic bird species within just 11,000 km² (Stattersfield & al., 1998). With its highly endemic flora (38% endemism in woody plants alone; Linares-Palomino, 2006), the Marañón valley can be considered as a biodiversity hotspot of global conservation priority in its own right. Although likely an underestimate, the high level of endemism in the Marañón SDTF flora is comparable to well-known oceanic island floras such as the Galapagos (43% endemism in vascular plant flora; Tye, 2000). The American Bird Conservancy has proposed the Marañón-Alto Mayo Conservation Corridor for protection (Angulo & al., 2008), but despite these international calls and the steadily accumulating evidence on their global conservation importance, the Marañón valley dry forests remain unprotected.

	dence on their global conservation importance, the Marañón ley dry forests remain unprotected.
	■ TAXONOMIC TREATMENT
	Key to Mimosa sect. Batocaulon ser. Andinae
1	Petiole including leaf rachis 0.3–4.5 cm long; leaves with 1–3 pairs of pinnae, 4–10 pairs of leaflets per pinna 2
1	Petiole including leaf rachis (1.5–)1.9–10.0 cm long; leaves with (3–)4–13 pairs of pinnae, 6–20 pairs of leaflets per pinna; if leaves with 3 pairs of pinnae, then each pinna with 9–17 pairs of leaflets
2	Petiole plus leaf rachis 2.0–4.5 cm; rachis of longer pinnae 2–4 cm; leaflets 4.5–7.5 mm long; inter-Andean Ecuador
2	Petiole plus leaf rachis 0.3–1.2 cm; rachis of longer pinnae 0.4–1.2 cm; leaflets 2–4 mm long; central and northern Peru
3	Capitula, excluding stamens, 4–5 mm in diameter; calyx 0.5–1.0 mm long; corolla 2–3 mm long; Dpto. Cajamarca to Dpto. Ancash, at 2100–3100 m elevation
3	Capitula, excluding stamens, 5–7 mm in diameter; calyx 1.5–2.0 mm long; corolla 3.0–3.5 mm long; Huancabamba valley, Dpto. Piura, at 1800–2500 m elevation.
4	Each pinna with 6–10 pairs of leaflets; leaflets 8–13 × 3.0–6.5 mm, weakly coriaceous
4	Each pinna with 8–20 pairs of leaflets; leaflets 1.6–5.0 × 0.5–1.8 mm, chartaceous
5	Leaves with 3–5 pairs of pinnae; peduncle 0.8–1.0(–1.1) cm long; at 500–800 m elevation
5	Leaves with 4–13 pairs of pinnae; peduncle 1.0–2.6 cm long; at 1700–3700 m elevation
6	Leaves with (5–)6–13 pairs of pinnae; leaflets 1.6–3.0 × 0.5–0.8 mm; capitula 5–6 mm long; inter-Andean valleys in Ecuador and Colombia
6	Leaves with 4–9 pairs of pinnae; leaflets 2.0–5.0 × 0.7–1.8 mm; capitula 7–35 mm long; inter-Andean valleys in Peru
7	Leaves with 6–9 pairs of pinnae, each with 14–18 pairs

- leaflets; capitula 7–15 mm long excluding stamens . . . . 8

#### **Description of Mimosa jaenensis**

Mimosa (sect. Batocaulon, ser. Andinae) jaenensis T.E. Särkinen, J.L. Marcelo-Peña & C.E. Hughes, sp. nov. – Type: PERU. Dpto. Cajamarca, Jaén, ca. 5 km NW from Jaén, close to Gota de Agua (5°41′59″ S 78°46′59″ W), 13 Apr 2008 (fls. and fruits), coll. T.E. Särkinen, A. Daza Y., H. Vandrot & S. D'Ugard 3062 (holotype: MOL; isotypes: FHO, K, NY, USM).

Mimosa montanae et M. weberbaueri in habitu generali arctissime affinis sed a M. montana pinnis pluribus (3–5 non 1–2) et foliolis per pinnam pluribus (9–17 non 4–8), pseudoracemis in surculis efoliatis portatis, et leguminibus lunatim incurvatis cum marginibus inter loculos constrictis differt; a M. weberbaueri rachidibus foliorum et pinnarum inermibus (haud aculeatis), pinnis paucioribus (3–5 non 5–9) et foliolis maximis brevioribus (1.5–3.0 mm non 3–5 mm), capitulis brevioribus (4-5 mm longis non 7-15(-35) mm), et leguminibus brevioribus (2.5–4.0 cm non 5–7 cm longis) cum replo inermi recedit; intra seriem Andinas ab omnibus aliis speciebus (M. caduca excepta) leguminibus indehiscentibus in articulos 1-seminales facile rumpentibus distincta; a M. caduca leguminibus inter loculos constrictis et foliolis multo minoribus  $(1.5-3.5 \text{ mm longis} \times 0.8-1.0 \text{ mm latis, non } 8-13 \times 3.0-6.5 \text{ mm})$ concoloribus haud discoloribus facile distinguenda.

