



Taxonomy and evolutionary history of the neotropical fern genus *Salpichlaena* (Blechnaceae)

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Key words

ferns
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Abstract *Salpichlaena* is a distinctive fern genus characterised by 2-pinnate climbing fronds with indeterminate growth. The number of species in the genus has been a matter of debate. Taxonomic studies are made difficult by within-frond variability in pinna morphology and size, and by herbarium material being incomplete. We systematically documented 62 morphological traits in 283 herbarium specimens and sequenced 52 *Salpichlaena* and 11 outgroup specimens. DNA sequences included plastid genes (*rbcL*, *rpoC1* and *rps4*), intergenic spacers (*rps4-tmS*, *trnH-psbA* and *trnG-trnR*) and a nuclear gene (*pgiC*). Phylogenetic analyses based on the plastid markers divided the samples into six major clades. We recognise the three deepest clades as distinct species (*S. hookeriana*, *S. papyrus* sp. nov. and *S. volubilis*), and each of the four shallower clades as a subspecies of *S. volubilis*. Furthermore, we suggest that a group of specimens, placed into different clades in the plastid and nuclear trees and showing mixed morphological characters, represent a fourth species of hybrid origin (*S. hybrida* sp. nov.). The most important diagnostic characters are: degree of lamina reduction in fertile pinnules; pinna/pinnule apex incisions, pinna/pinnule margin thickness and lamina texture in sterile pinna/pinnules; presence or absence of foliar buds; shape of scales; and the appearance of the abaxial surface of the lamina (uniform or with stomata on small white protuberances). Each of the four species can be identified by several diagnostic characters, and their geographical ranges are broad and partly overlapping. In contrast, the subspecies are mostly allopatric and their morphological limits are diffuse.

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INTRODUCTION

Blechnaceae is a sub-cosmopolitan fern family with about 267 species. The latest classification of the family (De Gasper et al. 2017) divided it into three monophyletic subfamilies:

1. *Woodwardioideae*, with 15 species and a largely north-temperate and amphioceanic distribution;
2. *Stenochlaenoideae*, with about 12 species in three tropical genera (including *Salpichlaena* J.Sm.); and
3. *Blechnoideae*, with about 239 species especially in the southern hemisphere but also in north-temperate regions (De Gasper et al. 2016).

Within the subfamily *Stenochlaenoideae*, *Salpichlaena* has been resolved as sister to the clade formed by *Stenochlaena* and *Telmatoblechnum* Perrie, D.J.Ohlsen & Brownsey (De Gasper et al. 2017).

Salpichlaena is a neotropical genus that occurs from Nicaragua to Bolivia, throughout Amazonia and the Atlantic coastal rain forest, and in the Lesser Antilles (Tryon & Tryon 1982). Adult plants are characterised by indeterminately growing twining rachises, which give the plants a climbing habit and make it possible for the fronds to reach up to the height of 15 m in the forest canopy. This highly unusual habit is only shared by one other fern genus, *Lygodium* Sw. (Tryon & Tryon 1982). Frond complexity in *Salpichlaena* increases during ontogeny: small juvenile plants produce simple fronds and larger juvenile plants 1-pinnate fronds, with each frond generally being longer (and having more pinnae) than the preceding one, until the plant is old enough to produce climbing indeterminately growing 2-pinnate fronds (Tuomisto & Groot 1995). According to Robbin

C. Moran (pers. comm.), adult plants in Central America may intermittently produce 1-pinnate fronds between the 2-pinnate ones, but we have not observed this phenomenon in Amazonia. Only the 2-pinnate fronds produce fertile pinnae, and these can be either monomorphic or dimorphic. If dimorphic, the fertile pinnules are narrower than the sterile, with the degree of fertile pinnule contraction depending on the species (Smith 1995).

The first species of *Salpichlaena* was described in 1824 as *Blechnum volubile* Kaulf. (Kaulffuss 1824) and transferred in 1841 to the new genus *Salpichlaena* as *S. volubilis* (Kaulf.) J.Sm. (Smith 1841). A second name, *Lomaria volubilis* Hook., appeared in 1860 (Hooker 1860) and was changed to *Spicanta hookeriana* by Kuntze in 1891 (Kuntze 1891). Later on, Alston (1932) transferred the species to *Salpichlaena* as *S. hookeriana* (Kuntze) Alston. In 1990, A.R. Smith made a new combination, *S. lomarioidea* (Baker) A.R.Sm., based on *Blechnum volubile* var. *lomarioidea* Baker (Smith 1990), but later he treated this as a synonym of *S. hookeriana* (Smith 1995). The most recent species described in the genus is *S. thalassica* Grayum & R.C.Moran (Moran 1990).

The number of taxa recognised within the genus *Salpichlaena*, as well as their delimitation and appropriate taxonomic rank, has been controversial. Different authors have given different taxonomic significance for the observed morphological variation. Some have recognised 'geotypes' (Vareschi 1969) or varieties (Baker 1870, Smith 1990) within broadly defined species. Tryon & Tryon (1982) denied the validity of *Lomaria volubilis* (*S. hookeriana*) even as a form and accepted only a single species. Murillo (2001) came to the same conclusion based on morphological investigation of Colombian material, and attributed the morphological variation to climatic and edaphic conditions. Giudice et al. (2008) accepted two species, *S. hookeriana* and *S. volubilis*, in their revision of the genus. They argued that the diagnostic characters of *S. thalassica*

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Table 1 List of taxa sampled for phylogenetic analysis and GenBank accession numbers.

Taxa	Voucher	GenBank accession number ²					
		<i>pgiC</i>	<i>rbcL</i>	<i>rpoC1</i>	<i>rps4 + rps4-trnS</i>	<i>trnH-psbA</i>	<i>trnG-trnR</i>
<i>Salpichlaena hookeriana</i> (Kuntze) Alston	Tuomisto 14123 (TUR)	MH178931	MH179035	MH178893	KJ628937	MH178987	MH178778
<i>Salpichlaena hookeriana</i> (Kuntze) Alston	Tuomisto 14956 (TUR)	MH178930	KJ628824	MH178892	MH178837	MH178986	MH178776
<i>Salpichlaena hookeriana</i> (Kuntze) Alston	Tuomisto 15436 (TUR)	MH178929	KJ628825	MH178891	MH178838	MH178985	MH178779
<i>Salpichlaena hookeriana</i> (Kuntze) Alston	Tuomisto 16902 (TUR)	–	MH179034	MH178890	MH178836	MH178984	MH178777
<i>Salpichlaena hybrida</i> sp. nov.	Christenhusz 2460 (TUR)	MH178928	MH179033	MH178889	MH178835	MH178983	MH178775
<i>Salpichlaena hybrida</i> sp. nov.	Lehtonen 1073 (TUR)	MH178927	MH179032	MH178888	MH178834	MH178982	MH178774
<i>Salpichlaena hybrida</i> sp. nov.	Tuomisto 15787 (TUR)	MH178926	MH179031	MH178887	MH178833	MH178981	MH178773
<i>Salpichlaena papyrus</i> sp. nov.	Cerón 6102 (AAU)	–	–	MH178881	MH178820	–	–
<i>Salpichlaena papyrus</i> sp. nov.	Elgaard 8079 (AAU)	–	MH179025	MH178896	MH178817	MH178970	–
<i>Salpichlaena papyrus</i> sp. nov.	Gómez 20878 (AAU)	–	–	MH178886	MH178827	MH178980	–
<i>Salpichlaena papyrus</i> sp. nov.	Hamilton 4121 (AAU)	–	–	MH178879	MH178815	MH178968	–
<i>Salpichlaena papyrus</i> sp. nov.	Hampshire 370 (AAU)	–	–	MH178880	MH178816	MH178969	–
<i>Salpichlaena papyrus</i> sp. nov.	Holm-Nielsen 4260 (AAU)	–	MH179028	MH178900	MH178822	MH178974	MH178765
<i>Salpichlaena papyrus</i> sp. nov.	Jones 165 (TUR)	MH178923	MH179022	MH178876	MH178829	MH178965	MH178767
<i>Salpichlaena papyrus</i> sp. nov.	Jones 610 (TUR)	MH178922	MH179021	MH178875	MH178831	MH178964	MH178772
<i>Salpichlaena papyrus</i> sp. nov.	Jones 933 (TUR)	MH178921	KJ628828	MH178874	KJ628936	MH178963	MH178770
<i>Salpichlaena papyrus</i> sp. nov.	Kessler 13352 (GOET)	MH178920	MH179020	–	MH178832	MH178962	MH178771
<i>Salpichlaena papyrus</i> sp. nov.	Lægaard 52003 (AAU)	–	MH179027	MH178882	MH178821	MH178973	–
<i>Salpichlaena papyrus</i> sp. nov.	Moran 3344 (AAU)	–	–	MH178885	MH178826	MH178979	–
<i>Salpichlaena papyrus</i> sp. nov.	Poulsen 80460 (AAU)	–	MH179026	MH178902	MH178818	MH178971	–
<i>Salpichlaena papyrus</i> sp. nov.	Testo 215 (AAU)	–	MH179030	MH178884	MH178825	MH178978	–
<i>Salpichlaena papyrus</i> sp. nov.	Tuomisto 15145 (TUR)	MH178925	MH179024	MH178878	MH178830	MH178967	MH178768
<i>Salpichlaena papyrus</i> sp. nov.	Tuomisto 15160 (TUR)	MH178924	MH179023	MH178877	MH178828	MH178966	MH178769
<i>Salpichlaena papyrus</i> sp. nov.	Øllgaard 1907 (AAU)	–	–	–	–	MH178976	–
<i>Salpichlaena papyrus</i> sp. nov.	Øllgaard 1488 2/2 (AAU)	–	MH179029	MH178883	MH178823	MH178975	MH178766
<i>Salpichlaena papyrus</i> sp. nov.	Øllgaard 2395 1/3 (AAU) ¹	–	–	MH178901	MH178819	MH178972	–
<i>Salpichlaena papyrus</i> sp. nov.	Øllgaard 105457 1/2 (AAU)	–	–	–	MH178824	MH178977	–
<i>Salpichlaena volubilis</i> subsp. <i>amazonica</i> subsp. nov.	Navarrete 1257 (AAU)	–	MH179019	MH178873	MH178810	MH178961	MH178758
<i>Salpichlaena volubilis</i> subsp. <i>amazonica</i> subsp. nov.	Navarrete 1509 (AAU)	–	MH179018	MH178872	MH178809	MH178960	MH178759
<i>Salpichlaena volubilis</i> subsp. <i>amazonica</i> subsp. nov.	Poulsen 80802 (AAU)	–	MH179017	MH178871	MH178808	MH178959	MH178760
<i>Salpichlaena volubilis</i> subsp. <i>amazonica</i> subsp. nov.	Tuomisto 14562 (TUR)	MH178918	MH179015	MH178869	MH178814	MH178958	MH178764
<i>Salpichlaena volubilis</i> subsp. <i>amazonica</i> subsp. nov.	Tuomisto 16010 (TUR)	MH178919	MH179016	MH178870	MH178813	–	MH178763
<i>Salpichlaena volubilis</i> subsp. <i>amazonica</i> subsp. nov.	Tuomisto 16118 (TUR)	MH178917	MH179014	MH178868	MH178812	–	MH178762
<i>Salpichlaena volubilis</i> subsp. <i>amazonica</i> subsp. nov.	Tuomisto 16550 (TUR)	MH178916	MH179013	MH178867	MH178811	–	MH178761
<i>Salpichlaena volubilis</i> subsp. <i>crenata</i> subsp. nov.	Christenhusz 2486 (TUR)	–	MH179012	MH178865	MH178806	MH178956	MH178757
<i>Salpichlaena volubilis</i> subsp. <i>crenata</i> subsp. nov.	Christenhusz 2553 (TUR)	MH178912	MH179008	MH178861	MH178801	MH178952	MH178755
<i>Salpichlaena volubilis</i> subsp. <i>crenata</i> subsp. nov.	Christenhusz 2729 (TUR)	MH178914	MH179010	MH178863	MH178802	MH178954	MH178751
<i>Salpichlaena volubilis</i> subsp. <i>crenata</i> subsp. nov.	Christenhusz 2756 (TUR)	MH178911	–	MH178860	–	MH178951	MH178752
<i>Salpichlaena volubilis</i> subsp. <i>crenata</i> subsp. nov.	Christenhusz 2821 (TUR)	MH178915	–	MH178866	MH178807	MH178957	–
<i>Salpichlaena volubilis</i> subsp. <i>crenata</i> subsp. nov.	Kessler 12906 (TUR)	MH178913	MH179009	MH178862	MH178803	MH178953	MH178753
<i>Salpichlaena volubilis</i> subsp. <i>crenata</i> subsp. nov.	Lehtonen 810 (TUR)	–	MH179011	MH178864	MH178805	MH178955	MH178756
<i>Salpichlaena volubilis</i> subsp. <i>crenata</i> subsp. nov.	Lehtonen 813 (TUR)	–	MH179007	MH178858	MH178800	MH178949	–
<i>Salpichlaena volubilis</i> subsp. <i>crenata</i> subsp. nov.	Lehtonen 985 (TUR)	–	MH179006	MH178857	MH178799	MH178948	–
<i>Salpichlaena volubilis</i> subsp. <i>crenata</i> subsp. nov.	Tuomisto 15651 (TUR)	MH178910	KJ628827	MH178859	MH178804	MH178950	MH178754
<i>Salpichlaena volubilis</i> subsp. <i>thalassica</i> comb & stat. nov.	Jones 804 (TUR)	KM114164	MH179004	MH178855	KJ628938	MH178946	MH178749
<i>Salpichlaena volubilis</i> subsp. <i>thalassica</i> comb & stat. nov.	Nee 11112 (AAU)	–	MH179005	MH178856	MH178796	MH178947	–
<i>Salpichlaena volubilis</i> subsp. <i>thalassica</i> comb & stat. nov.	Tuomisto 15159 (TUR)	MH178909	MH179003	MH178854	MH178798	MH178945	MH178748
<i>Salpichlaena volubilis</i> subsp. <i>thalassica</i> comb & stat. nov.	Tuomisto 15162 (TUR)	MH178908	MH179002	MH178853	MH178797	MH178944	MH178750
<i>Salpichlaena volubilis</i> subsp. <i>volubilis</i>	Christenhusz 4774 (TUR)	MH178906	MH179001	MH178851	MH178794	MH178942	MH178746
<i>Salpichlaena volubilis</i> subsp. <i>volubilis</i>	Christenhusz 4800 (TUR)	MH178907	MH178896	MH178852	MH178795	MH178943	MH178747
<i>Salpichlaena volubilis</i> subsp. <i>volubilis</i>	Lehtonen 601 (TUR)	MH178904	–	MH178849	MH178792	MH178940	MH178745
<i>Salpichlaena volubilis</i> subsp. <i>volubilis</i>	Lehtonen 637 (TUR)	MH178905	MH179000	MH178850	MH178793	MH178941	MH178744
<i>Blechnum cartilagineum</i> Sw.	2011-668 (Helsinki Botanical Garden)	MH178935	MH179043	MH178897	MH178846	MH178995	MH178788
<i>Blechnum francii</i> Rosenst.	2011-597 (Helsinki Botanical Garden)	MH178934	MH179042	MH178898	MH178845	MH178994	MH178787
<i>Blechnum loxense</i> (Kunth) Hook. ex Salomon	Christenhusz 6777 (H)	MH178933	MH179041	MH178899	MH178844	MH178993	MH178786
<i>Blechnum neohollandicum</i> Christenh.	2011-1120 (Helsinki Botanical Garden)	–	MH179040	MH178895	MH178843	MH178992	MH178785
<i>Blechnum occidentale</i> L.	Jones 1162 (TUR)	–	MH179039	–	MH178842	MH178991	MH178784
<i>Blechnum spicant</i> (L.) Roth	2011-0010 (Helsinki Botanical Garden)	–	MH179038	MH178894	MH178841	MH178990	MH178782
<i>Doodia caudata</i> (Cav.) R.Br.	Alanko 95365 (H)	–	MH179037	–	MH178840	MH178989	MH178781
<i>Sadleria cyatheoides</i> Kaulf.	1991-1232 (Royal Botanic Gardens, Kew)	MH178932	MH179036	–	MH178839	MH178988	MH178780
<i>Stenochlaena palustris</i> (Burm.) Bedd.	1972-367 (Helsinki Botanical Garden)	–	MH178999	MH178848	MH178791	MH178939	MH178743
<i>Telmatoblechnum serrulatum</i> (Rich.) Perrie, D.J.Ohlsen & Brownsey	Prado 1872 (SP)	MH178903	MH178998	–	MH178790	MH178938	MH178783
<i>Woodwardia unigemmata</i> (Makino) Nakai	2010-1132 (Helsinki Botanical Garden)	MH178936	MH178997	MH178847	MH178789	MH178937	MH178742

¹ Øllgaard 2395 is a mixed collection with sheet 1/3 representing *S. papyrus* and sheets 2–3/3 representing *S. volubilis* subsp. *amazonica*.² The accession numbers beginning with KJ were published in Lehtonen et al. (2015).

(elevation of occurrence and length of the petiolule of the basal fertile pinnule) were not consistent, and consequently synonymized this name under *S. volubilis*.

A pervasive problem for taxonomical studies on *Salpichlaena* is the morphological variability found in the herbarium material due to the climbing habit and indeterminate growth of the 2-pinnate fronds. Pinna size and morphology vary along the rachis and possibly also directly in response to height from the ground and/or light conditions in the forest canopy (pers. obs.). It is in practice impossible to collect an entire climbing frond, so herbarium material of *Salpichlaena* is almost always incomplete, and usually the label provides no information on the relative position of the preserved pinnae. Obviously, the non-climbing fronds would fit on a herbarium sheet, but they are never fertile. Since most collectors avoid gathering sterile material, the non-climbing fronds are poorly represented in herbaria. Consequently, specimens in herbaria are generally represented by one or two pinnae taken from an undefined part of the climbing frond, which complicates comparative taxonomic work. Such discrimination against non-climbing fronds is unnecessary, since our experience is that climbing and non-climbing fronds can usually be identified to species equally well: sterile pinnae have similar scales as well as similar lamina texture, margins and apices whether they are climbing or not.

As a complementary tool for traditional taxonomic methods, quite a few molecular methods for species delimitation have been developed (e.g., Doyle 1995, Brower 1999, Puillandre et al. 2012, Zhang et al. 2013). These take into account genetic relatedness and thereby can provide a more objective way than visual inspection to establish species boundaries.

Here we combine morphological and molecular methods:

1. to establish the delimitation among and number of species or other taxa in the genus *Salpichlaena*;
2. to propose a phylogenetic hypothesis for the evolutionary relationships of the taxa; and
3. to provide a key to the species.