Arborescent shrub 1.5-4.0 m high, multi-stemmed from the base, stems up to 3.5 cm in diameter, highly branching with stiff virgate shoots, woody stems cinnamon-brown, longitudinally striate or weakly ridged, eratically armed with short, 2.0–2.5(–4.0) mm long, straight, internodal aculei, flowering shoots conspicuous pseudoracemes of solitary or more often 2–3(–4)-nate capitula on essentially efoliate shoots exserted 10–15(–20) cm beyond foliage prior to anthesis, the whole plant more or less puberulent, the shoots, the leaf rachis including the petiole, stipules, leaflets and peduncles covered by fine whitish-grey hairs less than 0.3 mm and scattered livid reddish granules, the hornotinuous shoots and foliage often densely hairy, becoming less so with age. Stipules subulate-setiform,  $(2-)3-5 \times 0.5$  mm wide at base, persistent. Leaves bipinnate, 3-5-jugate, the leaf rachis (1.5-)1.9-3.0 cm long including a (5-)7-9(-12) mm long petiole, the distance between pinnae 5–8 mm, borne on a slightly swollen 1 mm long pulvinus, the rachis deeply grooved above, with minute 0.2–1.0 mm long spicules between most pinnae pairs, and ending in a short 0.3– 0.4 mm long, mucro. Leaflets (9–)11–15(–17) pairs per pinna, a pair of small subulate ca. 0.2–0.5 mm long paraphyllidia at base of each pinna, the pinnae (10–)14–17 mm long, deeply grooved and ending in a short pointed mucro, ca. 1 mm between leaflets, larger leaflets 1.5–3.5 × 0.8–1.0 mm, linear-oblong, apex acute, base truncately asymmetric, concolourous, weakly 1-nerved below, the midrib nearly centric, no venation visible below, sparsely pubescent below and on margins, nearly glabrous above. Capitula on (6–)8–10(–11) mm-long peduncles, globose or very weakly ellipsoid, lax, few (17-24)-flowered, deeply moriform in bud, the minute bracts greatly overtopped by flowers even in bud, the capitula without filaments 4–5 × 5.0–5.5 mm. Flowers sweetly scented, sessile, 5-merous, diplostemonous; floral bracts inconspicuous, 0.7–1.0 mm long, spathulate, puberulent, readily caducous prior to anthesis; calyx reduced to a 0.5-1.0 mm diminutive, subtruncate campanulate ring with a fimbriate margin, puberulent; corolla narrowly vase-shaped, the petals to 2.0–3.5 mm long, 1-nerved, sparsely puberulent in bud and glabrous when mature, pale whitishgreen, lobe tips acute; stamens 10, these 6-9 mm long, creamwhite, ovary short-stipitate, obovate  $1.0 \times 0.5$  mm, glabrous to densely hairy, style up to 7 mm. Fruit a craspedium, sessile or nearly so, in clusters of 1–2(–4) per capitulum, broadly oblong, lunately incurved, the margins clearly constricted between the seed chambers, strongly plano-compressed, the seed chambers suborbicular, low colliculate over seeds, the apex shortly acute,  $25-35(-40) \times 6-9$  mm; the valves chartaceous, glabrous or sparsely puberulent, green tinged reddish unripe, turning pale brown when ripe, 4-6(-7) seeds per pod, the pods breaking up readily into indehiscent 1-seeded articles to leave a persistent replum, setae or aculei completely absent, the replum glabrous to puberulent. Seeds suborbicular, lentiform, compressed 3 × 3 mm, the brown testa smooth and hard, marked on both sides by a horseshoe-shaped pleurogram with 90% arm extension and open towards the hilum. See Fig. 3.

Additional specimens examined. — PERU. Dpto. Cajamarca: Jaén, sector San Isidro, 14 Apr 2006, *J.-L. Marcelo-Peña 1989* (MOL); Jaén, sector Shanango, 18 Dec 2006, *J.-L. Marcelo-Peña 2241* (MOL); Jaén, district Bellavista, sector La Guayaba, 27 Mar 2008, *J.-L. Marcelo-Peña 3112* (E, MOL); Jaén, district Bellavista, sector Sambimera, 11 Aug 2009, *J.-L. Marcelo-Peña 4352* (MOL); rd from Jaén to San Ignacio, 19 Apr 2007, *T.E. Särkinen & al., 2177* (FHO, K, USM, MOL); Gota de Agua, nr central Jaén, Apr 2008, *T.E. Särkinen & al., 3070, 3044* (E, MOL).

**Etymology.** — *Mimosa jaenensis* is named after the town of Jaén to highlight the high endemic plant species diversity found in the local Jaén flora, including a set of notable highly restricted endemics such as *Ditaxis katharinae* Pax (Euphorbiaceae), *Mimosa lamolina* C.E. Hughes & G.P. Lewis (Leguminosae), *Esenbeckia cornuta* Engl. (Rutaceae), *Praecereus euchlorus* (F.A.C. Weber) N.P. Taylor subsp. *jaenensis* (Rauh & Backeb.) Ostolaza, *Rauhocereus riosaniensis* Backeb. subsp. *jaenensis* Backeb. (Cactaceae), *Clusia* sp. nov. ined. (Clusiaceae) (Marcelo-Peña & al., 2010), as well as for its importance in harbouring some of the last remaining reasonably intact areas of seasonally dry tropical forest in the Marañón valley. The forests in the Marañón valley are under severe anthropogenic pressure due to their accessibility and fertile soils, and

are in need of protection. Given that no official protected areas exist, it is fortunate that several private landowners in the area are actively conserving these important dry-forest remnants.

**Phenology.** — Flowering from December to April, fruiting from April to August.

**Distribution and habitat.** — *Mimosa jaenensis* is a narrowly restricted but locally abundant endemic of the seasonally dry tropical forests of a small part of the western side of the upper Marañón valley, between 500–800 m elevation, near to Jaén, Dpto. Cajamarca (Fig. 1). It forms an understorey shrub or small treelet in dry forest and adjacent secondary dry mattoral with commonly associated species including Caesalpinia cassioides Willd., Tephrosia cinerea (L.) Pers., Leucaena trichodes Benth., Cyathostegia mathewsii (Benth.) Schery, Cordia iguaguana I.M. Johnst., Capparis guaguaensis Steyerm., Tabebuia chrysantha (Jacq.) G. Nicholson, Ceiba insignis (Kunth) P.E. Gibbs & Semir, Sideroxylon obtusifolium (Roemer & Schultes) T.D. Penn., Ruprechtia aperta Pendry, Jatropha humboldtiana McVaugh, Capparis flexuosa (L.) L., Ditaxis dioica Kunth, Zanthoxylum rigidum Humb. & Bonpl., Praecereus euchlorus (F.A.C. Weber) N.P. Taylor, Rauhocereus riosaniensis Backeb., and Browningia altissima (F. Ritter) Buxb.

**Conservation status.** — *Mimosa jaenensis* is known only from localities close to Jaén, and despite being locally abundant, is undoubtedly globally rare and is hence provisionally assigned to threat status CRb1. However, botanical knowledge of the Marañón valley remains very incomplete, and more field surveys are needed to establish just how widely distributed this species is.

Mimosa jaenensis can be confidently placed in Barneby's M. ser. Andinae of sect. Batocaulon and fits within that series comfortably in terms of both morphology and geography. Furthermore, the molecular phylogeny supports ser. Andinae (albeit with some important adjustments) as a group of closely related species, as well as the placement of M. jaenensis within that group (see Results and Discussion).

Mimosa jaenensis can be distinguished from other members of ser. Andinae, apart from M. caduca, by the mode of fruit dehiscence. Both M. jaenensis and M. caduca have craspedia that break up readily into free-falling indehiscent 1-seeded articles, whereas in other members of ser. Andinae the pod valves separate from the replum either along the dorsal side, inertly opening to release the seeds from a single cavity (pseudofollicular dehiscence, e.g., M. andina), or along both sutures, later breaking tardily into 1-seeded articles (follicular dehiscence, e.g., M. montana).

In other respects, *M. jaenensis* is morphologically most similar to *M. montana* and *M. weberbaueri*, but it can be distinguished based on a combination of quantitative leaf traits, armature and inflorescence characters (Table 1). It differs from *M. montana* in having generally larger leaves with more pairs of pinnae and more leaflets on each pinna, bearing inflorescences on pseudoracemes on efoliate shoots, and in having lunately incurved pods with the margins markedly constricted between seed chambers. *Mimosa jaenensis* can be distinguished from *M. weberbaueri* in having smaller leaflets, unarmed leaf and pinnular rachises, smaller capitula, and shorter pods with an

unarmed replum. *Mimosa jaenensis* can also be easily distinguished from *M. caduca* based on leaves alone, as *M. jaenensis* has longer leaf rachises with smaller, concolourous leaflets, differing clearly from *M. caduca* which has short leaf rachises and large, conspicuously bicoloured leaflets which are convex and shiny dark green above and pallidly silky-pilosulous beneath.