MATERIALS AND METHODS

Morphological studies

We measured 62 morphological traits on 283 *Salpichlaena* specimens, and studied 1074 specimens deposited in AAU, CAY, INPA, K, P, TUR, US and USM herbaria (all herbarium acronyms according to Thiers, continuously updated). We observed the shape of fronds, pinnae and pinnules as well as their margin and apex type, lamina texture, lamina dimorphism and presence of foliar buds. We measured the fronds, pinnae, pinnules, petioles, petiolules and scales with a ruler and a caliper. We used the stereoscope and microscope to observe and measure scales, hairs, stomata and spores. In addition,

to infer the distribution and range of morphological variation within the taxa, we studied more than 1000 specimens from the digital collections of several herbaria (AAU, ALCB, AMAZ, BHCB, BM, CAY, CR, CVRD/VALE, F, FLOR, FURB, HUEFS, INPA, K, LE, MO, NY, P, RON, SP, SPF, UC, UEC, US, USM and Z). Digital images of BHCB, BM, CR, LE, MO, SPF, UC and Z herbaria were provided by the curators; ALCB, CVRD, FLOR, FURB, HUEFS, part of INPA, RON and UEC were obtained from INCT-Herbário Virtual da Flora e dos Fungos (<http://inct.splink.org.br>); F from Field Museum webpage (<http://emuweb.fieldmuseum.org/botany/detailed.php>); AAU, AMAZ, K, P, US and USM images were taken by GC; CAY by SL; and NY and SP by HT. Representative specimens for each geographical region are mentioned under Additional specimens seen. The complete list of specimens studied is provided in the Identification list of *Salpichlaena* specimens. Herbarium barcodes, named 'code(s)', are used when collector and collection number are not available.

Molecular studies

Laboratory procedures

We used herbarium material as well as silicagel dried material for DNA extractions (Table 1). Total genomic DNA was extracted from 52 *Salpichlaena* and 11 outgroup specimens (Table 1). For the extractions we used E.Z.N.A. SP Plant DNA Kit (Omega Bio-tek, Doraville, Georgia) following the protocol for dry samples or NucleoSpin Plant II kit (Macherey-Nagel, Germany). Polymerase chain reaction (PCR) amplifications were executed using PuReTaq Ready-To-Go (PCR) Beads (GE Healthcare UK Limited). PCR was used to amplify the plastid genes *rbcL*, *rpoC1* and *rps4*, and plastid intergenic spacers *rps4-trnS*, *trnH-psbA* and *trnG-trnR*, and the nuclear gene *pgiC*. The PCR tubes contained approximately 32 µl of solution composed by 25 µl of ddH₂O, 1 µl of each primer and 5 µl of the extraction template. PCR primers and protocols are detailed in Table 2. Purification and sequencing of the PCR products was done by Macrogen Inc. (Seoul, South Korea). Sample information and GenBank accession codes are listed in Table 1. The final data matrices and the resulting trees are available in TreeBASE (study number TB2:S22278).

Phylogenetic analyses

We used PhyDe version 1.0 (Müller et al. 2010) to examine the DNA sequences, to compare forward and reverse chromatograms and to edit them. The sequences were aligned with default parameters using MAFFT version 7.149 (Katoh & Standley 2013). We then used Bayesian Information Criterion to select the best model for each marker using jModelTest-2.1.10 (Darriba et al. 2012). Since variation in sequence length is generally considered to be phylogenetically relevant information (e.g., Giribet & Wheeler 1999, Simmons et al. 2001), we

Table 2 Primers and PCR protocols used for amplification and sequencing.

Marker	Primer name	Primer sequence	Reference	PCR protocol
pgiC	14F	GTGCTTCTGGGTCTTTTGGAGTG	Ishikawa et al. 2002	94° (3 min), 35 × 94° (45 sec), 50° (45 sec), 72° (90 sec), 72° (8 min)
	16R	GTTGTCCATTAGTTCCAGGTTCCCC		
rbcL	ESRBCL1361R	TCAGGACTCCACTTACTAGCTTCACG	Korall et al. 2006	94° (3 min), 35 × 94° (45 sec), 52° (30 sec), 72° (90 sec), 72° (5 min)
	ESRBCL1F	ATGTCACCACAAACGGAGACTAAAGC		
rpoC1	LP1	TATGAAACCAGAATGGATGG	Chase et al. 2007	94° (1 min), 35 × 94° (30 sec), 48° (40 sec), 72° (40 sec), 72° (5 min)
	LP5	CAAGAAGCATATCTTGASTYGG		
rps4 + rps4-trnS	trnSGGA	TTACCGAGGGTTTCGAATCCCTC	Shaw et al. 2005 Small et al. 2005	95° (2 min), 40 × 95° (1 min), 60° (1 min), 72° (1 min), 72° (7 min)
	rps4.5'	ATGTCSCGTTAYCGAGGACCT		
trnG-trnR	TRNG1F	GCGGGTATAGTTTAGTGGTAA	Nagalingum et al. 2007	94° (5 min), 30 × 94° (1 min), 47° (1 min), 72° (1 min), 72° (7 min)
	TRNR22R	CTATCCATTAGACGATGGACG		
trnH-psbA	psbA3'f	GTTATGCATGAACGTAATGCTC	Sang et al. 1997 Tate & Simpson 2003	94° (1 min), 40 × 94° (30 sec), 48° (40 sec), 72° (40 sec), 72° (5 min)
	trnH	CGCGCATGGTGGATTCACAATCC		

performed simple gap coding (Simmons & Ochoterena 2000) to the aligned sequences using SeqState 1.4.1 (Müller 2005). The aligned DNA sequences and binary coded gap data were combined for data analyses. Following the results of model testing, the evolutionary model for *pgiC*, *trnH-psbA*, *rps4*, *rps4-trnS* and *trnG-trnR* was set to HKY+G with default flat Dirichlet prior probability distribution and for *rbcL* and *rpoC1* to K80+G with a fixed (equal) prior probability distribution. For the binary coded gap data a Standard Discrete Model was applied with options coding = variable and rates = gamma to accommodate lack of constant characters and variable rates of change. We performed Bayesian inference with MrBayes version 3.2 (Ronquist et al. 2012) to build phylogenetic trees for each marker. Four chains of 10 000 000 generations were run sampling every 1 000th generation. After verifying that the resulting trees had no supported conflict (PP > 0.75), we combined the five plastid datasets with SequenceMatrix (Meier et al. 2006). However, conflict was observed between the trees of plastid and nuclear markers and the nuclear *pgiC* was analysed separately. Final trees were inferred as above, except that for *pgiC* 5 000 000 more generations were run in order to achieve convergence. The first 25 % of trees were discarded as burn-in and a 50 % majority rule consensus tree was calculated from the remaining trees. FigTree v. 1.4 (Rambaut 2006–2012) was used for editing the tree.

Molecular species delimitation

We applied two molecular species delimitation methods to our chloroplast dataset to investigate putative species boundaries within *Salpichlaena*. First, we analysed the aligned sequences using Automatic Barcode Gap Discovery (ABGD; Puillandre et al. 2012) on the webserver (<http://www.wabi.snv.jussieu.fr/public/abgd/abgdweb.html>). This method assumes that the degree of sequence divergence is larger between than within species, and that the interspecific sequence divergence range does not overlap with the intraspecific divergence range, resulting in a barcode gap in pairwise differences between individual sequences (Puillandre et al. 2012). We detected barcode gaps separately for each molecular marker using an intraspecific prior divergence ranging from $P = 0.001$ to $P = 0.1$, the default proxy for the minimum gap width $X = 1.5$, and applying the Kimura 2-Parameter evolution model (Kimura 1980). Out-group sequences were excluded from the alignments before the analyses. ABGD allows recursive partitioning in which the initial partitions can be further split if an additional barcode gap is detected inside the partition (Puillandre et al. 2012). This generally results in a higher number of putative species and poorer match with established taxonomies (Puillandre et al. 2012). We therefore ignored recursive partitioning here and only consider the initial partitions.

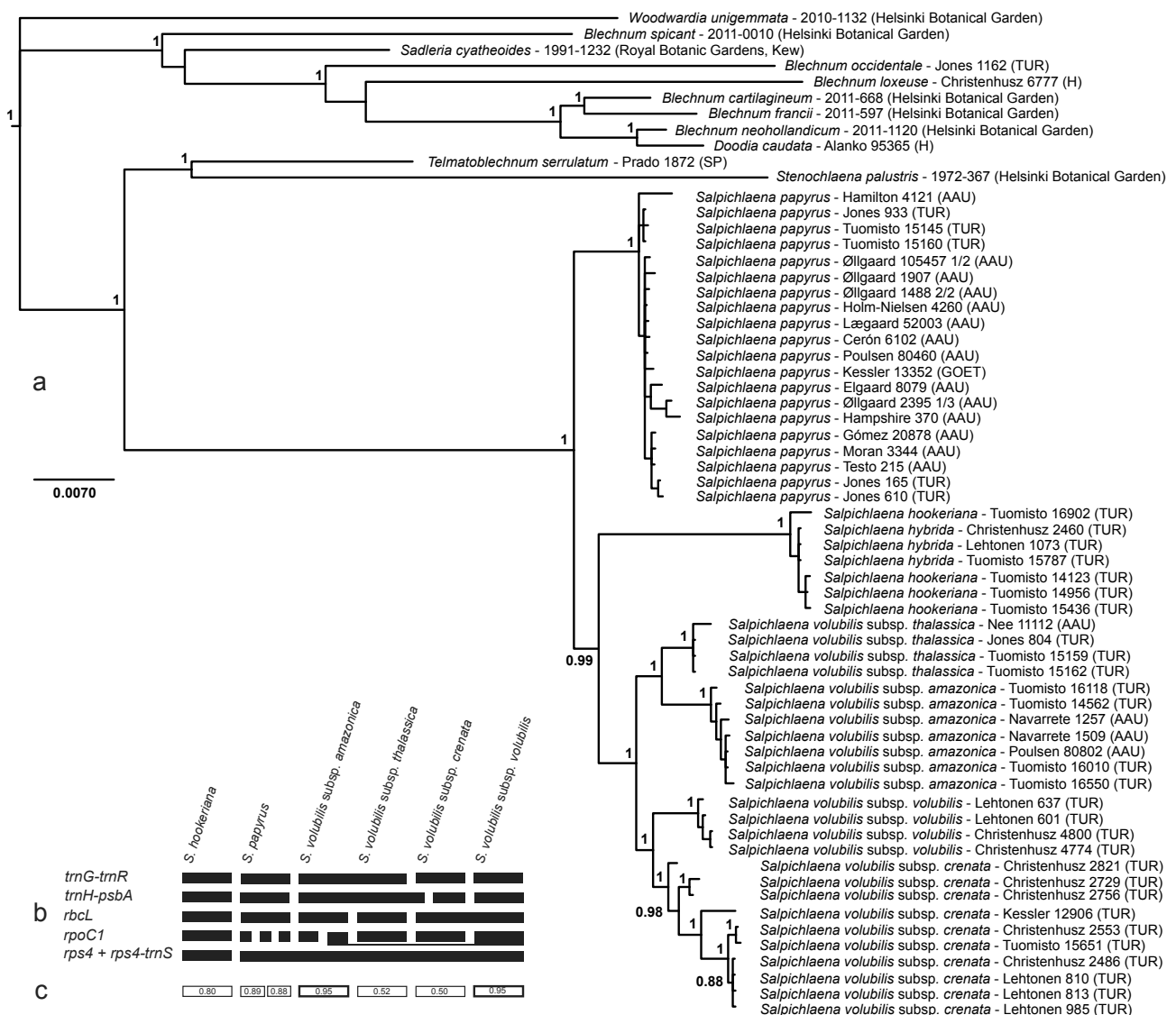


Fig. 1 Plastid phylogeny and species delimitation. a. A Bayesian majority rule consensus tree based on the combined data of five plastid markers with posterior probabilities shown at the nodes; b. ABGD species delimitation at prior maximum divergence of intraspecific diversity 1.67×10^{-3} ; c. bPTP species delimitation with posterior probabilities.

In addition, we applied a Bayesian implementation of the Poisson Tree Processes model (bPTP) to delimit species boundaries based on a phylogenetic input tree and the number of substitutions on its branches (Zhang et al. 2013). This method assumes that the number of substitutions is significantly higher between species than within species. We used the tree obtained from a combined analysis of five plastid markers as input tree and ran 200 000 MCMC generations in the bPTP webserver (<http://species.h-its.org/ptp/>) with a thinning value of 100 and 15 % burn-in.

RESULTS

Molecular phylogenetics

The alignment of the combined plastid markers consisted of 3950 base pairs. The resulting phylogenetic tree shows a well supported *Salpichlaena* as sister to a well supported clade formed by *Telematoblechnum* and *Stenochlaena* (Fig. 1). Within *Salpichlaena*, the tree shows six major clades with high support. We recognise the three deepest clades at species level: *S. hookeriana*, *S. papyrus* sp. nov. and *S. volubilis*. Within *S. volubilis*, we recognise the four distinct clades at subspecific level: subsp. *amazonica* subsp. nov., subsp. *crenata* subsp. nov., subsp. *thalassica* stat. nov. and subsp. *volubilis* (Fig. 1).

Our nuclear phylogenetic tree is generally very poorly resolved, but it shows *S. hookeriana*, *S. volubilis* subsp. *amazonica* and *S. volubilis* subsp. *thalassica* as well-supported clades. *Salpichlaena volubilis* subsp. *crenata*, *S. papyrus* and *S. volubilis* subsp. *volubilis* remain unresolved (Fig. 2). A set of specimens that are unresolved within *S. hookeriana* in the plastid tree are

nested in a single clade with high support within *S. volubilis* subsp. *amazonica* in the nuclear tree. We propose that these specimens represent a new species that has emerged from a single hybridization event between *S. hookeriana* (the maternal parent) and *S. volubilis* subsp. *amazonica* (the paternal parent), and recognise this taxon as *S. hybrida* sp. nov.

Morphology

We found that the most useful characters to differentiate *Salpichlaena* species and subspecies are: degree of foliar dimorphism, apical incisions and texture of the lamina, margin type, shape of the scales on the abaxial axes, presence or absence of foliar buds, and the appearance of the abaxial surface of the lamina. A single character is typically not enough for reliable identification, but two or three characters in combination usually are.

Salpichlaena hookeriana and *S. papyrus* differ from *S. volubilis* and *S. hybrida* by having strongly serrate apices in sterile pinnae and pinnules (Fig. 3). Apices are entire in *S. hybrida* and *S. volubilis*, although in some subspecies of *S. volubilis* they can be crenate or even slightly serrate (Fig. 3). Because serration is generally less obvious in fertile pinnules, *S. papyrus* is most reliably distinguished from *S. volubilis* on the basis of sterile pinnules.

Salpichlaena hookeriana is unique in its foliar dimorphism, which is so strong that fertile pinnules are almost devoid of lamina (Fig. 5). Furthermore, *S. hookeriana* often has a foliar bud at the base of one or more pinnae or pinnules in the climbing fronds (Fig. 4b), a character that is extremely rare in *S. papyrus* and has never been observed in *S. hybrida* or *S. volubilis*.

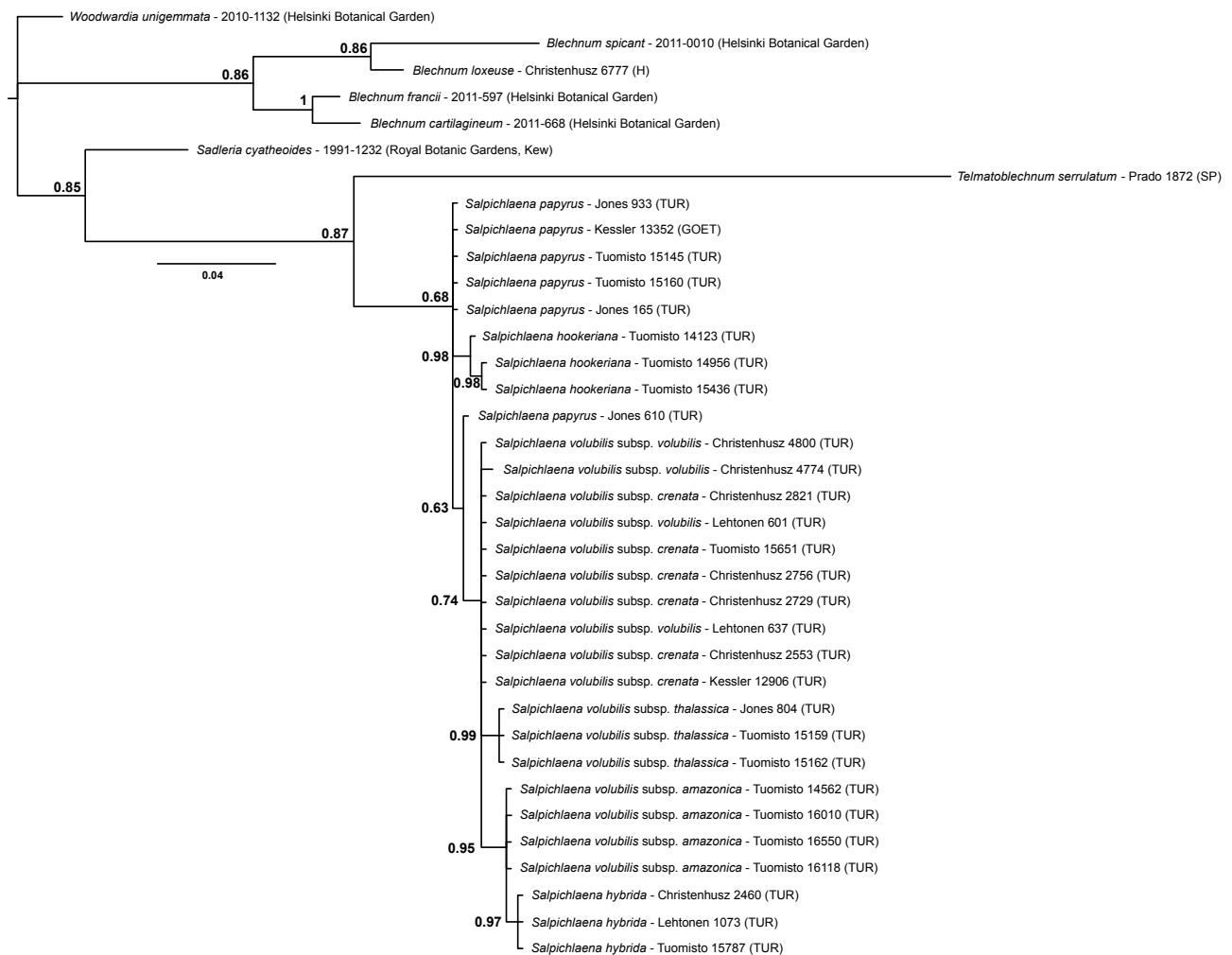


Fig. 2 A Bayesian majority rule consensus tree based on the nuclear *pgiC* gene with posterior probabilities shown at the nodes.