#### **■** ACKNOWLEDGEMENTS

We thank Carlos Reynel for support in Peru, the Instituto Nacional de Recursos Naturales, Lima for permission to collect plant material, Rosemary Wise for the elegant illustration, Terry Pennington for assistance with transport for fieldwork, Hervé Vandrot, Sylvia D'Ugard and Maria Baden for assistance in the field, Bente Klitgaard, Gwilym Lewis and Laszlo Csiba at the Royal Botanic Gardens, Kew for permission to extract DNA from herbarium samples and for assistance in the laboratory, and Robert Mill for translating the Latin diagnosis. This research was supported by Osk. Huttunen Fund (Osk. Huttusen Säätiö), Helsingin Sanomat Fund (Helsingin Sanomain Säätiö), Ehrnrooth Fund (Ella ja Georg Ehrnroothin Säätiö), Davis Expedition Fund (T.E. Särkinen), and by a Royal Society University Research Fellowship (C.E. Hughes).

#### **■ LITERATURE CITED**

Angulo, F., Palomino, W., Arnal, H., Aucca, C. & Uchofen, O. 2008.

Corredor de Conservación de Aves Marañón – Alto Mayo: Análisis de Distribución de Aves de Alta Prioridad de Conservación e Identificación de Propuestas de Áreas para su Conservación.

Cusco, Perú: Asociación Ecosistemas Andinos & American Bird Conservancy.

**Atahuachi, M. & Hughes, C.E.** 2006. Two new species of *Mimosa* endemic to Bolivia. *Brittonia* 58: 59–65.

Barneby, R.C. 1991. Sensitivae Censitae—A description of the genus *Mimosa* Linnaeus (Mimosaceae) in the New World. *Mem. New York Bot. Gard.* 65: 1–835.

Barneby, R.C. 1992. Centennial beans: A miscellany of American fabales. *Brittonia* 44: 224–239.

**Barneby, R.C.** 1993. Increments to the genus *Mimosa* (Mimosaceae) from South America. *Brittonia* 45: 328–332.

Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K.L., Meier, R., Winker, K., Ingram, K.K. & Das, I. 2006. Cryptic species as a window on diversity and conservation. *Trends Ecol. Evol.* 22: 148–155.

**Bonaccorso, E.** 2009. Historical biogeography and speciation in the Neotropical highlands: Molecular phylogenetics of the jay genus *Cyanolyca. Molec. Phylog. Evol.* 50: 618–632.

Bregman, R. 1996. The genus Matucana: Biology and systematics of fascinating Peruvian cacti. Rotterdam: A.A. Balkema.

Bridgewater, S., Pennington, R.T., Reynel, C., Daza Y., A. & Pennington, T.D. 2003. A preliminary floristic and phytogeographic analysis of the woody flora of seasonally dry forests in northern Peru. *Candollea* 58: 129–141.

Condon, M.A., Scheffer, S.J., Lewis, M.L. & Swensen, S.M. 2008. Hidden neotropical diversity: Greater than the sum of its parts. *Science* 320: 928–931.

Duno de Stefano, R., Fernandez-Concha, G.C., Can-Itza, L.L. & Lavin, M. 2010. The morphological and phylogenetic distinctions of *Coursetia greenmanii* (Leguminosae): Taxonomic and ecological implications. *Syst. Bot.* 35: 289–295.