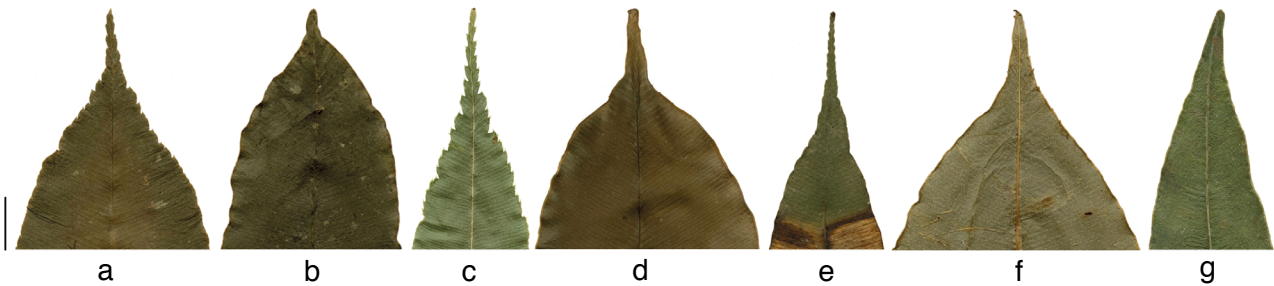


Fig. 3 Sterile pinnule apices of *Salpichlaena*. a. *S. hookeriana*; b. *S. hybrida*; c. *S. papyrus*; d. *S. volubilis* subsp. *amazonica*; e. *S. volubilis* subsp. *crenata*; f. *S. volubilis* subsp. *thalassica*; g. *S. volubilis* subsp. *volubilis* (a. Tuomisto 12785; b. Christenhusz 2460 3/3; c. Jones 165; d. Tuomisto 16550; e. Christenhusz 2729; f. Tuomisto 15144; g. Christenhusz 4950 2/4; all TUR). — Scale bar: 1 cm.



Fig. 4 *Salpichlaena*. a. Habit of a climbing adult *S. volubilis* subsp. *volubilis*; b. foliar bud of *S. hookeriana*; c. sori covered by indusia, *S. volubilis* subsp. *volubilis*; d. costal scales of *S. papyrus*; e. abaxial lamina of *S. volubilis* subsp. *thalassica* with stomata on white laminal protuberances; f. abaxial lamina of *S. volubilis* subsp. *amazonica* uniform without white protuberances; g. non-climbing fronds of *S. volubilis* subsp. *amazonica* (b. Cárdenas 1755; c. Christenhusz 4800 2/2; d. Jones 165; e. Jones 650; f. Navarrete 1509; b–e. TUR; f. AAU). — Scale bar: 1 cm.

Salpichlaena papyrus differs from all other species in that the scales on costulae, costae and rachises are either broad and resemble crumpled paper or are ovate with small or no appendices (Fig. 4d). In the other species, scales are more slender and have long appendices.

Although we did not find clear-cut differences between the *S. volubilis* subspecies, we found some character combinations that usually identify them.

Fronds, pinnae and pinnules of subsp. *amazonica* and subsp. *thalassica* have cartilaginous margins and entire or almost entire apices with a few small, sometimes serration-like teeth that are limited to the cartilaginous margin and do not cut into the lamina tissue (Fig. 3d, f). These subspecies have also chartaceous to coriaceous texture and generally broader sterile pinnules (2.4–8.6 cm) than the other taxa (1.2–5 cm). Under the stereoscope, subsp. *thalassica* can usually be differentiated from subsp. *amazonica* by the location of the stomata on small whitish protuberances of the lamina, whereas in *S. amazonica* the abaxial side of the lamina looks uniform (Fig. 4e–f).

The key characters to differentiate *S. volubilis* subsp. *volubilis* from the other taxa are the entire frond/pinna/pinnule apices (Fig. 3g), herbaceous lamina texture, and lack of cartilaginous margin in sterile pinnae (in fertile pinnae, both the lamina and the margin are slightly thickened). *Salpichlaena volubilis* subsp. *crenata* has crenate (Fig. 3e) to slightly serrate pinnule apices, but in contrast to subsp. *thalassica* and subsp. *amazonica*, the incisions cut through the only slightly cartilaginous margin to the lamina.

In accordance with its postulated hybrid origin, *S. hybrida* shares characters with both *S. hookeriana* and *S. volubilis* subsp. *amazonica*. The length and width of pinnae in the 1-pinnate non-climbing fronds are similar to those in subsp. *amazonica*, but *S. hybrida* has a more herbaceous lamina texture. In contrast, pinnules in the 2-pinnate climbing fronds of *S. hybrida* resemble more the pinnules of *S. hookeriana* in size, texture and shape, but the pinnule apices are entire in the former and serrate in the latter.

Species delimitation analyses

The number of species delimited by ABGD varied depending on the molecular marker and the prior maximum intraspecific divergence (P) that was used (Table 3; Fig. 1b). The most consistent results were obtained with *rbcl*, *trnH-psbA* and *trnG-trnR*, all of which recognised five taxa throughout the P values used. Out of the five taxa, however, only *S. papyrus* and *S. hookeriana* were identically delimited by these markers. Within *S. volubilis*, alternative delimitations emerged. Both *trnH-psbA* and *trnG-trnR* indicated that *S. volubilis* subsp. *thalassica* and subsp. *amazonica* are conspecific, whereas *rbcl* recognised them as distinct species. On the other hand, subsp. *crenata* and subsp. *volubilis* were grouped together as a single species by *rbcl*, but recognised as separate species by *trnG-trnR* and mixed as two non-monophyletic species by *trnH-psbA*. The remaining molecular

markers (*rps4*, *rps4-trnS*, *rpoC1*) were less conclusive, although *S. hookeriana* was consistently recognised (Fig. 1b)

The bPTP analysis recognised seven species within *Salpichlaena*, but only two of them received a Bayesian posterior value $\geq 95\%$ (*S. volubilis* subsp. *amazonica* Bpp = 0.99 and subsp. *volubilis* Bpp = 0.95). Two species were recognised within *S. papyrus* (Bpp = 0.89 and Bpp = 0.88). The remaining species recognised by bPTP were *S. hookeriana* (Bpp = 0.80), *S. volubilis* subsp. *thalassica* (Bpp = 0.52) and *S. volubilis* subsp. *crenata* (Bpp = 0.50) (Fig. 1c).

DISCUSSION

The phylogenetic position of *Salpichlaena* as sister to the clade formed by *Telmatoblechnum* and *Stenochlaena* in our tree is congruent with the current understanding of the evolutionary history of *Blechnaceae* (Lehtonen 2011, Perrie et al. 2014, De Gasper et al. 2017).

Based on our results, we suggest a new classification for *Salpichlaena*: it contains four species, one of which has four subspecies. Out of the formerly described species, we accept two, *S. hookeriana* and *S. volubilis*, at the species rank, but place *S. thalassica* at the subspecific rank within *S. volubilis*. We describe two new species, *S. papyrus* and *S. hybrida*, and two new subspecies, *S. volubilis* subsp. *amazonica* and *S. volubilis* subsp. *crenata*.

On morphological grounds, we have considered *S. hookeriana*, *S. papyrus* and *S. volubilis* as distinct species for some time already (see Tuomisto & Groot 1995 for discussion on *S. hookeriana* and *S. volubilis*; *S. papyrus* was referred to as *Salpichlaena* sp. 1 in Jones et al. 2006, 2008). Here we recognise all three at the species rank. They are morphologically distinct and the fact that they form well-supported clades in the plastid phylogeny despite overlapping distributions in Amazonia suggests that they are independent evolutionary lineages. Furthermore, the species delimitation analyses were mostly congruent at this level: both ABGD and bPTP invariably supported *S. hookeriana* as distinct species, and almost always recognised *S. papyrus*.

A group of specimens from the Guyana shield was found to have some morphological characters of *S. hookeriana* and others similar to *S. volubilis* subsp. *amazonica*. We were able to sequence some of these specimens, and they consistently grouped together with *S. hookeriana* in the plastid phylogeny but were nested as a clade within *S. volubilis* subsp. *amazonica* in the nuclear *pgiC* tree. Based on this, we suggest that they represent hybrids between the two taxa. Because the chloroplast genome is maternally inherited in ferns (Gastony & Yatskievych 1992, Vogel et al. 1998), we consider *S. hookeriana* as the maternal progenitor and *S. volubilis* subsp. *amazonica* as the paternal progenitor. Interestingly, the proposed hybrids seem to be absent from most of Amazonia where the putative parent taxa co-occur. The distribution of the three species only

Table 3 The number of species delimited using aligned sequence matrices and ABGD with prior maximum divergence of intraspecific diversity ranging from 0.001 to 0.1.

Marker	1.00×10^3	1.67×10^3	2.78×10^3	4.64×10^3	7.74×10^3	1.29×10^2	2.15×10^2
<i>rbcl</i>	5	5	5	5	1	–	–
<i>rpoC1</i>	8	8	2	2	1	–	–
<i>rps4 + rps4-trnS</i>	20	2	2	2	1	–	–
<i>trnH-psbA</i>	5	5	1	–	–	–	–
<i>trnG-trnR</i>	5	5	5	5	5	2	1
<i>pgiC</i>	8	8	1	–	–	–	–

overlaps in northern Brazil and in the Guianas, which may be the area where the original hybridization took place. Unfortunately, we have not been able to study the morphology or viability of the spores, as none of the physical specimens we have had access to was fertile.

The *S. volubilis* clade is a taxonomical challenge. The specimens vary morphologically and different molecular species delimitation analyses gave different suggestions on how to split it. The ABGD delimitation split this clade differently for each molecular marker, and none of these delimitations was congruent with the bPTP delimitation, which split the clade into four species (Fig. 1b–c). However, the four clades recognised in the plastid consensus tree received high support. Mostly we found these four clades allopatric and morphologically distinguishable, but specimens with intermediate characteristics were found especially in the areas where two clades meet. Such behaviour is considered typical for taxa of subspecific rank (Mayr 1942, Patten 2015).

Salpichlaena volubilis subsp. *thalassica* can usually be identified from *S. volubilis* subsp. *amazonica* by the location of stomata on white laminal protuberances in the former. However, in the northernmost part of the Andes, this characteristic is not so obvious and morphological delimitation of these taxa may not be possible. Likewise, some specimens of *S. volubilis* subsp. *amazonica* approach in their appearance *S. volubilis* subsp. *crenata*. *Salpichlaena volubilis* subsp. *crenata* from the Caribbean and northern South America and *S. volubilis* subsp. *volubilis* from the Atlantic Forest are generally distinct, but again, some specimens are morphologically indistinguishable. Within *S. volubilis* subsp. *crenata*, there are four smaller well-supported clades with specimens of somewhat distinct morphologies between the clades. Such variability could suggest the presence of further subspecies in this clade, but we did not have enough material from the relevant areas to test if the differences are consistent.

Our conclusions disagree with those of Vareschi (1968), who recognised *S. volubilis* as a single species having two 'geotypes'. His drawings indicate the presence of big scales in the axes of 'geotype' *euvolubilis* (Fig. T100-2 in Vareschi 1968) and strong frond dimorphism in 'geotype' *maegdefrauiana* (Fig. T100-3,4 in Vareschi 1968). We conclude that the former 'geotype' corresponds to *S. papyrus* and the latter to *S. hookeriana*. Similarly, Murillo (2001) accepted only one polymorphic species in the genus based solely on material from Colombia. We have checked the specimens listed in her publication and found them to represent three taxa as defined here: *S. hookeriana* (e.g., Schultes 15410, US), *S. papyrus* (e.g., Forero 5461, US) and *S. volubilis* subsp. *thalassica* (e.g., Haught 1299, US). Murillo (2001) based her conclusion on the variability of characters and on the measurements of pinnae and pinnules. Although we agree that *Salpichlaena* is morphologically highly variable, we find characters like foliar dimorphism, incisions of pinna and pinnule apices, and shape of scales consistent enough to be used to delimit morphologically cohesive groups. The fact that these correspond with groups identified by molecular markers further supports treating them as different taxa.

Moran (1990) originally described *S. thalassica* on the basis of blue-green fronds, the occurrence of the species on higher elevations and the long stalks of the basal fertile pinnules. Giudice et al. (2008) disagreed with the significance of these characters and pointed out that the length of the basal fertile pinnule stalk did not correlate with the elevation when viewed over a larger geographical extent. In addition, since they could not observe the colour differences in herbarium material, they did not find support for separating *S. thalassica* from *S. volubilis*.

We did not have an opportunity to make a systematic study of frond colour in the field, and since herbarium specimens invariably lose their original lamina colour, we are unable to confirm whether the colour is a diagnostic character. The length of the petiolule of the basal fertile pinnule seems not to be diagnostic: it differs little between subsp. *thalassica* (up to 1.7 cm) and the other taxa (up to 1.5 cm).

Given that Grayum & Moran in Moran (1990) focused on specimens from Costa Rica and Panama, it seems clear that they were comparing *S. volubilis* subsp. *thalassica* with *S. papyrus*. Hence, we agree with their original conclusion that there are two distinct species in the area. However, they happened to describe as a new species the one we consider to be distinct from the type of *S. volubilis* only at the subspecies level.

We agree with Giudice et al. (2008) that important diagnostic characters to differentiate *S. hookeriana* from *S. volubilis* are foliar dimorphism and presence of foliar buds. They also mentioned the appearance of the costal scales, which we found to be useful to distinguish *S. papyrus* (whose scales are more generally formless and resemble crumpled paper) from all the other taxa (whose scales are lanceolate to ovoid and always have long appendices). Giudice et al. (2008) also mentioned that *S. hookeriana* can be differentiated from *S. volubilis* by the presence of glandular hairs on the abaxial surface of the costa, but we have observed microscopic hairs more often in *S. volubilis* subsp. *thalassica* and subsp. *amazonica* than in *S. hookeriana*.

A major obstacle for *Salpichlaena* taxonomy is that herbarium specimens tend to be incomplete. Although it is unpractical to collect an entire climbing frond, it is important to collect both sterile and fertile material. The taxon-specific diagnostic characters are, for most *Salpichlaena* taxa, much more obvious in sterile than in fertile pinnae. Therefore, sterile specimens (including those consisting of non-climbing fronds only) can usually be identified all the way to the subspecific level, but specimens consisting of fertile pinnae only are more difficult to identify.

TAXONOMIC TREATMENT

Salpichlaena

Salpichlaena J.Sm. (1841) 168. — Type: *Salpichlaena volubilis* (Kaulf.) J.Sm. (1841) 168.

Terrestrial. *Rhizome* long-creeping, dorsiventral, 0.3–0.8 cm diam; scales 2–5(–9) mm long, brown to black, usually with a lighter margin. *Fronde*s almost monomorphic to strongly dimorphic, with twining rachises, up to 15 m long. *Petioles* abaxially terete, adaxially sulcated with one omega-shaped vascular bundle, glabrous, with catenate hairs and yellowish to brown scales. *Laminae* entire in juveniles, 1- (or 2-)pinnate in non-climbing and 2-pinnate in climbing fronds. *Pinnae* subopposite to opposite; herbaceous to coriaceous, margin cartilaginous to not cartilaginous, catenate hairs of 2 or 3 cells on abaxial side of the lamina, mostly on the veins; axes glabrous, sparsely hairy or scaly, veins parallel, simple or once-forked. *Pinnules* subopposite to opposite (alternate), fertile ones generally narrower than sterile, lanceolate, elliptic to oblanceolate, petiolulate to sessile or winged; apex acuminate, attenuate, caudate, cuspidate or cuneate, with entire, crenate or serrate margin, base round to attenuate. *Sori* linear at both sides of the costule covered by a firm dark-brown indusium that opens towards the costa, paraphyses absent. *Spores* monoletate, ellipsoid-reniform with vesicles on the surface, monoletate, 0.7–1 µm; *n* = 40 (Walker 1973; count from Trinidad).

IDENTIFICATION KEY TO SPECIES

- 1. Fertile pinnae almost without lamina; apices of sterile pinnae/pinnules serrate; pinnae/pinnules elliptic; laminar buds common in climbing fronds at the pinna bases 1. *S. hookeriana*
- 1. Fertile pinnae with lamina; apices of sterile pinnae/pinnules entire, crenate or serrate; if serrate, pinnae/pinnules lanceolate; laminar buds in climbing fronds absent or very rare 2
- 2. Apices of sterile pinnae/pinnules obviously serrate; costal scales broad and shapeless, like crumpled paper, or ovate with or without small appendices 3. *S. papyrus*
- 2. Apices of sterile pinnae/pinnules entire, crenate to slightly serrate; costal scales lanceolate or ovate, always with long appendices 3
- 3. Sterile pinnae/pinnules broadly elliptic to oblanceolate, herbaceous, margin sometimes slightly cartilaginous. 2. *S. hybrida*
- 3. Sterile pinnae/pinnules of variable shape; if broadly elliptic, then chartaceous-coriaceous with clearly cartilaginous margin, if lanceolate, then herbaceous-chartaceous with only slightly or not at all cartilaginous margin 4. *S. volubilis*

1. *Salpichlaena hookeriana* (Kuntze) Alston — Fig. 3a, 4b, 5; Map 1

Salpichlaena hookeriana (Kuntze) Alston (1932) 312.
Lomaria volubilis Hook. (1860) 39. — *Blechnum volubile* Kaulf. var. *lomarioidea* Baker (1870) 428. Replacement name for *Lomaria volubilis* Hook. at a new rank. — *Spicanta hookeriana* Kuntze (1891) 821. Replacement name for *L. volubilis* Hook., non *Spicanta volubilis* (Kaulf.) Kuntze. — *Salpichlaena lomarioidea* (Baker) A.R.Sm. (1990) 250, nom. illeg. superfl. — Type: *Spruce R 1263* (lectotype K K000633415, designated here; isoelectotypes

K K000633413, K000633414, NY 02617982, 02617987, P P00347482), Brazil, Amazonas, Barra.

Etymology. Species named after William Jackson Hooker (1785–1865).

Non-climbing and sterile climbing fronds with herbaceous (chartaceous) lamina texture, pinnae and pinnule margins not cartilaginous; scales on abaxial axes lanceolate with long, sometimes bifurcated appendices (stick-like scales formed by a long apical row of cells and usually two shorter lateral basal cells); stomata rarely on white laminal protuberances. *Non-climbing* entire fronds up to 27 by 2.4 cm. Non-climbing 1-pinnate fronds 34–77 cm. Pinnae up to 6 pairs; apical one elliptic (lanceolate), 8.7–20.5 by 1.9–4.3 cm; lateral ones elliptic, oblanceolate (lanceolate), 9–19.7 by 1.8–4.4 cm; apex acuminate (attenuate), with serrate margin; base acute. *Climbing* fronds with pinnae strongly dimorphic, fertile pinnae almost without any laminar tissue. Pinnules opposite to subopposite. *Fertile pinnules* in 1–7 pairs; apical one linear, 12.4–36.3 by 0.1–0.4 cm; lateral ones linear, 8.4–31 by 0.1–0.4 cm. *Sterile pinnules* in 2–6 pairs; apical one elliptic (lanceolate), 12.7–35 by 2.4–5.8 cm, apex acuminate (attenuate) with serrate margin, serration sometimes extending more than 1/4 of the length of the pinnule, base acute, equilateral to slightly oblique; lateral ones elliptic (oblanceolate, lanceolate), 9–24.3 cm, apex acuminate, attenuate, base obtuse, cuneate, acute, equilateral to oblique; petiolulate, sessile, rarely winged; sometimes foliar buds on the base of pinnule.