- **Fortunato, R.H. & Palese, R.** 1999. Una especie nueva del género *Mimosa* L. (Fabaceae-Mimosaceae) para el Chaco boliviano: *M. craspedisetosa. Candollea* 54: 83–87.
- Funk, D.J. & Omland, K.E. 2003. Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Rev. Ecol. Evol. Syst.* 34: 397–423.
- Grether, R. & Martinez-Bernal, A. 1996. *Mimosa tejupilcana*, a new species of series *Plurijugae* (Leguminosae) from the State of México, Mexico. *Syst. Bot.* 21: 617–621.
- Hall, T. 1999–2007. BioEdit Sequence Alignment Editor. Carlsbad, California: Ibis Biosciences.
- Hebert, P.D.N., Penton, E.H., Burns, J.M., Janzen, D.H. & Hallwachs, W. 2004. Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly Astraptes fulgerator. Proc. Natl. Acad. Sci. U.S.A. 101: 14812–14817.
- Hensold, R. 1999. Las angiospermas del Departamento de Cajamarca, Perú. *Arnaldoa* 6: 141–184.
- **Huelsenbeck, J.P. & Ronquist, F.** 2003. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17: 754–755.
- **Hughes**, C.E. 2005. Four new legumes in forty-eight hours. *Oxford Pl. Syst. Newslett.* 12: 6–7.
- Hughes, C.E., Daza, A. & Hawkins, J.A. 2003. A new palo verde (Parkinsonia—Leguminosae: Caesalpinioideae) from Peru. Kew Bull. 58: 467–472.
- Hughes, C.E., Lewis, G.P., Daza, A. & Reynel, C. 2004. *Maraniona*: A new dalbergioid legume genus (Leguminosae, Papilionoideae) from Peru. *Syst. Bot.* 29: 366–374.
- **Knapp, S.** 2002. Assessing patterns of plant endemism in Neotropical uplands. *Bot. Rev.* 68: 22–37.
- Koch, C., Venegas, P.J. & Böhme, W. 2006. A remarkable discovery: Description of a big-growing new gecko (Squamata: Gekkonidae: *Phyllopezus*) from northwestern Peru. *Salamandra* 42: 145–150.
- Lavin, M. 1988. Systematics of *Coursetia* (Leguminosae Papilionoideae). *Syst. Bot. Monogr.* 21: 1–167.
- Lavin, M. 2006. Floristic and geographical stability of discontinous seasonally dry tropical forests explains patterns of plant phylogeny and endemism. Pp. 433–447 in: Pennington, R.T., Lewis, G.P. & Ratter, J.A. (eds.), Neotropical savannas and seasonally dry forests. Boca Raton: Taylor & Francis.
- Lavin, M., Wojciechowski, M.F., Gasson, P., Hughes, C.E. & Wheeler, E. 2003. Phylogeny of robinioid legumes revisited: Coursetia and Gliricidia recircumscribed and a biogeographical appraisal of the Caribbean endemics. Syst. Bot. 28: 387–409.
- **Lewis, G.P.** 1998. Caesalpinia: *A revision of the* Poincianella-Erythrostemon *group*. Kew: Royal Botanic Gardens, Kew.
- Lewis, G.P., Hughes, C.E., Daza, A., Solange Sotoyo, J. & Simon, M.F. 2010. Three new legumes endemic to the Marañón valley, Peru. Kew Bull. 65: 209–220.
- Linares-Palomino, R. 2006. Phytogeography and floristics of seasonally dry tropical forests in Peru. Pp. 257–280 in: Pennington, R.T., Lewis, G.P. & Ratter, J.A. (eds.), Neotropical savannas and seasonally dry forests. Boca Raton: Taylor & Francis.
- Linares-Palomino, R. & Pennington, R.T. 2007. Lista anotada de plantas leñosas en bosques estacionalmente seco del Perú—una nueva haramienta en Internet para estudios taxonómicos, ecológicos y de biodiversidad. Arnaldoa 14: 149–152.
- Lötters, S., Schulte, R. & Duellman, W.E. 2004. A new and critically endangered species of *Atelopus* from the Andes of northern Peru (Anura: Bufonidae). *Revista Esp. Herpetol*. 18: 101–109.
- **Macbride, J.F.** 1930. Spermatophytes, mostly Peruvian. *Fieldiana* 8: 1–130.
- Macbride, J.F. 1943. Flora of Peru, Family Leguminosae. *Publ. Field Mus. Nat. Hist., Bot. Ser.* 13: 3–507.
- Marcelo-Peña, J.L., Pennington, R.T., Reynel, C. & Zevallos, P. 2010. Guia ilustrada de la flora leñosa de los bosques estacionalmente secos de Jaén, Perú. Lima: Universidad Nacional Agraria La Molina; Edinburgh: Royal Botanic Garden Edinburgh.