Distribution — *Salpichlaena hookeriana* occurs mostly in Amazonia, reaching Mato Grosso do Sul in the south.

Habitat & Ecology — Primary lowland rain forest. Grows in poorly drained areas including palm swamps, near creeks and less often near paths. On brownish sandy and clay soil. Altitude 50–700 m.

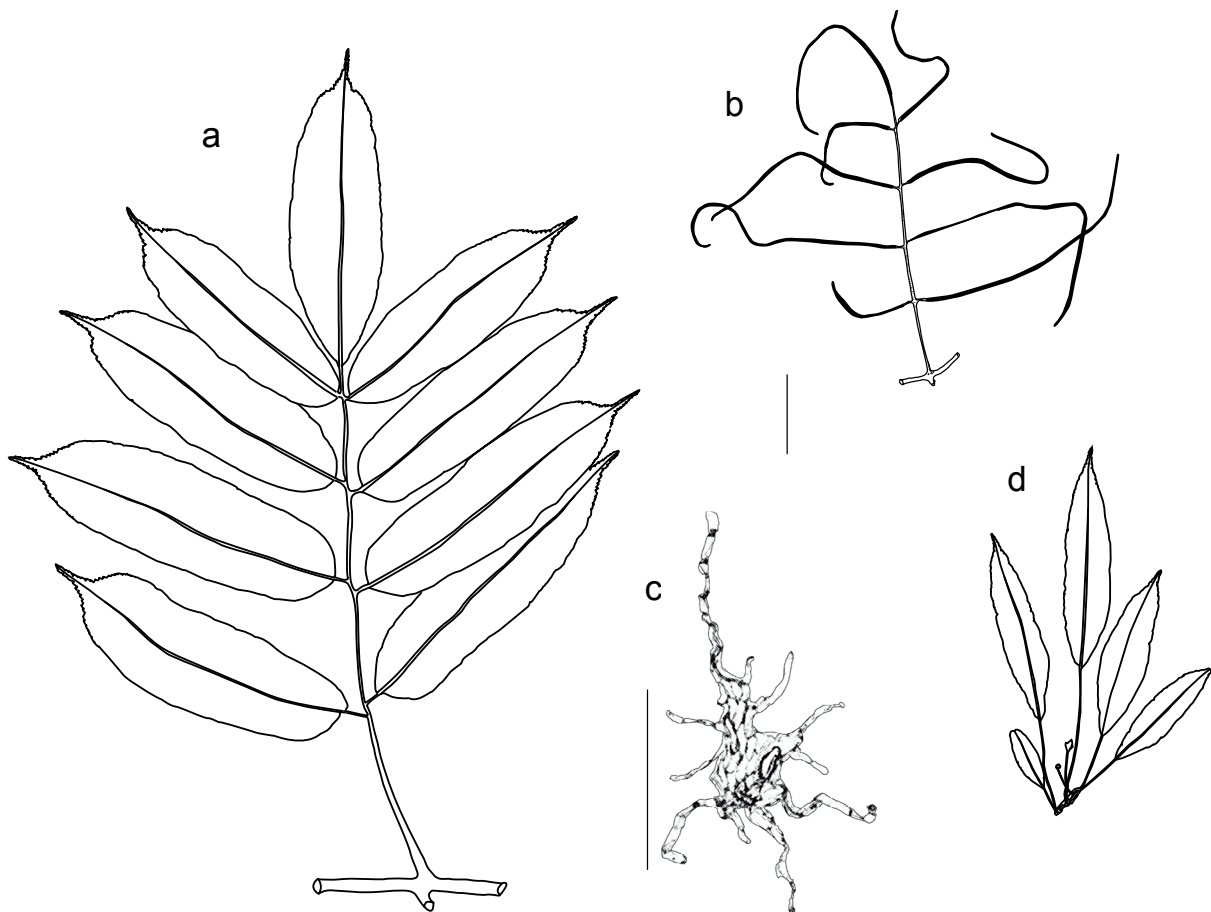
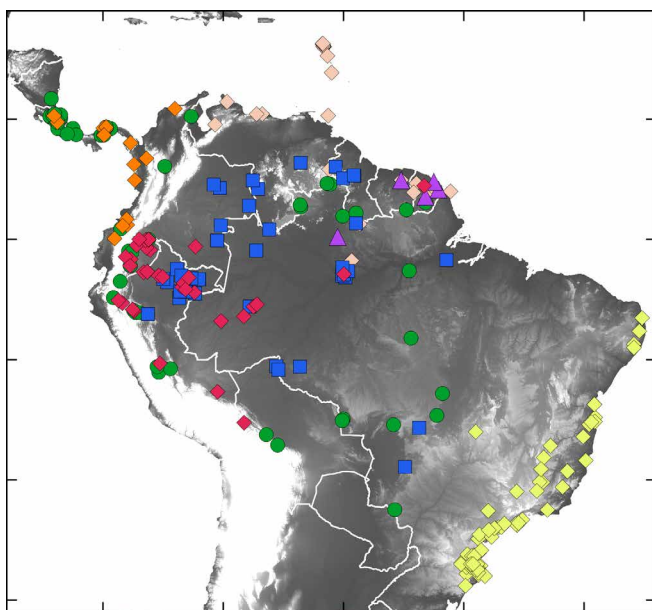


Fig. 5 *Salpichlaena hookeriana*. a. Sterile pinna; b. fertile pinna; c. costal scale; d. juvenile (a. Tuomisto 16902; b. Tuomisto 15436; c. Cárdenas 1754; d. Tuomisto 14771; all TUR). — Scale bar: a–b, d = 5 cm; c = 0.5 mm.

Additional specimens seen. BOLIVIA, Beni, 5 km NW of Guayamerin, 24 Jan. 1978, *Anderson WR 11824* (US). – BRAZIL, Amazonas, Mun. Presidente Figueiredo, na margen da Rodovia AM-240, 2 Feb. 2008, *Prado J et al. 1863* (NY, SP, TUR); Carauari, 3–5 km north-west from the village of Lago do Pupunha, Rio Juruá, S5°34' W67°48', 100–140 m, 12 June 2012, *Tuomisto H et al. 16902* (SP, TUR); Rio Preto da Eva, S2°37' W59°37', 80–120 m, 23 Jan. 2008, *Tuomisto et al. 15436* (INPA, SP, TUR). – COLOMBIA, Vaupés, Río Piraparaná (tributary of Río Apaporis), Caño Teemeefia, S0°15' W70°30', 10 Sept. 1952, *Schultes RE & Cabrera I 17449* (US); Vichada, Gaviotas, Caño Urimica, 130–160 m, 8 Dec. 1972, *Murillo TM 1582* (AAU, P). – GUYANA, Potaro-Siparuni, Pakaraima Mts, Ireng River, 4 km upstream from Kurutuik Falls along Topaima stream, N5°05'00" W60°02'00", 685 m, 27 Oct. 1994, *Mutchnick P et al. 240* (CAY, US); Upper Takutu-Upper Essequibo, Acarai Mts, 8 km S of Sipu River, N01°21' 58' 57", 610 m, 3 Sept. 1998, *Clarke D et al. 7429* (CAY, US). – PERU, Loreto, Loreto, Río Pucacuro, S3°17' W74°59', 100–200 m, 14 Jan. 2005, *Tuomisto H et al. 14123* (AMAZ, TUR, UC, USM); Loreto, Río Tigre, S3°33' W74°39', 100–200 m, 6 Feb. 2005, *Tuomisto H et al. 14956* (AMAZ, TUR); Mariscal Ramón Castilla, Río Yaguasyacu, 2–5 km SW from the village of Puerto Izango, S3°18' W72°1', 100–150 m, 23 May 1997, *Tuomisto H et al. 11252* (AAU, AMAZ, TUR, UC, USM); Mariscal Ramón Castilla, Río Yaguasyacu, 2 km S from the village of Puerto Izango, S3°19' W72°00', 100–150 m, 20 Aug. 1998, *Tuomisto H et al. 12677* (AMAZ, TUR, USM); Maynas, Estación Biológica Quebrada Blanco, S4°21' W73°9', 110 m, 17 Sept. 2010, *Cárdenas GG et al. 1755* (AMAZ, TUR); Requena, Río Ucayali, 2 km N from the biological station Jenaro Herrera, S4°52' W73°39', 100–200 m, 18 Sept. 1998, *Tuomisto H et al. 12785* (AMAZ, TUR, USM). – VENEZUELA, Amazonas, Cerro Sipapo (Paráque), 2 Feb. 1949, *Maguire B & Politi L 28766* (K, US).

Notes — *Salpichlaena hookeriana* is unique within the genus in the nearly complete absence of laminar tissue in fertile pinnules. Serrate apices of the sterile pinnae and the presence of foliar buds differentiate it from *S. hybrida* and *S. volubilis*. Foliar buds are common on climbing fronds and occur at the base of the pinnae and sometimes at the base of pinnules. They are more frequent in sterile than in fertile pinnae. Foliar buds have also been seen in *S. papyrus*, but only rarely. The non-climbing fronds of the *S. hookeriana* can be separated from the co-occurring *S. volubilis* subsp. *amazonica* by smaller size and higher number of pinnae.

The clearly serrate pinna/pinnule apices is a character that *S. hookeriana* shares with *S. papyrus* but not with the other species. The sterile fronds of these two species can be differentiated by the scales: in *S. hookeriana*, scales are lanceolate



Map 1 Distribution of *Salpichlaena hookeriana* (Kuntze) Alston (■), *S. hybrida* Lehtonen, G.G.Cárdenas & Tuomisto (▲), *S. papyrus* G.G.Cárdenas, Tuomisto & Lehtonen (●), *S. volubilis* (Kaulf.) J.Sm. subsp. *volubilis* (◆), *S. volubilis* subsp. *amazonica* G.G.Cárdenas & Tuomisto (◆), *S. volubilis* subsp. *crenata* G.G.Cárdenas & Tuomisto (◆), *S. volubilis* subsp. *thalassica* (Grayum & R.C. Moran) G.G.Cárdenas & Tuomisto (◆).

and have long appendices, whereas in *S. papyrus* they are formless and resemble crumpled paper and usually lack appendices. In addition, *S. hookeriana* has elliptic pinnules with herbaceous texture whereas *S. papyrus* has more lanceolate chartaceous pinnules.

2. *Salpichlaena hybrida* Lehtonen, G.G.Cárdenas & Tuomisto, sp. nov. — Fig. 3b, 6; Map 1

Intermediate between *S. hookeriana* and *S. volubilis* subsp. *amazonica*. Differs from the former by lack of foliar buds, presence of laminar tissue in fertile pinnae and larger pinnae in the non-climbing fronds; and from the latter by the herbaceous texture of the lamina and thin rather than cartilaginous pinna/pinnule margin. — Type: *Christenhusz, M.J.M., Bollendorff, S.M., Maas, P.J.M. & Maas-van de Kamer, H. 2460* (holo TUR (mounted on three sheets: 576477, 576478, 576479); iso CAY, NY, U), French Guiana, Commune Montsinéry-Tonnégrande, Bagne des Annamites, km 15 along Route Départementale 5, near Rivière de Tonnégrande, N4°48' W52°29', 21 Feb. 2003.

Etymology. The specific epithet refers to the postulated hybrid origin of the species.

Climbing and non-climbing fronds with herbaceous lamina texture, pinnae and pinnule margins not cartilaginous (to slightly cartilaginous); scales on abaxial axes lanceolate with long appendices sometimes divided and bifurcate, some stick-like scales formed by a long apical row of cells and usually two shorter basal lateral cells; stomata rarely on white laminal protuberances. *Non-climbing* 1-pinnate fronds 62–151 cm. Pinnae up to 4 pairs; apical one elliptic (oblanceolate), 22.6–46 by 6.4–8 cm; lateral ones oblanceolate, 22.7–35 by 6–7.2 cm; apex acuminate (caudate), with entire (slightly serrate) margin; base obtuse, acute. *Climbing* fronds with dimorphic pinnae. Pinnules opposite to subopposite. *Fertile pinnules* in up to 6 pairs; apical one elliptic, lanceolate, slightly oblanceolate, 20 by 4.1 cm, apex caudate, entire, base acute, oblique up to 0.1 cm; lateral ones elliptic (oblanceolate), 19.5 by 4.1 cm, apex caudate, entire, base obtuse, slightly oblique. *Sterile pinnules* in 2–4 pairs; apical one elliptic, slightly oblanceolate, 13–20 by 3.8–6.6 cm, apex acuminate (caudate), entire to slightly serrate, base acute, slightly oblique; lateral ones oblanceolate, 9.5–15.8 by 2.9 cm, apex acuminate, caudate, entire, base obtuse, equilateral to oblique; petiolulate, rarely sessile or winged.

Distribution — *Salpichlaena hybrida* occurs in northern Brazil (Roraima), French Guiana and Suriname.

Habitat & Ecology — Terra firme rain forest, on white sand and poorly drained soil, close to creeks and paths. Altitude 0–130 m.

Additional specimens seen (paratypes). BRAZIL, Roraima, Rorainópolis, about 5 km W along a side road starting at km 120–130 (RR) of the Manaus - Boa Vista road, N0°13' W60°29', 80–130 m, 18 Feb. 2008, *Tuomisto H et al. 15787* (TUR). – FRENCH GUIANA, Cayenne, road N2 from Régina to Saint-Georges de l'Oyapock, km 127, N4°9' W52°6', 70 m, 29 Oct. 2013, *Lehtonen S & Geniez C 1073* (CAY, TUR); environs du lieu-dit 'Roche-bateau', sur la Crique Nouvelle-France, 11 Mar. 1976, *Raynal A & Tirel C 18572* (P). – SURINAME, Brokopondo, Brownsberg Nature Park, Mazaroni vallen, waterfalls on very steep slope of at least 60°, N4°56' W55°12', 400–500 m, 6 Mar. 2003, *Christenhusz MJM & Bollendorff SM 2581* (TUR).

Notes — The climbing sterile pinnae are elliptic and similar in appearance to those of *S. hookeriana*, but the pinnule apices are entire instead of serrate. Non-climbing fronds are similar to those of *S. volubilis* subsp. *amazonica* in having large pinnae, but in *S. hybrida* they have herbaceous texture and lack the cartilaginous margin. *Salpichlaena hybrida* can be differentiated from *S. papyrus* by the entire pinnule apices and by the scales similar to those in *S. hookeriana* in contrast to the scales of *S. papyrus* resembling crumpled paper. *Salpichlaena hybrida* differs from *S. volubilis* subsp. *volubilis* by shorter and broader pinnules, and from *S. volubilis* subsp. *crenata* by shorter pinnules and by thinner lamina texture.

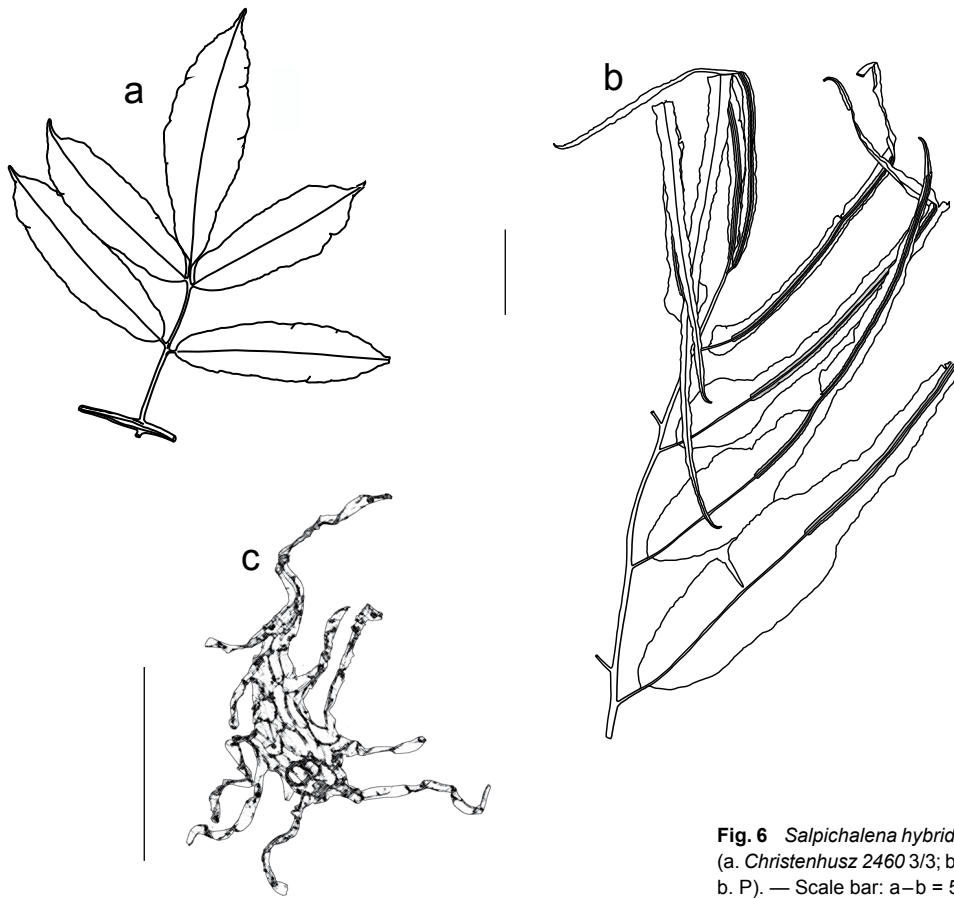


Fig. 6 *Salpichlaena hybrida*. a. Sterile pinna; b. fertile pinna; c. costal scale (a. Christenhusz 2460 3/3; b. Raynal 18572; c. Christenhusz 2460; a, c. TUR; b. P). — Scale bar: a–b = 5 cm; c = 0.5 mm.

We did not have physical access to fertile specimens of *S. hybrida* and the description of the fertile state is based on a few morphologically identified specimens seen as digital images. Hence, we do not have molecular support for the identification of the fertile specimens. Among the specimens seen, *Raynal A & Tirel C 18572* (P01326148) can be considered most typical as it clearly shows mixed characters of the presumed parental taxa.

3. *Salpichlaena papyrus* G.G.Cárdenas, Tuomisto & Lehtonen, *sp. nov.* — Fig. 3c, 7; Map 1

Salpichlaena papyrus can be recognised by its scales on the abaxial axes having an appearance of crumpled paper, or being broadly ovate with no appendices or only small ones. — Type: *Jones M & Olivas P 165* (holo CR (CR0241094), iso LSCR, TUR (mounted on two sheets: 591746, 591747), USJ), Costa Rica, Heredia, Sarapiquí, La Selva Biological Station, nearest grid post P1000:50, N10°26' W84°1', 50–150 m, 7 Aug. 2001.

Etymology. The specific epithet refers to the scales, which have the distinctive appearance of crumpled paper.

Climbing and non-climbing fronds with herbaceous, chartaceous (to coriaceous) lamina texture, pinnae and pinnule margins not cartilaginous (to slightly cartilaginous); scales on abaxial axes formless resembling crumpled paper or ovate with no appendices or only short ones (1–3 cells); stomata often on white protuberances of the lamina. *Non-climbing* entire fronds up to 32 by 3 cm. *Non-climbing* 1-pinnate fronds 20–80 cm. Pinnae up to 9 pairs, apical one lanceolate (elliptic), 11.2–22.2 by 2–2.7 cm; lateral ones lanceolate, parallel-sided (elliptic), 6.3–19.2 by 1.5–2.8 cm; basal ones rarely pinnate; apex acuminate (attenuate), with serrate margin; base obtuse. *Climbing* fronds with pinnae almost monomorphic, although fertile pinnae usually narrower than sterile. Pinnules subopposite to opposite (alternate). *Fertile pinnules* in 2–11 pairs; apical one lanceolate, lanceolate-elliptic, elliptic-lanceolate (falcate), 12–27.7 by

0.8–2.1 cm, apex attenuate, serrate margin (to entire), base obtuse, cuneate, equilateral to oblique; lateral ones lanceolate, elliptic, elliptic-lanceolate, parallel-sided (falcate), 12.6–22.7 by 0.6–1.8 cm, apex attenuate, long-attenuate, acuminate, caudate or serrate, base obtuse, equilateral to slightly oblique. *Sterile pinnules* in 3–10 pairs; apical one lanceolate, parallel-sided (elliptic), 10.7–24.5 by 0.9–3.7 cm, apex attenuate, acuminate, serrate margin, base round, acute, equilateral to oblique; lateral ones lanceolate, parallel-sided (elliptic), 9.6–20.4 by 1.8–3.3 cm, apex acuminate, attenuate (caudate), serrate margin, base obtuse (acute), equilateral to oblique; petiolulate, sessile, rarely winged. Foliar buds rarely present at the base of pinnules.

Distribution — *Salpichlaena papyrus* occurs in Central America in Costa Rica, Nicaragua and Panama, and in South America in Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru and Venezuela.

Habitat & Ecology — In primary rain forests on variable topographies on relatively well-illuminated sites near paths, tree fall gaps, streams, cliffs and ravines, also along forest borders and in disturbed forests. Reported from clayey to loamy soils. Altitude 50–1830 m.

Additional specimens seen (paratypes). BOLIVIA, Beni, Ballivián, al sud de la Misión Fatima, 950 m, 24 May 1988, *Beck G, et al. 16372* (F). — BRAZIL, Mato Grosso, Chapada dos Guimaraes, Veu das Noivas, 16 Feb. 1988, *Salino A 402* (AAU, BHCB, UEC). — COLOMBIA, Meta, Llanos, 457 m, Mar. 1948, *Sandeman C 5868* (K); Nariño, 2 km E of Barbacoas, just s of Río Telembí, N1°40' W78°8', 100 m, 13 Oct. 1943, *Fosberg FR 21245* (US). — COSTA RICA, Cartago, forest near the entrance to Parque Nacional Tapanti, 1270 m, 3 Aug. 1983, *Moran R 3344* (AAU, MO); Heredia, Sarapiquí, La Selva biological station, nearest grid post 3400:750, N10°26' W84°1', 50–150 m, 21 May 2007, *Jones M & Putkonen M 610* (TUR); San Jose, Parque Nacional Braulio Carrillo, Estación La Montura, Sendero A de 0–250 m, 22 Jan. 1984, *Gómez LD et al. 20878* (AAU). — ECUADOR, Morona-Santiago, Mutintz, SE of Makuma, c. 1 km along trail to Tunantz, S2°11' W77°44', 675 m, 31 Oct. 1996, *Øllgaard B & Navarrete H 1907* (AAU); Zamora-Chinchipec, Rd. Zumba-San Andres, km 1–4, N4°50' W79°8', 1300–1500 m, 24 May 2001, *Elgaard Madsen J & Rosales*



Fig. 7 *Salpichlaena papyrus*. a. Sterile pinna; b. fertile pinna; c. costal scale; d. juvenile (a–c. Jones 165; d. Tuomisto 15145; all TUR). — Scale bar: a–b, d = 5 cm; c = 0.5 mm.

C 8079 (AAU); Pastaza, Sarayacu, S01°46' W77°29', 12 Apr. 2007, *Sirén A et al. 64* (QCA, TUR). — FRENCH GUIANA, Sommet tabulaire, centre ouest, Tête de crique marécageuse avec éboulis éclairée et ensoleillée, ± 45 km ES de Saül, 600–650 m, *Cremers 6502* (CAY, Z). — GUYANA, Cuyuni-Mazaruni, Mt Maringma, southern slopes of summit escarpment, Arabarú River, N5°12'16.6" W60°34'35.9", 1360 m, 23 June 2004, *Clarke et al. 12005* (US); *Schomburgk 1140* (K). — NICARAGUA, Rio San Juan, San Juan del Norte, Reserva Indio-Maiz, N11°07' W83°54', 100 m, 18 Sept. 1998, *Rueda R et al. 8780* (US). — PANAMA, Coclé, 3-mountain ridge above El Valle, N8°40' W80°10', 900–1000 m, 24 July 1983, *Hamilton C et al. 4121* (AAU); Colón, Sierra Llorona, collected in forest at P32, N9°21' W79°44', 285 m, 5 Mar. 2008, *Jones M & Mitre D 933* (TUR). — PARAGUAY, in regione calcarea cursus superioris fluminis Apa, Sept. 1913, *Hassler 11969* (K, Z). — PERU, San Martín, Rioja, Sol de Oro, S5°54' W77°27', 1343 m, 17 June 2015, *Suominen L et al. 286* (TUR). — VENEZUELA, Bolívar, Alto Caroni, alrededores de Santa Elena de Uairen, 25 Apr. 1946, *Lasser 1642* (K, US); Zulia, Ayapa, Sierra Perijá, west of Machiques, 1320 m, Dec. 1947, *Ginés 137* (US).

Notes — *Salpichlaena papyrus* shares the serrate pinnule apices with *S. hookeriana*, but can be differentiated from it in any ontogenetical state by the scales that are formless and resembling crumpled paper, and in the fertile state by the presence of laminar tissue in the fertile pinnules. Furthermore, the usually higher number of pinnules, more lanceolate pinnule shape and more chartaceous texture of lamina are distinguishing characters.

The scales in *S. papyrus* are unlike those in any other species with an appearance of crumpled paper without clear shape (more often on the costa), or ovate with no appendices or only small ones (1 or 2 cells) (more often on the rachis and petiolule). Specimens with ovate scales and longer appendices have been observed in Peru, Bolivia and South-East Brazil. Scales on the rachises and petiolules are often big enough to be easily observed by the naked eye.

The serrate pinnule apices of *S. papyrus* are usually distinctive enough to allow differentiating it from *S. volubilis* and *S. hybrida*. However, the serration is less clear in fertile pinnules, which also have thicker lamina texture and more tendency towards a cartilaginous margin than the sterile pinnules do. Therefore, material consisting only of fertile pinnae can be difficult to identify to species, especially if the fronds are already so old that the scales have been eroded.

Foliar buds exist but are very rare in *S. papyrus*: out of the more than 300 specimens we studied, only two had foliar buds (*Øllgaard 105457* AAU and *Holm-Nielsen et al. 25341*, AAU, both from Ecuador). This contrasts with *S. hookeriana*, where foliar buds are very common. The non-climbing fronds in *S. papyrus* are sometimes 2-pinnate, a character that we have not observed in any other taxa.

Salpichlaena papyrus and *S. volubilis* subsp. *thalassica* are the only *Salpichlaena* taxa occurring in Central America and along the western side of the Andes, where they are broadly sympatric. The non-climbing fronds of *S. papyrus* usually are smaller and have higher number of pinnae than *S. volubilis* subsp. *thalassica*.

4. *Salpichlaena volubilis* (Kaulf.) J.Sm. — Fig. 3d–g, 8–11; Map 1

Salpichlaena volubilis (Kaulf.) J.Sm. (1841) 168.

Blechnum volubile Kaulf. (1824) 159. — *Spicanta volubilis* (Kaulf.) Kuntze (1891) 821. — Type: Korte A & Kniess A 2825 (neotype FLORFLOR0059465, designated here; isoneotype FURB FURB06861), Brazil, Santa Catarina, Ascurra, Guaricanas, S27°00'00" W49°24'36", 281 m, 15 Mar. 2010.

Blechnum scandens Bory (1828) 272. — *Salpichlaena scandens* (Bory) C.Presl (1851) 122. — Type: Brazil, Sta. Catherine, *Durville s.n.* 1827 (lectotype P00347471 designated here).

Etymology. The specific epithet refers to the twining petioles and rachises.

Climbing and non-climbing fronds with herbaceous to coriaceous lamina texture, pinnae and pinnule margins with or without cartilaginous margin; scales on abaxial axes either stick-like (formed by a long apical row of cells and usually two lateral smaller rows of cells) or lanceolate with small or large body of cells and always with long appendices; stomata located on small white laminal protuberances or not. *Non-climbing* entire fronds up to 53 by 6.8 cm. Non-climbing 1-pinnate fronds 45–135 cm. Pinnae up to 6 pairs; apical one lanceolate, elliptic, 16.3–45.5 by 2–9.5 cm; lateral ones lanceolate, elliptic, parallel-sided, oblanceolate, 18–32.2 by 1.7–7.7 cm; apex acuminate, attenuate, cuspidate, entire, entire with few small teeth on the cartilaginous margin, crenate; base obtuse, acute. *Climbing* fronds with pinnae slightly dimorphic, fertile pinnae generally narrower than sterile. Pinnules opposite to alternate; in 1–7 pairs, lanceolate, elliptic, oblanceolate, parallel-sided; petiolulate, sessile (winged); apex acuminate, attenuate, caudate (apiculate, cuneate, cuspidate, falcate), entire, almost entire with few small teeth (sometimes serration-like) on the cartilaginous margin, slightly crenate, slightly serrate, base obtuse, cuneate, acute, attenuate, equilateral to oblique.

Distribution — *Salpichlaena volubilis* is widely distributed, occurring from Central America to the Lesser Antilles and southern Brazil. Each of the four subspecies has a different distribution. *Salpichlaena volubilis* subsp. *amazonica* occurs in Western Amazonia, along the eastern slopes of the Andes and in French Guiana; *S. volubilis* subsp. *crenata* occurs in the Lesser Antilles and in the northern part of South America; *S. volubilis* subsp. *thalassica* occurs in Central America and

along the western side of the Andes in northeastern South America and *S. volubilis* subsp. *volubilis* occurs in the Atlantic rain forest of southeastern Brazil.

Notes — Apices of frond, pinna and pinnule of *S. volubilis* are entire, crenate to only slightly serrate, which differentiates it from *S. hookeriana* and *S. papyrus*, whose apices are obviously serrate. Most subspecies of *S. volubilis* differ from *S. hybrida* by their more chartaceous-coriaceous lamina texture and the presence of a cartilaginous margin. Only *S. volubilis* subsp. *volubilis* has equally herbaceous texture and non-cartilaginous margin, but it differs from *S. hybrida* by having lanceolate rather than elliptic pinnules. Distinguishing characters to identify *S. volubilis* subspecies are in Table 4.

We have been unable to locate any of the original material of *Blechnum volubile* collected by Von Chamisso. The type specimen was not found in LE where Von Chamisso's collection is kept. Therefore, we designate here a neotype for *Blechnum volubile*. We have chosen a specimen collected close to Santa Catarina Island, because according to Von Chamisso's diary (Von Chamisso 1821) this is the most probable place from where he could have collected the original material. Our results suggest that only one *Salpichlaena* taxon occurs in the Brazilian Atlantic Forest, and the name *S. volubilis* should be applied to this taxon.

Two different sources have received credit for the first publication of the name *Salpichlaena volubilis*, 'The Journal of Botany vol. 4', and 'Genera Filicum', both by Hooker. 'The Journal of Botany' has priority. It was published in 1841, whereas 'Genera Filicum' was probably published in 1842 (Staffeu & Cowan 1979).

a. subsp. *volubilis* — Fig. 3g, 4a, 8; Map 1

Climbing and non-climbing fronds with herbaceous to chartaceous lamina texture, pinnae and pinnule margins not cartilaginous, or sometimes slightly cartilaginous in fertile specimens; scales on abaxial axes lanceolate and ovate with long appendices, sometimes stick-like; stomata not on white laminal protuberances. *Non-climbing* entire fronds up to 33 by 2.3 cm. Non-climbing 1-pinnate fronds 45–101 cm. Pinnae up to 6 pairs; apical one lanceolate, elliptic, 16.3–25.5 by 2–3.5 cm; lateral ones lanceolate (elliptic), 11.3–27.5 by 1.7–3.5 cm; apex acuminate, with entire margin; base obtuse. *Climbing* fronds with pinnules subopposite to opposite. *Fertile pinnules* in 3–7 pairs; apical one lanceolate, oblanceolate, elliptic, 12.9–18.2 by 0.75–1.8 cm, apex acuminate, attenuate (round or fan-shaped tip caused by the apical division of the main vein), entire, base

Table 4 Distinguishing characters to identify *Salpichlaena volubilis* subspecies.

Characteristic	<i>Salpichlaena volubilis</i> subspecies			
	<i>amazonica</i>	<i>crenata</i>	<i>thalassica</i>	<i>volubilis</i>
Lamina texture	chartaceous, coriaceous (herbaceous)	chartaceous, herbaceous (coriaceous)	chartaceous, herbaceous, coriaceous	herbaceous (chartaceous)
Margin texture	cartilaginous	slightly cartilaginous (cartilaginous)	cartilaginous	not cartilaginous, but sometimes yellowish
Apex margin	entire or with few small teeth cutting only into the cartilaginous margin	crenate or slightly serrate	entire or with few small teeth cutting only into the cartilaginous margin	entire
Abaxial scales	stick-like and lanceolate with long appendices	lanceolate and stick-like	stick-like and lanceolate with long appendices	lanceolate to ovate with long appendices
Lateral pinnule shape	elliptic, lanceolate, oblanceolate	lanceolate, elliptic (parallel sided)	elliptic, lanceolate (parallel sided)	lanceolate
Number of lateral pinnae (non-climbing)	up to 3	up to 3	up to 4	up to 6
Number of lateral pinnules (climbing)	1–6	1–5	1–6	2–5
Abaxial lamina surface	uniform	uniform	stomata on whitish protuberances	uniform

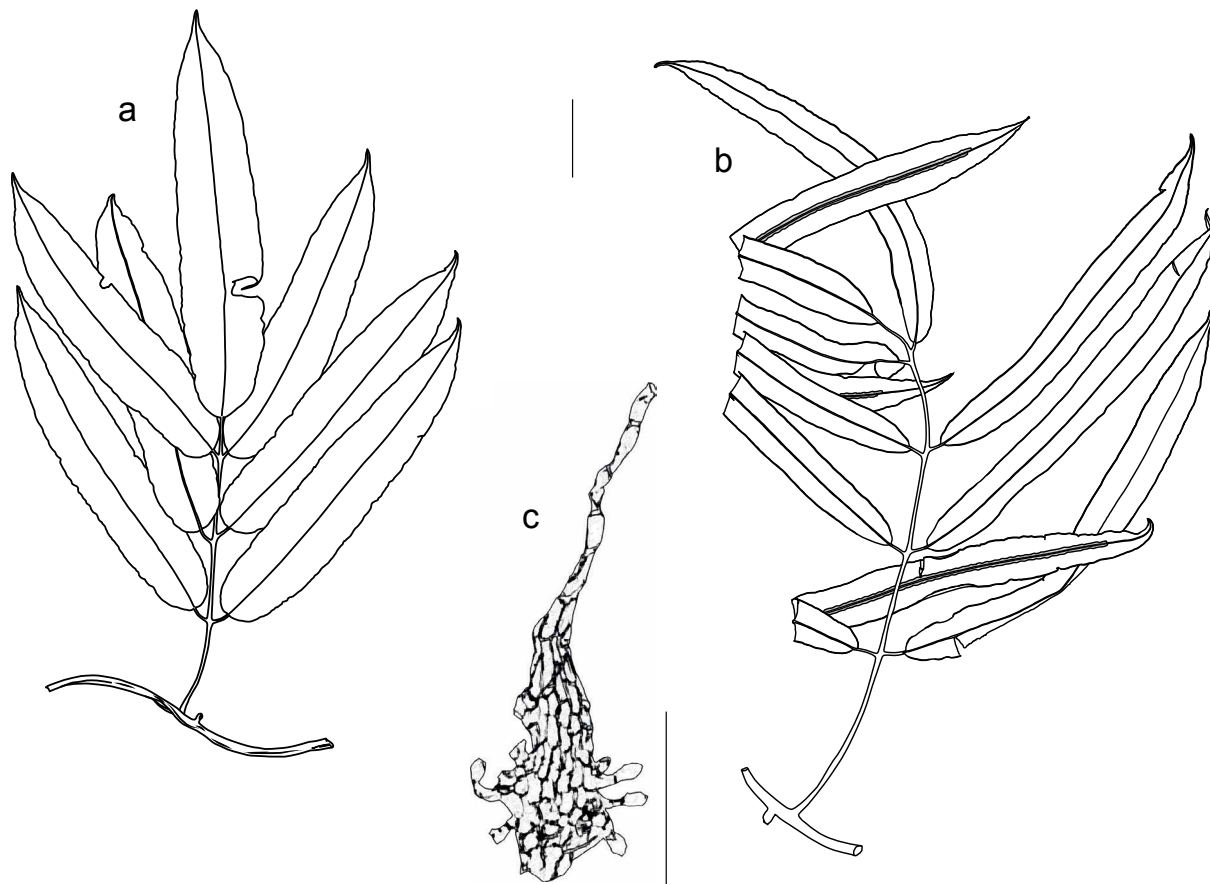


Fig. 8 *Salpichlaena volubilis* subsp. *volubilis*. a. Sterile pinna; b. fertile pinna; c. costal scale (a. *Christenhusz* 49552/2; b. *Christenhusz* 48311/2; c. *Lehtonen* 601; all TUR). — Scale bar: a–b = 5 cm, c = 0.5 mm.

obtuse, equilateral; lateral ones elliptic, parallel-sided, slightly oblanceolate, 12–13.6 by 0.69–1.5 cm, apex acuminate-attenuate (round or fan-shaped tip caused by the apical division of the main vein), base obtuse, attenuate, equilateral. *Sterile pinnules* in 2–5 pairs; apical one lanceolate, elliptic, 17.5 by 2.2 cm, apex acuminate, entire (round or fan-shaped tip caused by the apical division of the main vein), base obtuse, equilateral; lateral ones lanceolate, 13.6 by 1.9 cm, apex, acuminate, entire (round or fan-shaped tip caused by the apical division of the main vein), base obtuse, equilateral; petiolulate, sometimes winged.