- Molbo, D., Machado, C.A., Sevenster, J.G., Keller, L. & Herre, E.A. 2003. Cryptic species of fig-pollinating wasps: Implications for the evolution of the fig-wasp mutualism, sex allocation, and precision of adaptation. *Proc. Natl. Acad. Sci. U.S.A.* 100: 5867–5872.
- Morawetz, W. & Raedig, C. 2007. Angiosperm biodiversity, endemism and conservation in the Neotropics. *Taxon* 56: 1245–1254.
- Pendry, C.A. 2004. Monograph of *Ruprechtia* (Polygonaceae). *Syst. Bot. Monogr.* 67: 1–113.
- Pennington, R.T., Lavin, M. & Oliveira-Filho, A. 2009. Woody plant diversity, evolution and ecology in the tropics: Perspectives from seasonally dry tropical forests. <u>Annual Rev. Ecol. Evol. Syst.</u> 40: 437–457
- Pennington, R.T., Daza, A. & Lavin, M. In press. Poissonia eriantha (Leguminosae) from Cuzco, Peru: An overlooked species underscores a pattern of narrow endemism common to seasonally dry neotropical vegetation. Syst. Bot.
- Pennington, R.T., Lavin, M., Särkinen, T., Lewis, G.P., Klitgaard, B.B. & Hughes, C.E. 2010. Contrasting plant diversification histories within the Andean biodiversity hotspot. *Proc. Natl. Acad. Sci. U.S.A.* 107: 13783–13787.
- **Posada, D. & Crandall, K.A.** 1998. Modeltest: Testing the model of substitution. *Bioinformatics* 14: 817–818.
- Queiroz, L.P. de & Lavin, M. In press. Coursetia (Leguminosae) from eastern Brazil: The monophyly of three caatinga-inhabiting species is revealed by nuclear ribosomal and chloroplast DNA sequence analysis. Syst. Bot.
- Queiroz, L.P. de & Lewis, G.P. 2000. A new species of *Mimosa* endemic to the Chapada Diamantina, Bahia, Brazil. *Kew Bull.* 54: 983–986.
- **Reeder, T.W.** 1996. A new species of *Pholidobolus* (Squamata: Gymnophthalmidae) from the Huancabamba Depression of northern Peru. *Herpetologica* 52: 282–289.
- Ronquist, F. & Huelsenbeck, J.P. 2005. MRBAYES 3: Bayesian phylogenetic inference under mixed models. <u>Bioinformatics</u> 19: 1572–1574
- Shaw, J., Lickey, E.B., Beck, J.T., Farmer, S.B., Liu, W.S., Miller, J., Siripun, K.C., Winder, C.T., Schilling, E.E. & Small, R.L. 2005. The tortoise and the hare II: Relative utility of 21 non-coding chloroplast DNA sequences for phylogenetic analysis. *Amer. J. Bot.* 92: 142–166.
- Simon, M.F., Grether, R., de Queiroz, L., Skema, C., Pennington, R.T. & Hughes, C.E. 2009. Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in-situ evolution of adaptations to fire. *Proc. Natl. Acad. Sci. U.S.A.* 106: 20359–20364.
- Simon, M.F., Hughes, C.E. & Harris, S.A. 2010. Four new species of *Mimosa* (Leguminosae) from the central highlands of Brazil. *Syst. Bot.* 35: 277–288.
- Smith, M.A., Rodriguez, J.J., Whitfield, J.B., Deans, A.R., Janzen, D.J., Hallwachs, W. & Hebert, P.D.N. 2008. Extreme diversity of tropical parasitoid wasps exposed by iterative integration of natural history, DNA barcoding, morphology, and collections. *Proc. Natl. Acad. Sci. U.S.A.* 105: 12359–12364.
- Sotuyo, S., Delgado-Salinas, A., Chase, M.W., Lewis, G.P. & Oyama, K. 2007. Cryptic speciation in the *Caesalpinia hintonii* complex in seasonally dry Mexican forest. *Ann. Bot.* 100: 1307–1314.
- Stattersfield, A.J., Crosby, M.J., Long, A.J. & Wege, D.C. 1998. Endemic bird areas of the world: Priorities for biodiversity conservation. Cambridge: BirdLife International.
- **Thompson, F.G.** 1982. A new land snail of the genus *Euglandina* from Peru. *Proc. Biol. Soc. Washington* 95: 763–765.
- **Trontelj, P. & Fišer, C.** 2009. Cryptic species diversity should not be trivialised. *Syst. Biodivers.* 7: 1–3.
- Tye, A. 2000. Las plantas vasculares endemicas de Galapagos. Pp. 24–28 in: Valencia, R., Pitman, N., Leon-Yanez, S. & Jorgensen, P.M. (eds.), Libro rojo de las plantas endemicas del Ecuador 2000. Quito: Herbario QCA, Pontificia Universidad Católica del Ecuador.