Distribution — *Salpichlaena volubilis* subsp. *volubilis* occurs in the Atlantic rain forest in southeastern Brazil.

Habitat & Ecology — Terra firme, primary and disturbed Atlantic rain forest. Near open places like waterfalls and ravines. On hills, mid-slope and flat terrain. On clay soil. Altitude 0–1175 m.

Additional specimens seen. BRAZIL, Bahia, Litoral Sul, Ituberá, Pacangê, S13°43' W39°08', 10 Apr. 2006, *Valadão R & Guedes ML* 38 (ALCB); El Moricano, 1836, *Blanchet J* 2487 (K, NY); Espírito Santo, Conceição da Barra, Floresta Nacional do Rio Preto, S18°22'22.8" W39°51'01.5", 27 m, 10 June 2009, *Salino A et al.* 14313 (BHCB); Reserva Natural da CVRD-LINHARES, Jueirana Facão, *Folli DA* 5469 (CVRD); Paraná, Mun. Matinhos, Matinhos, Morro do Teleférico, S25°51' W48°33', 0–10 m, 14 Feb. 2008, *Christenhusz MJM et al.* 4774 (TUR); Pernambuco, Jaqueira, Usina Colônia (Serra do Quengo), S8°42'50.4" W35°50'25.8", 713 m, 3 Apr. 2002, *Lopes M & Pietrobom MRS* 550 (HUEFS, INPA); Rio de Janeiro, *Miers* 177 (K); Santa Catarina, Guabiruba, Aymoré, S27°05'24" W49°02'58", 256 m, 28 Oct. 2009, *Stival-Santos A et al.* 1123 (FLOR, FURB); Jaraguá do Sul, along the road to Campo Alegre, near Rio Itapocuzinho, S26°21' W49°8', 140 m, 10 Feb. 2008, *Christenhusz MJM et al.* 4743 (TUR); São Paulo, Parque Estadual das Fontes do Ipiranga, trail near the border of the zoo, S23°39' W46°37', 800 m, 19 Feb. 2008, *Christenhusz MJM et al.* 4800 (NY, TUR); Mun. Tapiraí, fazenda São José, S24°1' W47°27', 300 m, 24 Feb. 2008, *Lehtonen S et al.* 601 (SP, TUR); Parque Estadual da Serra do Mar, Núcleo Caraguatatuba, estrada da Intermediária, Rio Pardo, S23°40' W45°39', 715 m, 8 Mar. 2008,

Lehtonen S et al. 637 (SP, TUR); Iporanga, *Prado J et al.* 956 (INPA, NY); Brotas, Mata do Veiro Municipal, 14 July 1991, *Salino* 934 (BHCB, UEC).

Note — *Salpichlaena volubilis* subsp. *volubilis* differs from the other subspecies by its narrow pinnules with herbaceous (to chartaceous) lamina texture and non-cartilaginous to only slightly cartilaginous margin. Some specimens of subsp. *crenata* with nearly entire pinnule apices and lanceolate pinnules approach subsp. *volubilis* and cannot be reliably identified. We place the specimens from the Atlantic rain forest to subsp. *volubilis* and the specimens from eastern Amazonia, the Caribbean and Guyanas to subsp. *crenata*, but the distinction in morphology is diffuse and the amount of genetic variation within subsp. *crenata* is high.

b. subsp. *amazonica* G.G.Cárdenas & Tuomisto, *subsp. nov.* — Fig. 3d, 4f, 9; Map 1

Salpichlaena volubilis subsp. *amazonica* can be recognised by its chartaceous to coriaceous lamina texture, clearly cartilaginous pinnule margins, long and wide pinnules and uniform abaxial lamina. — Type: *Tuomisto H, Moulatlet G, Ruokolainen K & Castro D* 16904 (holotype SP; isotype INPA, TUR (mounted on four sheets: 606298–606301)), Brazil, Amazonas, Carauari, c. 7 km south from the village of Vila Ramalho, Rio Juruá, S5°35' W67°29', 100 m, 14 June 2012.

Etymology. The name refers to the geographical distribution of the subspecies in Amazonia.

Climbing and non-climbing fronds with chartaceous to coriaceous lamina texture, pinnae and pinnule margins clearly cartilaginous; scales on abaxial axes stick-like, formed by a long apical row of cells and usually two lateral smaller rows of cells, and sometimes also lanceolate scales with long appendices; stomata not (or very rarely) on white laminal protuberances. *Non-climbing* entire fronds up to 53 by 6.8 cm. *Non-climbing* 1-pinnate fronds

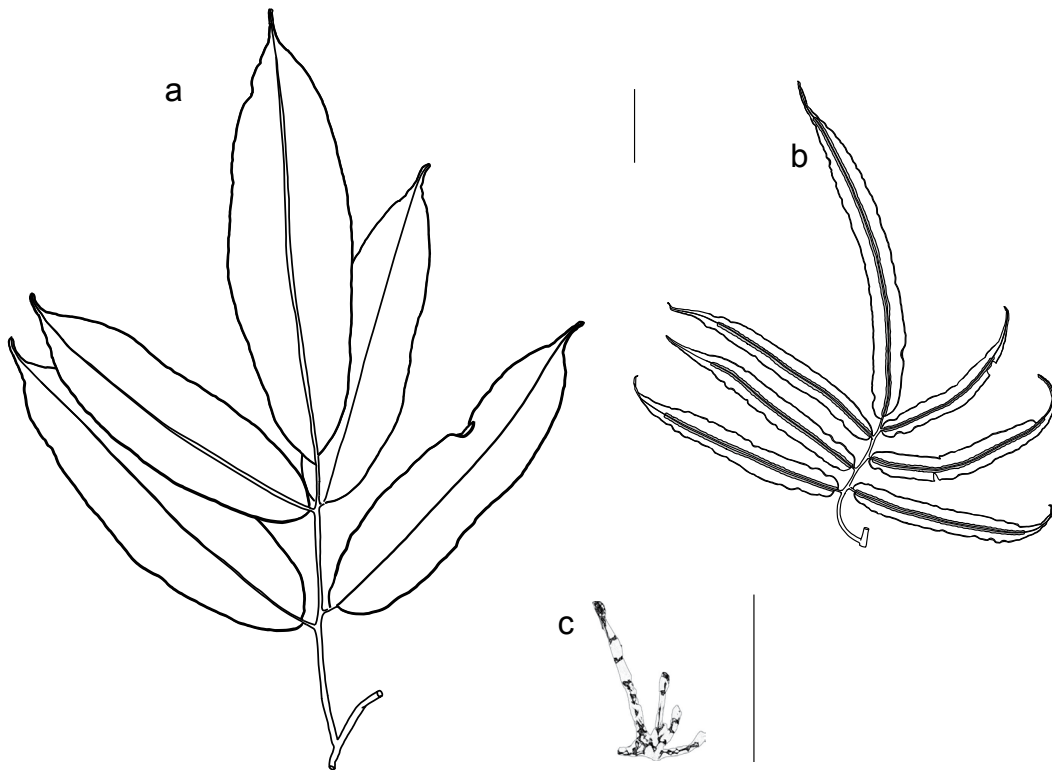


Fig. 9 *Salpichlaena volubilis* subsp. *amazonica*. a. Sterile pinna; b. fertile pinna; c. costal scale (a. Tuomisto 16904; b. Tuomisto 14562; c. Tuomisto 16010; all TUR). — Scale bar: a–b = 5 cm; c = 0.5 mm.

65–135 cm. Pinnae up to 3 pairs; apical one elliptic, lanceolate, 21.7–45.5 by 5.4–9.5 cm; lateral ones elliptic, oblanceolate, 18.5–30.8 by 5–7.7 cm; apex acuminate, cuspidate, with entire margin or with few small teeth on the cartilaginous margin; base obtuse, acute. *Climbing* fronds with pinnules subopposite to alternate. *Fertile pinnules* in 1–7 pairs; apical one lanceolate, elliptic (parallel-sided), 21–38.3 by 1.2–3.9 cm, apex attenuate, long-attenuate, acuminate, entire or with few small teeth (sometimes serration-like) on the cartilaginous border, base acute, strongly oblique; lateral ones elliptic-oblanceolate, lanceolate, parallel-sided, 14–25 by 1.6–2.2 cm, apex acuminate, attenuate, entire or with few small teeth (sometimes serration-like) on the cartilaginous border, base obtuse, equilateral. *Sterile pinnules* in 1–6 pairs; apical one elliptic, lanceolate or oblanceolate, 19.3–36.7 by 3.7–8.8 cm, apex acuminate, cuspidate, apicular, entire or with few small teeth (sometimes serration-like) on the cartilaginous border, base obtuse, acute, equilateral to strongly oblique; lateral ones elliptic, lanceolate, oblanceolate, 15.2–35.2 by 3.7–8.6 cm, apex cuspidate, acuminate (attenuate, apicular), entire or with few small teeth (sometimes serration-like) on the cartilaginous border, base obtuse, acute, equilateral to oblique; petiolulate, sessile (winged).

Distribution — *Salpichlaena volubilis* subsp. *amazonica* occurs mostly in Western Amazonia (eastern slopes of the Andes) with a few occurrences in Central Amazonia and the Guyana Shield, in Bolivia, Brazil, Colombia, Ecuador, French Guiana and Peru.

Habitat & Ecology — Tropical rain forest, usually in terra firme, rarely in periodically inundated areas or swamps. On hills, mid-slope and flat terrain. On loamy soil. Altitude 50–1500 (–2378) m.

Additional specimens seen (paratypes). BOLIVIA, La Paz, puente de Tora (near Tipuani), 800 m, Cárdenas M 1287 (US); near Inglis-Inglis, 1524 m, 16 Aug. 1902, Williams RS 1295 (US). — BRAZIL, Amazonas, Carauari, c. 4 km south from the village of Bom Jesus, Rio Juruá, S5°24' W67°12', 100 m, 30 Mar. 2012, Tuomisto H et al. 16010 (SP, TUR); Itamarati, c. 5 km north-west from the town of Itamarati, Rio Juruá, S6°24' W68°17', 120–150 m, 8 Apr.

2012, Tuomisto H et al. 16118 (SP, TUR); Eirunepe, c. 3 km south from the village of Vila União, Rio Juruá, S6°47' W70°11', 140 m, 1 May 2012, Tuomisto H et al. 16550 (SP, TUR). — COLOMBIA, Amazonas, Rio Caquetá, Araracuara, 24 Sept. 1991, Vester H & Matapi A 653 (Z); Caquetá, Valparaiso, via Morelia-Valparaiso, finca Las Palmeras, N1°11'3.5" W75°39'21.6", 250 m, 19 Oct. 2010, Rodríguez WD et al. 7001 (NY). — ECUADOR, Morona-Santiago, comunidad Shuar de Mutints, faldas orientales de la Cordillera del Cutucú, S2°11' W77°44', 600 m, Navarrete H 1257 (AAU); Napo, Parque Nacional Yasuní, S0°40' W76°23', 250–280 m, 30 Jan. 1996, Navarrete H 1509 (AAU); Pastaza, Sarayacu, S01°52' W77°14', 1 Dec. 2007, Sirén A et al. 2023 (QCA, TUR); Sucumbios, Reserva Faunística Cuyabeno, one-hectare plot c. 1 km north of Laguna Grande and surroundings, S0°00' W76°12', 265 m, Poulsen A 80802 (AAU). — FRENCH GUIANA, D.Z. du Haut-Kourcibo, Bassin du Sinnamary, N4°28'23" W53°17'18", 80 m, 19 Apr. 1991, de Granville JJ et al. 11333 (CAY, US). — PERU, Amazonas, Bagua, along road from Chiriaco towards Bagua, S05°16'57" W78°23'10", 750 m, 21 Mar. 2001, Van der Werff H. et al. 16278 (MO); Cajamarca, San Ignacio, Huarango, S5°03'50" W78°43'19", 2378 m, 27 Aug. 2007, Perea J et al. 3902 (AAU, US); Loreto, Loreto, Upper Rio Pastaza, ± 20 km northwest of Nuevo Andoas community, S2°44' W76°37', 250 m, 26 Mar. 2005, Higgins M & Ruiz F 139 (TUR); Ramón Castilla, rio Yavarí-Mirín, S4°25' W72°23', 100–200 m, 23 Mar. 2002, Cárdenas GG & Salovaara K 1290 (AMAZ, TUR, USM); Madre de Dios, Manu, Eastern bank of rio Colorado, 10 km from its confluence with rio Madre de Dios, S12°40' W70°28', 250–350 m, 2 Nov. 1998, Tuomisto H et al. 13601 (TUR); San Martín, Rioja, Yaracyacu, S5°58' W77°24', 1381 m, 10 June 2015, Suominen L et al. 219 (TUR); Pasco, Oxapampa, Palcazu Valley, Iscozacín, S10°12' W75°15', 400 m, 12 Jan. 1984, Foster R et al. 7894 (F, USM).

Notes — In general appearance, *S. volubilis* subsp. *amazonica* is similar to subsp. *thalassica* and non-climbing fronds can be confused with *S. hybrida*. However, usually subsp. *amazonica* can be distinguished from subsp. *thalassica* by the uniform appearance of the abaxial lamina in contrast to the typical white protuberances of the lamina associated with stomata in subsp. *thalassica*. The chartaceous-coriaceous lamina texture and cartilaginous pinnule margins distinguish subsp. *amazonica* from *S. hybrida* and also from subsp. *volubilis*, both of which have herbaceous texture and non-cartilaginous (or only slightly cartilaginous) margins. It is more difficult to separate subsp. *amazonica* from subsp. *crenata* because their characters sometimes overlap. In subsp. *amazonica*, the pinnule apices are entire

or have small teeth that do not cut into the lamina, in contrast to subsp. *crenata* whose pinnule apices are usually crenate (sometimes slightly serrated or entire). Subsp. *amazonica* has wider pinnules, more chartaceous-herbaceous texture, and an obvious cartilaginous margin that is absent or not so obvious in subsp. *crenata*.

In the northern Andes, *S. volubilis* subsp. *amazonica* and subsp. *thalassica* are difficult to separate on morphological grounds. The distribution of our sequenced specimens suggests that *S. volubilis* subsp. *amazonica* is restricted to the eastern side of the Andes, whereas subsp. *thalassica* occurs only on the western side.

c. subsp. *crenata* G.G.Cárdenas & Tuomisto, *subsp. nov.* — Fig. 3e, 10; Map 1

Distinguished from all other *Salpichlaena* taxa by the crenate to slightly dentate-serrate apices of the sterile pinnules. — Type: *Christenhusz MJM & Katzer F 3988* (holotype TUR (mounted on two sheets 581127, 581128); isotypes NY 02007148, 02730089, P P01419530), Guadeloupe, Basse Terre, comm. Saint-Rose, Sofaïa, route forestier de Sofaïa, Trace de Baille-Argent-Sofaïa, down to the crossing with Rivière Moustique, N16°17' W61°44', 460 m, 8 Mar. 2005.

Etymology. The infraspecific epithet refers to the crenate pinnule apices.

Climbing and non-climbing fronds with chartaceous, herbaceous (coriaceous) lamina texture, pinnae and pinnule margins slightly cartilaginous to cartilaginous; scales on abaxial axes lanceolate with long appendices, some scales stick-like with a long apical row of cells and usually two smaller lateral cells; stomata rarely on white laminal protuberances. *Non-climbing* entire fronds up to 35 by 3.8 cm. *Non-climbing* 1-pinnate fronds 65–91 cm. Pinnae up to 3 pairs; apical one lanceolate (elliptic), 22.5–40.7 by 3.9–5.5 cm; lateral ones lanceolate, elliptic, 18.5–29.5 by 3.9–4.4 cm; apex attenuate, with entire, crenate margin; base acute, obtuse. *Climbing* fronds with pinnules subopposite (opposite, alternate). *Fertile pinnules* in 1–5 pairs; apical one elliptic, parallel-sided, lanceolate, 17.7–33.2 by 1.8–3.3 cm, apex caudate, acuminate, slightly serrate, entire margin, base acute, slightly oblique; lateral ones lanceolate, parallel-sided, slightly oblanceolate, 10–26 by 1.2–2.9 cm, apex slightly caudate, acuminate, attenuate with slightly crenate or slightly serrate margin, sometimes with a round or fan-shaped tip caused by the apical division of the main vein, base obtuse, cuneate, equilateral to slightly oblique. *Sterile pinnules* in 1–5 pairs; apical one lanceolate, elliptic, (parallel-sided), 16–28.8 by 2.2–6.5 cm, apex acuminate, caudate, attenuate, slightly crenate, slightly serrate, sometimes with a round or fan-shaped tip caused by the apical division of the main vein, base acute, ob-

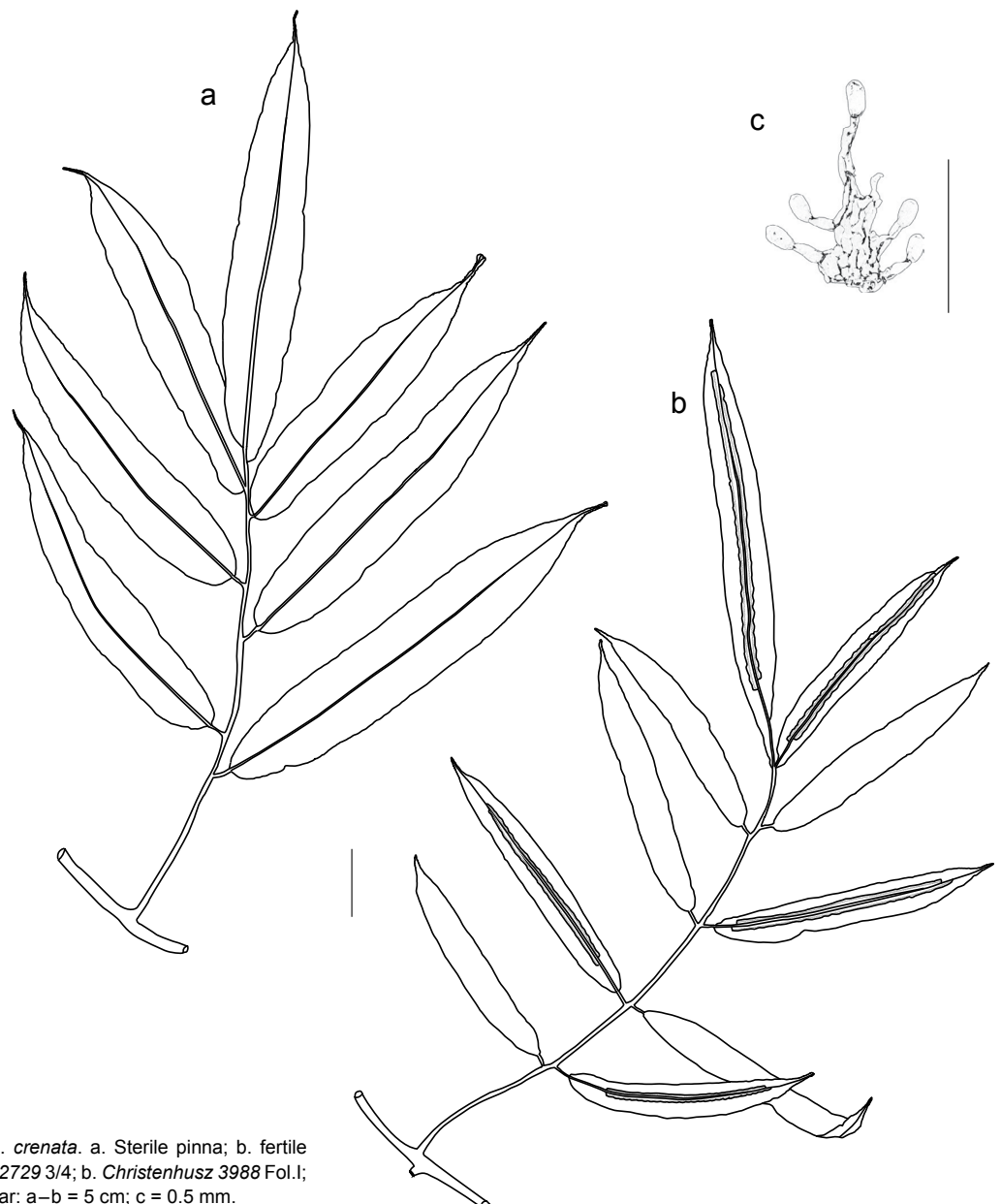


Fig. 10 *Salpichlaena volubilis* subsp. *crenata*. a. Sterile pinna; b. fertile pinna; c. costal scale (a. *Christenhusz 2729 3/4*; b. *Christenhusz 3988* Fol.I.; c. *Kessler 12906*; all TUR). — Scale bar: a–b = 5 cm; c = 0.5 mm.

tuse, cuneate (lobate), oblique; lateral ones lanceolate, elliptic (parallel-sided, falcate), 9–26.3 by 1.8–4.7 cm; apex attenuate, slightly crenate, slightly serrate, base acute, obtuse, equilateral to oblique; petiolulate (sessile or winged).

Distribution — *Salpichlaena volubilis* subsp. *crenata* occurs in the Lesser Antilles and in the northern part of South America, in Brazil, Dominica, Guadeloupe, French Guiana, Guyana, Martinique, Santa Lucia, Suriname, Trinidad and Tobago, Venezuela.

Habitat & Ecology — Terra firme primary rain forest, subtropical and transitional cloud forests. Along paths and along steep creekbanks. In hills and flat terrain. On clay and sandy soil. Altitude 70–1123 m.

Additional specimens seen (paratypes). BRAZIL, Amapá, Rivière Haut Jari, N54°46' W2°28', 400 m, 17 Aug. 1993, *de Granville JJ et al. 12339* (CAY, Z); Amazonas, Presidente Figueiredo, Reserva Biológica Uatumã, close to the easternmost point of the lake, S1°45' W59°19', 90–140 m, 6 Feb. 2008, *Tuomisto H et al. 15651* (TUR). — DOMINICA, rainforest bordering Imperial Road, Sylvania to Mahaut River, 549 m, 13 and 23 Aug. 1938, *Hodge WH 98* (NY, US); Syndicate Estate, north-west slopes of Morne Diablotins, 10 Oct. 1983, *Whitefoord C & Eddy A 3965* (US). — FRENCH GUIANA, Cayenne, Réserve Naturelle des Nouragues, camp Inselberg, white quartz sand derived from the inselberg, along a small creek, N4°5' W52°40', 200 m, 5 Oct. 2013, *Lehtonen S et al. 813* (CAY, TUR); road N2 from Régina to Saint-Georges de l'Oyapock, km 159, N4°00' W51°57', 70 m, 23 Oct. 2013, *Lehtonen S & Geniez C 985* (CAY, TUR); Montagne Cacao, SE de Cayenne, *Cremers 7819* (CAY, P, Z). — GUADELOUPE, Basse Terre, Capesterre-Belle-Eau, Grand-Étang, along D4 road from St. Sauveur to Chutes du Carbet, N16°2' W61°37', 400 m, 30 Mar. 2003, *Christenhusz MJM & Bollendorff S 2729* (TUR); Sainte-Rose, Source Sulfureuse de Sofaïa, along the trail down to Saut des Trois Cornes, steep slopes with creek gullies, N16°18' W61°43', 400 m, 2 Apr. 2003, *Christenhusz MJM & Paajanen MT 2756* (TUR). — GUYANA, Cuyuni-Mazaruni, Waukayengtipu, slope, N5°49'30" W61°11'40", 1300 m, 10 July 1997, *Clarke HD et al. 5530* (CAY, US); Upper Takutu-Upper Essequibo, Acarai Mts, Kashinar Mt, summit

and surrounding slopes, N1°17' W58°39', 825–975 m, 2 Mar. 1994, *Henkel TW et al. 4903* (CAY, US). — MARTINIQUE, 1886, *Père Duss 1700* (NY). — SANTA LUCIA, forest between Quillesse and head of Murray Hill road, Apr. 22–May 18 1950, *Howard RA 11691* (P); Morne Lacombe at 1200', Aug. 1934, *Box HE 419* (US). — SURINAME, Brokopondo, Brownsberg Nature Park, steep slope on lateritic soil along path leading to Leoval, N4°57' W55°11', 400–500 m, 5 Mar. 2003, *Christenhusz MJM & Bollendorff S 2553* (TUR); Brownsberg Nature Park, Koemboeval, N4°56' W55°11', 400–500 m, 8 Mar. 2003, *Christenhusz MJM & Bollendorff S 2627* (TUR). — TRINIDAD AND TOBAGO, Tobago, road from Parlatuvier to Roxborough, near Gilpin Trace, 500 m, 28 Dec. 2002, *Kessler M 12906* (TUR); Trinidad, Arima valley, north range, Forestry Trail, 600 m, 24 Mar. 1959, *Cowan RS & Simmonds NW 1202* (P, US). — VENEZUELA, Vargas, cordillera de la Costa, serranía del litoral, Monumento Natural Pico Codazzi, Carretera Arco de la Colonia Tovar-Pto. Cruz, 2.5 km desde el Arco, SE del centro turístico Villa Bahareque, N10°26' W67°13.5', 1850–1950 m, 15 Aug. 1999, *Mostacero J & Castillo R 259* (US).

Note — Most specimens of *S. volubilis* subsp. *crenata* differ from all the other subspecies by the crenate to slightly dentate-serrate apices on sterile pinnules. When only slightly serrate (or practically entire), subsp. *crenata* may be confused with subsp. *amazonica* or subsp. *thalassica*, but the serrations in the latter two are, when present, merely small teeth in the cartilaginous border and they do not cut into the lamina, as they do in subsp. *crenata*. Fertile pinnules of subsp. *crenata* may have entire apices, and then they can be confused with fertile pinnae of the other subspecies of *S. volubilis*.

d. subsp. *thalassica* (Grayum & R.C. Moran) G.G.Cárdenas & Tuomisto, *comb & stat. nov.* — Fig. 3f, 4e, 11; Map 1

Salpichlaena thalassica Grayum & R.C.Moran (in Moran 1990) 591, 593. — Type: *Grayum & Chazdon 6833* (holotype MO; isotype CR), Costa Rica, Heredia, forest between Río Peje and Río Sardinalito, Atlantic slope of Volcán Barva, N10°17' W84°4.5', 800–1000 m, 7 Apr. 1986.

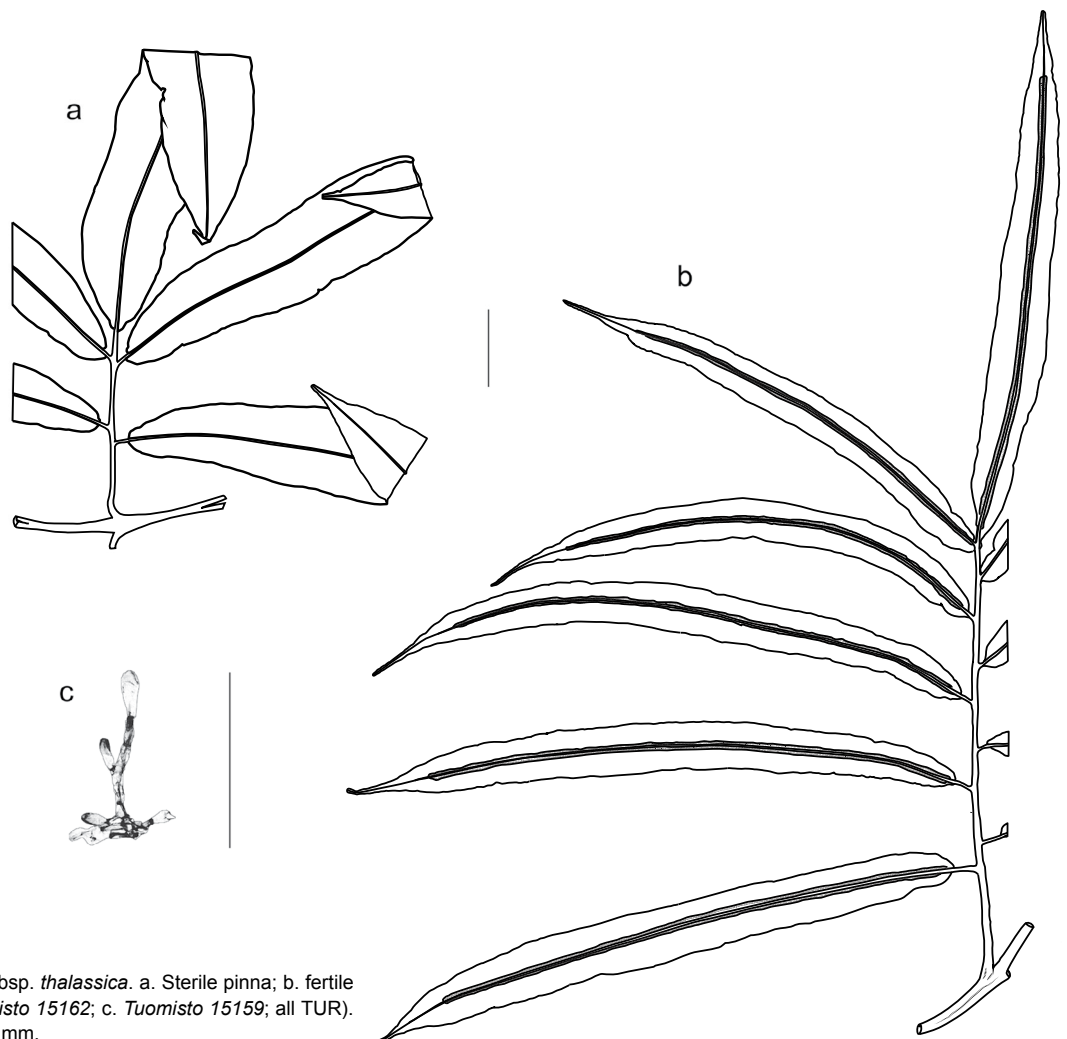


Fig. 11 *Salpichlaena volubilis* subsp. *thalassica*. a. Sterile pinna; b. fertile pinna; c. costal scale (a–b. *Tuomisto 15162*; c. *Tuomisto 15159*; all TUR). — Scale bar: a–b = 5 cm, c = 0.5 mm.

Etymology. The name refers to the bluish green colour of the fronds observed in the field.

Climbing and non-climbing fronds with chartaceous, herbaceous, coriaceous lamina texture, pinnae and pinnule margins cartilaginous; scales on abaxial axes stick-like formed by a long apical row of cells and usually two lateral smaller rows of cells and sometimes lanceolate scales with long appendices; stomata on white laminal protuberances. *Non-climbing* entire fronds up to 45 by 5 cm. Non-climbing 1-pinnate fronds 66–128 cm. Pinnae up to 4 pairs; apical one elliptic, lanceolate, 25–42 by 5.3–6.3 cm; lateral ones elliptic, parallel-sided, 18–32.2 by 3.7–5.5 cm; apex acuminate, attenuate, with entire margin; base obtuse. *Climbing* fronds with pinnules subopposite to opposite (alternate). *Fertile pinnules* in 1–5 pairs; apical one elliptic, lanceolate, parallel-sided, 18.2–30.2 by 1.1–3.1 cm, apex acuminate, attenuate (falcate), entire (slightly serrate), base cuneate, obtuse, acute, equilateral to strongly oblique; lateral ones elliptic (lanceolate, parallel-sided, falcate), 13.2–27.9 by 0.9–2.65 cm, apex acuminate, attenuate, or sometimes with a round, divided or fan-shaped tip caused by the apical division of the main vein, entire or with few small teeth (sometimes serration-like) on the cartilaginous border, base acute, obtuse, slightly oblique. *Sterile pinnules* in 1–6 pairs; apical one elliptic, lanceolate, (parallel-sided), 23–34.4 by 2.2–7.7 cm, apex acuminate, attenuate (cuspidate), entire, slightly serrate, base acute (lobate) equilateral to strongly oblique; lateral ones elliptic (lanceolate, parallel-sided), 17.3–27.7 by 2.4–6.9 cm; apex acuminate, attenuate (cuspidate, cuneate), entire or with few small teeth (sometimes serration-like) on the cartilaginous border; base obtuse, acute, entire to oblique; petiolulate, sessile (winged).

Distribution — *Salpichlaena volubilis* subsp. *thalassica* occurs in Central America and on the western side of the Andes in northeastern South America; Colombia, Costa Rica, Ecuador, Nicaragua, Panama.

Habitat & Ecology — Near stream valleys. On hills, mid-slope and flat terrain. Altitude 25–2400 m.

Additional specimens seen. COLOMBIA, Chocó, area of Baudó, on left bank of Rio Baudó, about 1.5 km upstream of stuary, 11 Feb.–28 Mar. 1967, *Fuchs HP & Zanella L 21894* (AAU, K, USM); Magdalena, Sierra Nevada de Santa Marta, Cerro Ratón, serranía de San Javier, N10°53' W74°01', 1900 m, 5 Aug. 1972, *Forero E & Kirkbride Jr H 672* (MO, US); Nariño, Ricárte, 1300 m, 18 May 1941, *Von Sneidern K A.603* (AAU, MO); Valle, Cordillera Occidental, vertiente occidental: hoyá del río Anchicayá, quebrada del Danubio, 300–350 m, 20 Dec. 1942, *Cuatrecasas J 13726* (US). – COSTA RICA, Heredia, Braulio Carrillo National Park, N10°20' W84°10', 1215 m, 13 Nov. 1986, *Hennipman E et al. 6893* (Z); San José, Tapantí, a lo largo del sendero Quebrada Segunta, 9 Apr. 1986, *Berrocál J & Sánchez J 122* (CR); Mts 5 miles S of Cartago, 1800 m, 12 May 1906, *Maxon WR 512* (US). – ECUADOR, Carchi, Maldonado, 1500 m, 8 Oct. 1981, *Werling L & Leth-Nissen S 428A, 428B* (AAU); Esmeraldas, Playa Grande, ± 2 km SE San Francisco de Cayapas, along Rio Cayapas, 16 Aug. 1967, *Sparre B 18058* (P); Pichincha, Reserva Forestal ENDESA, Río Silanche, 'Corporación Forestal Juan Manuel Durini', km 113 de la carretera Quito-Pto. Quito, faldas occidentales, N0°05' W79°02', 650–700 m, 17 Aug. 1984, *Jaramillo J 7016* (AAU). – NICARAGUA, Zelaya, cerro La Pimiena N13°44'40" W84°59'55", 1000–1200 m, 14 Apr. 1979, *Grijalva A 346* (CR); Cerro el Hormiguero, W range, N13°44' W85°00', 1100–1183 m, *Pipoly J 5182* (MO). – PANAMA, Colón, Santa Rita, STRI tree plot 32, N9°21' W79°44', 400 m, 20 Oct. 2005, *Tuomisto H et al. 15141* (PMA, TUR); Sierra Llorona, N9°21' W79°44', 285 m, 5 Mar. 2008, *Jones M & Mitre D 881* (TUR); Panama, Cerro Campana National Park, N8°41' W79°56', 850–900 m, 25 Oct. 2005, *Tuomisto H & Aguilar 15159* (PMA, TUR); Las Pavas, N9°08' W79°54', 87 m, 19 May 2008, *Jones M 1110* (TUR); PN Soberanía, N9°10' W79°45', 215 m, 23 Jan. 2008, *Jones M et al. 650* (TUR); PN Soberanía, N9°10' W79°45', 90 m, 15 Feb. 2008, *Jones M et al. 804* (TUR).

Notes — *Salpichlaena volubilis* subsp. *thalassica* shares with subsp. *amazonica* the chartaceous-coriaceous texture, cartilaginous margin, and the entire pinnule apices, which sometimes can have a few small teeth. However, the appearance of the

abaxial lamina sets subsp. *thalassica* apart from subsp. *amazonica*. In subsp. *thalassica*, the stomata are usually located on the top of small whitish laminal protuberances, which can be so conspicuous that they are visible to the naked eye as small white spots on the abaxial side of the lamina. In contrast, the epidermal surface of subsp. *amazonica* generally lacks the white protuberances altogether, but sometimes they may irregularly occur close to the lamina borders. Subsp. *thalassica* differs from subsp. *volubilis* and subsp. *crenata* by the presence of cartilaginous pinna margin and thicker lamina texture.

The paratype *Hampshire & Whitefoord 370* (BM) does not belong to *S. volubilis* subsp. *thalassica* but instead represents *S. papyrus*.

NAMES EXCLUDED FROM *SALPICHLAENA*

The following names do not belong to *Salpichlaena* (Perrie et al. 2014, De Gasper et al. 2016, Hassler 2018).

Salpichlaena adnata (Reinw. ex de Vriese) Trevis. (1868–1869) 576 = *Blechnopsis orientalis* (L.) C.Presl (1851) 117.

Salpichlaena brasiliensis (Desv.) Trevis. (1868–1869) 574 = *Neoblechnum brasiliense* (Desv.) Gasper & V.A.O.Dittrich (in De Gasper et al. 2016) 214.

Salpichlaena cartilaginea (Sw.) Trevis. (1868–1869) 575 = *Oceaniopteris cartilaginea* (Sw.) Gasper & Salino (in De Gasper et al. 2016) 214.

Salpichlaena cumingiana (C.Presl) Fée (1850–1852) 79 = *Blechnopsis orientalis* (L.) C.Presl (1851) 117.

Salpichlaena denticulata (Sw.) Trevis. (1868–1869) 575 = *Telmatoblechnum indicum* (Burm.) Perrie, D.J.Ohlsen & Brownsey (in Perrie et al. 2014) 755.

Salpichlaena elongata (C.Presl) Trevis. (1868–1869) 575 = *Blechnopsis orientalis* (L.) C.Presl (1851) 117.

Salpichlaena finlaysoniana (Wall. ex Hook. & Grev.) Fée (1850–1852) 79 = *Blechnopsis finlaysoniana* (Wall. ex Hook. & Grev.) C.Presl (1851) 116.