- Venegas, P.J., Townsend, J.H., Koch, C. & Böhme, W. 2008. Two new sympatric species of leaf-toed Geckos (Gekkonidae: *Phyllodactylus*) from the Balsas region of the upper Marañón valley, Peru. *J. Herpetol.* 42: 386–396.
- Vieites, D.R., Wollenberg, K.C., Andreone, F., Köhler, J., Glaw, F. & Vences, M. 2009. Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. <u>Proc. Natl. Acad. Sci. U.S.A.</u> 106: 8267–8272.
- Weigend, M. 2002. Observations on the biogeography of the
- Amotape-Huancabamba zone in northern Peru. <u>Bot. Rev. 68:</u> 38–54.
- Weigend, M., Gottschling, M., Hilger, H.H. & Nürk, N.M. 2010. Five new species of *Lithospermum* L. (Boraginaceae tribe Lithospermeae) in Andean South America: Another radiation in the Amotape-Huancabamba Zone. *Taxon* 59: 1161–1179.
- Young, K.R., Ulloa, C.U., Luteyn, J.L. & Knapp, S. 2002. Plant evolution and endemism in Andean South America: An introduction. *Bot. Rev.* 68: 4–21.

**Appendix.** GenBank accession numbers and voucher details including species name, collection number, herbarium acronym, and location (major division followed by country) for the 80 *Mimosa trnD-trnT* sequences generated for this study. Details for published Andean *Mimosa* sequences are also included, but voucher details for all other species are found in Simon & al. (2009). The new species, including the three candidate species, are labelled *M. jaenensis*, *M. cf. weberbaueri* 1, *M. cf. weberbaueri* 2, and *M. montana* var. *sandemanii*.

M. andina Benth., Lewis 2271 (K), Azuay, Ecuador, HM353071; M. andina, Lewis 2288 (K), Azuay, Ecuador, HM353072; M. boliviana Benth., Hughes 2283 (FHO), Cochabamba, Bolivia, HM353073; M. boliviana, Särkinen 2056 (FHO), La Paz, Bolivia, HM353074; M. boliviana, Wood 19036 (K), La Paz, Bolivia, HM353075; M. boliviana, Wood 15184 (K), Cochabamba, Bolivia, HM353076; M. boliviana, Hughes 2426 (FHO), La Paz, Bolivia, FJ982009; M. caduca (Willd.) Poir., Lewis 2990 (K), Loja, Ecuador, HM353077; M. caduca, Lewis 2376 (K), Loja, Ecuador, HM353078; M. caduca, Lewis 2916 (K), Loja, Ecuador, HM353079; M. caduca, Lewis 3006 (K), Loja, Ecuador, HM353080; M. cf. incarum, Pennington 1715 (E), Amazonas, Peru, HM353081; M. cf. polycarpa Kunth var. polycarpa, Eastwood 89 (FHO), La Libertad, Peru, HM353082; M. cf. polycarpa var. redundans Barneby, Pennington, R.T. 1642 (FHO), Cajamarca, Peru, HM353083; M. cf. rusbyana Barneby & Fortunato, Marcelo-Peña 4573 (E), Huancavelica, Peru, HM353084; M. cf. weberbaueri 1 Harms, Hughes 2043 (FHO), Ancash, Peru, FJ982229; M. cf. weberbaueri 2, Pennington, T.D. 17821 (K), Amazonas, Peru, HM353085; M. cf. weberbaueri 2, Pennington, T.D. 17903 (K), Amazonas, Peru, FJ981990; M. ctenodes Barneby, Hughes 2212 (FHO), Cajamarca, Peru, FJ982036; M. detinens Benth., Sanchez 46 (MO), Bolivia, FJ982046; M. farinosa Griseb., Wood 21535 (K), Bolivia, HM353086; M. hexandra M.Micheli, Simon 711 (FHO), Brazil, FJ982084; M. hexandra, Fabian-Martinez 128 (MEXU), Mexico, FJ982083; M. incarum Barneby, Pennington R.T. 1630 (FHO), Cajamarca, Peru, HM353087; M. jaenensis sp. nov., Särkinen 2177 (FHO), Cajamarca, Peru, HM353088; M. jaenensis, Särkinen 3062 (FHO), Cajamarca, Peru, HM353089; M. jaenensis, Särkinen 3044 (FHO), Cajamarca, Peru, HM353090; M. jaenensis, Särkinen 3070 (FHO), Cajamarca, Peru, HM353091; M. lamolina C.E. Hughes & G.P. Lewis, Hughes 2648 (FHO), Cajamarca, Peru, FJ982101; M. lamolina, Vandrot 226 (FHO), Cajamarca, Peru, HM353092; M. lepidota Herzog, Wood 19178 (K), Cochabamba, Bolivia, HM353093; M. lepidota, Wood 14443 (K), Chuquisaca, Bolivia, HM353094; M. lepidota, Wood 20099 (K), Tarija, Bolivia, HM353095; M. lepidota, Wood 22495 (K), Chuquisaca, Bolivia, HM353096; M. lepidota, Hughes 2469 (FHO), Santa Cruz, Bolivia, FJ982107; M. loxensis Barneby, Lewis 3082 (K), Loja, Ecuador, HM353097; M. loxensis, Lewis 2987 (K), Loja, Ecuador, FJ98211; M. montana Kunth var. montana, Särkinen 2223 (FHO), Loja, Ecuador, HM353098; M. montana var. montana, Hughes 2225 (FHO), Ancash, Peru, FJ982125; M. montana var. sandemanii Barneby, Eastwood 125 (FHO), Piura, Peru, HM353099; M. nothacacia Barneby, Lewis 3291 (K), Loja, Ecuador, HM353100; M. nothacacia, Lewis 3039 (K), Loja, Ecuador, HM353101; M. nothacacia, Lewis 2353, Loja, Ecuador, FJ982132; M. pectinatipinna Burkart, Särkinen 3101 (FHO), Cajamarca, Peru, HM353102; M. pectinatipinna, Särkinen 2188 (FHO), Cajamarca, Peru, HM353103; M. pectinatipinna, Pennington R.T. 783 (FHO), Amazonas, Peru, HM353104; M. pectinatipinna, Pennington T.D. 17650 (FHO), Amazonas, Peru, HM353105; M. pectinatipinna, Pennington R.T. 806 (FHO), Cajamarca, Peru, HM353106; M. pectinatipinna, Hughes 2036 (FHO), Cajamarca, Peru, FJ982144; M. polycarpa Kunth var. polycarpa, Eastwood 100 (FHO), Cajamarca, Peru, HM353107; M. polycarpa var. redundans Barneby, Pennington R.T. 1685 (E), Amazonas, Peru, HM353108; M. polycarpa var. redundans, Hughes 2656 (FHO), Cajamarca, Peru, HM353109; M. polycarpa var. redundans, Hughes 2206 (FHO), Cajamarca, Peru, FJ982092; M. polycarpa var. subandina Barneby, Särkinen 2061 (FHO), La Paz, Bolivia, HM353110; M. polycarpa var. subandina, Hughes 2432 (FHO), Santa Cruz, Bolivia, HM353111; M. quitensis Benth., Klitgaard 647 (K), Pichincha, Ecuador, HM353112; M. quitensis, Balslev 62442 (K), Tungurahua, Ecuador, HM353113; M. quitensis, Cornejo 5760 (K), Chimborazo, Ecuador, HM353114; M. quitensis, Vargas 270 (K), Pichincha, Ecuador, HM353115; M. quitensis, Lewis 2856 (K), Loja, Ecuador, HM353116; M. revoluta Benth., Hughes 2260 (FHO), La Paz, Bolivia, HM353117; M. revoluta, Hughes 2429 (FHO), La Paz, Bolivia, HM353118; M. revoluta, Wood 11291 (K), La Paz, Bolivia, HM353119; M. revoluta, Wood 18682 (K), Cochabamba, Bolivia, HM353120; M. revoluta, Eastwood 64 (FHO), La Libertad, Peru, HM353121; M. revoluta, Eastwood 103 (FHO), Cajamarca, Peru, HM353122; M. revoluta, Hughes 2278 (FHO), Cochabamba, Bolivia, FJ982174; M. rusbyana Barneby & Fortunato, Wood 20607 (K), La Paz, Bolivia, HM353123; M. rusbyana, Särkinen 2071 (FHO), La Paz, Bolivia, FJ982180; M. sp. 5 (sect. Mimosa ser. Mimosa subser. Polycarpae Barneby), Särkinen 3089 (FHO), Cajamarca, Peru, HM353124; M. sp. 5, Hughes 2642 (FHO), Cajamarca, Peru, HM353125; M. townsendii Barneby, Klitgaard 229 (K), Loja, Ecuador, HM353126; M. townsendii, Lewis 2914 (K), Loja, Ecuador, HM353127; M. townsendii, Lozano 1031 (K), Loja, Ecuador, HM353128; M. townsendii, Lozano 943 (K), Loja, Ecuador, HM353129; M. townsendii, Lewis 3025 (K), Loja, Ecuador, FJ982210; M. weberbaueri Harms, Eastwood 53 (FHO), La Libertad, Peru, HM353130; M. weberbaueri, Eastwood 96 (FHO), Cajamarca, Peru, HM353131; M. woodii Atahuachi & C.E.Hughes, Wood 20945 (K), Cochabamba, Bolivia, HM353132; M. woodii, Hughes 2285 (FHO), Cochabamba, Bolivia, FJ982231.