Salpichlaena imbricata (Blume) Trevis. (1868–1869) 575 = *Blechnopsis orientalis* (L.) C.Presl (1851) 117.

Salpichlaena latifolia (C.Presl) Trevis. (1868–1869) 575 = *Blechnopsis finlaysoniana* (Wall. ex Hook. & Grev.) C.Presl (1851) 116.

Salpichlaena longifolia (Cav.) Trevis. (1868–1869) 575 = *Blechnopsis orientalis* (L.) C.Presl (1851) 117.

Salpichlaena malaccensis (C.Presl) Trevis. (1868–1869) 576 = *Telmatoblechnum indicum* (Burm.) Perrie, D.J.Ohlsen & Brownsey (in Perrie et al. 2014) 755.

Salpichlaena nitida (C.Presl) Trevis. (1868–1869) 574 = *Blechnopsis orientalis* (L.) C.Presl (1851) 117.

Salpichlaena orientalis (L.) Fée (1850–1852) 79 = *Blechnopsis orientalis* (L.) C.Presl (1851) 117.

Salpichlaena patersonii (R.Br.) Fée (1850–1852) 79 = *Austroblechnum patersonii* (R.Br.) Gasper & V.A.O.Dittrich subsp. *patersonii* (in De Gasper et al. 2016) 203.

Salpichlaena pectinata (C.Presl) Trevis. (1868–1869) 575 = *Blechnopsis orientalis* (L.) C.Presl (1851) 117.

Salpichlaena pyrophylla (Blume) Trevis. (1868–1869) 575 = *Blechnopsis orientalis* (L.) C.Presl (1851) 117.

Salpichlaena serrulata (Rich.) Trevis. (1868–1869) 576 = *Telmatoblechnum serrulatum* (Rich.) Perrie, D.J.Ohlsen & Brownsey (in Perrie et al. 2014) 755.

Salpichlaena stenophylla (C.Presl) Trevis. (1868–1869) 575 = *Blechnopsis orientalis* (L.) C.Presl (1851) 117.

Salpichlaena striata (C.Presl) Trevis. (1868–1869) 576 = *Telmatoblechnum indicum* (Burm.) Perrie, D.J.Ohlsen & Brownsey (in Perrie et al. 2014) 755.

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IDENTIFICATION LIST OF *SALPICHLAENA* SPECIMENS

Herbarium barcodes, named 'code(s)', are used when collector and collection number are not available.

Salpichlaena

hook = *S. hookeriana*
hybr = *S. hybrida*
papy = *S. papyrus*

amaz = *S. volubilis* subsp. *amazonica*
cren = *S. volubilis* subsp. *crenata*
thal = *S. volubilis* subsp. *thalassica*
volu = *S. volubilis* subsp. *volubilis*

- Abedrabbo S & Calderón M 6 (AAU): thal – Almeida TE 2704 (BHCB): papy; 4024 (BHCB): papy – Almeida TE et al. 3229 (BHCB, UEC): volu – Al-lard HA 21386 (US): amaz – Allen PH 1899 (US): papy – Allorge P code P01419536 (P): cren; code P00347447 (P): cren – Anderson WR 11824 (US): hook – André R-F 3400 (K): papy – Anon. 246 code K000902257 (K): volu; 3072 code K000902264 (K): volu; P00398445 (P): cren; code P01419527 (P): cren; code P01419528 (P): cren; code P01619505 (P): cren; code P01622130 (P): cren; code 0095754 (US): volu; 64a code 1176938 (US): volu – Antar GM & Caetano VB 1131 (SPF): volu – Appun CF 995 (K): hook – Araujo L & Coelho D 363 (INPA): hook – Araújo B et al. 455 (F, US): papy – Archer WA 1922 (US): papy; 1928 (US): papy – Arevalo E (K): hook – Argent et al. 6427 (K, NY, P): papy – Arruda AJ & Gonçalves A 381 (BHCB): volu – Assunção PACL 385 (INPA, K, NY, SP): hook – Athayde FPF 216 (INPA): volu.
- Bailey LH & Bailey EZ T16 (US): cren; 968 (US) volu – Baldeón S et al. 2989 (USM): papy – Barfod A et al. 48060 (AAU): papy; 48177 (AAU): thal; 48598 (AAU): thal; 48756 (AAU): papy – Barreto KD et al. 2808 (BHCB): volu – Barrier S 2356 (NY, P, US): cren; 2885 (NY, P): cren; 3274 (P): cren – Bartlett HH & Lasser T 16930 (US): thal – Batista ER et al. 101 (UEC): volu – Baudouin A 343 (P): cren – Beck HT et al. 1605 (NY): cren – Beck St G et al. 16372 (F): papy – Belem RP 3589 (AAU, NY): volu – Betancur J et al. 18084 (NY): papy – Berrocal J & Sánchez J 122 (CR): thal; 123 (CR): thal – Billiet F et al. 6445 (CAY): cren – Bianchini RS & Prudente CM 1627 (NY): volu – Bittencourt F & Schmitt MR 52 (FURB): volu – Blanchet J 2487 (K, NY): volu – Boom BM 1330 (US): papy – Borchsenius F 120 (AAU): thal – Boudrie M 3641 (CAY): cren; 4034 (CAY, P): cren – Box HE 419 (US): cren; 446 (US): cren – Brade s.n. code 00814261 (NY): volu – Brandbyge J & Asanza CE 30172 (AAU): papy; Brandbyge et al. 33742 (AAU, P): papy; 36017B (AAU): amaz; 36107 (AAU): amaz – Brant AE & Martinez GE 1386 (K, MO): thal – Breier TB & Budke JC 609 (UEC): volu – Brown CA CR-200 (US): papy – Buchtien O 91 (US): amaz; 1049 (US): amaz – Bunting GS & Licht L 886 (US): papy – Burchell WJ 2602 (K): volu – Burger WC & Liesner RL 6807 (MO): thal – Bussmann RW et al. 17145 (MO, NY): papy – BW 323 (P, US): cren.
- Cadorin TJ et al. 67 (FURB): volu; 95 (FURB): volu; 119 (FURB): volu; 2242 (FURB): volu; 440 (FURB): volu; 458 (FURB): volu; 1064 (FURB): volu; 1858 (FURB): volu; 1825 (FURB): volu; 2302 (FURB): volu; 2457 (FURB): volu; 2971 (FURB): volu – Callejas R et al. 8571 (AAU): papy – Campos J & Cano O 4700 (USM): papy – Cárdenas D et al. 42016 (NY): papy – Cárdenas GG & Salovaara K 1290 (AMAZ, TUR, USM): amaz – Cárdenas GG et al. 535 (TUR): amaz; 772 (TUR): amaz; 1373 (AMAZ, TUR, USM): hook; 1751 (TUR): hook; 1753 (TUR): hook; 1754 (AMAZ, TUR): hook; 1755 (AMAZ, TUR): hook; 1948 (TUR): hook – Cárdenas M 1287 (US): amaz – Carneiro IA 73 (BHCB): papy – Carpenter JB & Carpenter MB 621a (US): papy – Carvajal A 77 (AAU): papy – Ceolin L s.n. (FURB): volu – Cerón CE 2684 (AAU): papy; 3324 (AAU): amaz; Cerón C 6102 (AAU): papy – Chagas J 122 (INPA, US): hook – Christenhusz MJM & Bollendorff S 2553 (TUR): cren; 2561 (TUR): cren; 2581 (TUR): hybr; 2627 (TUR): cren; 2639 (TUR): cren; 2729 (TUR): cren – Christenhusz MJM & Katzer 3949 (P, TUR): cren; 3988 (NY, P, TUR): cren; 3999 (P, TUR): cren; 4120 (P, TUR): cren; 4139 (P, TUR): cren – Christenhusz MJM & Paajanen MT 2734 (TUR): cren; 2756 (TUR): cren; 2800 (TUR): cren; 2821 (TUR): cren – Christenhusz MJM et al. 2065 (TUR, USM): hook; 2457 (TUR): cren; 2460 (TUR): hybr; 2486 (TUR): cren; 4743 (TUR): volu; 4774 (TUR): volu; 4800 (NY, TUR): volu; 4831 (TUR): volu; 4950 (NY, TUR): volu; 4955 (TUR): volu – Clark HL 7209 (INPA): hook – Clarke HD et al. 5530 (CAY, US): cren; 9566 (US): hook; 10128 (US): cren; 11472 (US): cren; 12005 (US): papy – Clarke D et al. 7429 (CAY, US): hook; 7543 (CAY, US): cren – Coelho L 1011 (INPA, US): hook – Conant DS et al. 881 (INPA, K, NY): hook; 930 (INPA, K, NY, US, Z): hook – Cook OF & Doyle CB 119 (US): papy; 180 (US): papy; 489 (US): papy – Cooper JJ code 154308 (US): papy – Coquille 92 code P00347470 (P): volu – Correa MD & Montenegro A 10415 (US): thal – Costa MAS et al. 797 (INPA, NY, SP): hook – Cowan RS & Simmonds NW 1202 (P, US): cren – Cremers G 6502 (CAY, Z): papy; 7819 (CAY, P, Z): cren; 10027 (CAY, US, Z): cren – Cremers G & De Granville JJ 13622 (CAY, P, US): cren – Croat TB 19543 (AAU): amaz; 20008 (US): hook; 20350 (US, USM): hook; 20788 (USM): amaz; 22759 (US): papy; 36687 (MO): papy – Couret 190 (US): amaz – Cuatrecasas J 7871 (US): papy; 13726 (US): thal; 14426 (US): papy; 16579 (US): thal; 16580 (US): thal; 17446 (US): thal – Cunha MFM 56 (RON): hook – Curran HM 137 (US): thal.
- Da Silva MR 1578 (SPF): volu; 1618 (SPF): volu – Day 384 (NY): cren – De Freitas CAA 639 (BHCB, INPA): papy – De Granville JJ B5130 (CAY): cren – De Granville et al. 11333 (CAY, US): amaz; 12339 (CAY, Z): cren; 12373 (P, US, Z): papy – De la Sota E 5155 (US): papy – Delnatte C 1379 (CAY): cren – Denslow J 2223B (US): thal – Devia AW & Prado F 2337 (US): papy – Dreveck S & Carneiro FE 1874 (FURB): volu; 1889 (FURB): volu – Duarte AP 2413 (K, NY): volu; 6729 (K): volu – Dudley TR 10451 (USM): papy – Duke JA 15681 (US): thal – Durville 1827 code P00347471 (P): volu – Dusén P 8759 (US): volu; 14134 (K, NY, US): volu; 14397 (Z): volu.

- Elgaard J & Rosales C 8079 (AAU): papy – Esposto N 637 (USM): papy – Ewan JA 15777 (US): thal; 16044 (US): papy; 16054 (US): thal; 16681 (US): papy; 16834 (US): thal.
- Fay A & Fay L 2674 (AAU): papy; 3762 (AAU, US): amaz; 4065 (AAU, US): papy – Feldmann J 75 (P): cren; 76 (P): cren; code P01419534 (P): cren; code P00347435 (P): cren; code P00347436 (P): cren; code P01419535 (P): cren – Fendler A 75: cren (US) – Ferreira S et al. 195 (NY): volu – Feuillet C 4583 (US): cren – Fiaschi P et al. 3712 (SPF): volu – Figueiredo JB & De Lima SG 562 (BHCB): volu – Flores M 32 (USM): hook; 136 (AAU, USM): amaz; 264 (AAU): hook; 265 (AAU): hook; 267 (AAU): hook; 414 (AAU): amaz; 705 (INPA): hook; 719 (INPA): hook; 738 (INPA): hook; 751 (INPA): hook; 795 (INPA): hook – Flores M & Lima J 825 (INPA): amaz; Flores M et al. 245 (AAU): amaz – Folli DA 5469 (CVRD): volu – Fonnegra R et al. 1974 (AAU, K): thal – Forero & Kirkbride JrH 672 (MO, US): thal; Forero et al. 5461 (US): papy – Forzza RC et al. 1310 (NY, SPF): volu – Fosberg FR 19551 (US): thal; 21245 (US): papy – Foster R & d'Achille B 10100 (F): amaz; Foster R et al. 7894 (F, USM): amaz – Freitas CA 658 (SP): hook; 678 (SP): hook – Freitas CA et al. 630 (INPA): hook – Fuchs HP & Zanella L 21894 (AAU, K, USM): thal – Fundación Biológica Puerto Rastrojo 4308 (K): hook – Funez LA 962 (FURB): volu.
- Galeano G et al. 2384 (US): thal – Gasper AL 580 (FURB): volu – Gasper AL et al. 2294 (FURB): volu – Gentry A & Emmons L 39651 (F): hook – Gentry A & Juncosa A 41014 (AAU): thal – Gentry A & Mori S 13754 (US): thal – Ginés Hno. 137 (US): papy; 4308 (US): cren; 4467 (US): cren; 4511 (US): cren – Glaziou A 12346 (LE, US): hook; s.n. code 814263 (NY): volu – Glaziou/Schwacke 10026 code P01419539 (P): hook – Goeden E s.n. (Z): volu – Gómez LD et al. 20541 (AAU): papy; 20878 (AAU): papy – Grant ML 10104 (US): papy – Grayum MH & Chazdon R 6833 (CR, MO): thal – Grijalva A 346 (CR): thal – Grubb PJ et al. 1182 (US): papy – Guedes ML et al. 11567 (ALCB): volu.
- Haber WA ex et al. 5383 (US): thal – Hamilton C & Davidse G 2725 (AAU): papy; 2806 (AAU): papy – Hamilton C et al. 4121 (AAU): papy – Hampshire RJ & Whiteford C 370 (AAU, BM): papy – Harley RM & Souza R 10051 (K, NY, US, P): papy – Harling H & Andersson L (AAU): papy – Hassler DE 10093 (K): papy; 11969 (K, Z): papy – Haught O 1299 (US): thal; 5342 (US): papy – Henkel TW & Hoffman B 89 (US): cren – Henkel TW et al. 1918 (US): cren; 4903 (CAY, US): cren; 6004 (US): hook – Hennipman J et al. 6837 (Z): thal; 6856 (Z): papy; 6893 (Z): thal – Hermann FJ 11009 (US): hook – Herrera H & Arosemena L 1781 (AAU): thal – Hiendlmayer R 1626 or s.n. code FURB06889 (FURB): volu – Higgins M & Ruiz F 139 (TUR): amaz; 306 (TUR): amaz; 333 (TUR): amaz; 351 (TUR): amaz; 397 (TUR): amaz; 434 (TUR): amaz; 444 (TUR): hook; 808 (TUR): amaz; 996 (TUR): amaz; 1051 (TUR): amaz; 1179 (TUR): amaz; 1244 (TUR): amaz; 1272 (TUR): amaz; 1315 (TUR): amaz; 1330 (TUR): amaz – Hitchcock AS 17374 (US): hook – Hochne W 2645 (K, SPF): volu – Hodge WH 98 (NY, US): cren – Hoff M 6897 (CAY, Z): cren – Holm-Nielsen L & Jeppesen S 445 (AAU): papy; 669 (AAU): papy; 798 (AAU): amaz – Holm-Nielsen L et al. 4260 (AAU): papy; 20176 (AAU): amaz; 25341 (AAU): papy; 25818 (AAU): thal – Holm RW & Iltis HH 209 (P): papy – Holst BK et al. 8708 (US): papy – Howard RA 11691 (P): cren.
- Idrobo JM 489 (US): papy – Idrobo JM & Schultes RE (US): papy – Irwin HS et al. 8751 (K, NY, P, US): papy; 10803 (NY, US): volu.
- Jameson W 730 (K): papy – Jaramillo J 7016 (AAU): thal – Jaramillo RM et al. 5204 (P): thal – Jardim JG et al. 539 (NY): volu – Jenman GS 1466 (K): hook – Jimenez I 59 (AAU): papy; 81 (AAU): papy – Jiménez MA 2324 (US): papy – Jones M 955 (TUR): thal; 1029 (TUR): thal; 1094 (TUR): thal; 1110 (TUR): thal – Jones M & Mitre D 881 (TUR): thal; 933 (TUR): papy – Jones M & Olivas P 165 (TUR): papy; 500 (TUR): papy – Jones M & Putkonen 610 (TUR): papy – Jones M et al. 13 (TUR): papy; 114 (TUR): papy; 650 (TUR): thal; 666 (TUR): thal; 804 (TUR): thal – Jönsson G 552a (NY, US): volu – Joseph BroA 727 (US): thal.
- Kennedy H et al. 2491 (US): thal – Kessler M 12906 (TUR): cren – Kessler M et al. 13352 (UC): papy – Killip EP 2901 (US): thal; 5105 (US): thal; 7761 (US): papy; 14831 (US): thal; 22323 (US): thal – Killip EP & Cuatrecasas J 38704 (US): papy – Killip EP & García H 33347 (US): papy – Killip EP & Smith AC 23923 (US): papy; 25565 (US): papy; 26954 (US): hook – Klug G 1126 (US): hook; 3197 (K, US): papy; 3614 (K, US): papy – Korte A & Kniess A 414 (FURB): volu; 836 (FURB): volu; 962 (FURB): volu; 1975 (FURB): volu; 2221 (FURB): volu; 2309 (FURB): volu; 2470 (FURB): volu; 2537 (FURB): volu; 2638 (FURB): volu; 2825 (FURB, UFSC): volu; 3048 (FURB): volu; 3183 (FURB): volu; 3434 (FURB): volu; 3889 (FURB): volu; 4038 (FURB): volu; 4345 (FURB): volu; 4527 (FURB): volu; 6167 (FURB): volu – Kozera C & de O Dittrich VA 1198 (UEC): volu – Kozera C & Kozera OP 1387 (UEC): volu – Kramer KU & Hatschbach G 10811 (Z): volu – Kvist LP & Asanza E 40763 (AAU): papy – Kvist LP et al. 48944 (AAU): thal.
- Labiak PH et al. 3889 (HUEFS): volu – Langsdorff code 01042386 (LE) volu – Langsdorff & Riedel 173 (LE) volu – Lasser T 1642 (K, US): papy – Lehmannium 8948 (K, US): papy; K.K.21 (K): thal – Lehtonen S & Geniez C 985 (CAY, TUR): cren; 1073 (CAY, TUR): hybr – Lehtonen S et al. 601 (SP, TUR): volu; 637 (SP, TUR): volu; 810 (CAY, TUR): cren; 813 (CAY, TUR): cren – Lellinger DB 2023 (US): hook – Læggaard S 51671 (AAU): thal; 52003 (AAU): papy – L'Herminier FL code 2427006 (US): cren; code 2427421 (US): cren; code P00347452 (P): cren; code P00347453 (P): cren; code P00347454 (P): cren; code P00347455 (P): cren; code P00347456 (P): cren; s.n./1 (NY): cren – León H et al. 1435 (Z): thal – Leprieur M 345 (P): cren; code P01419523 (P): cren – Lewis WH et al. 1947 (US): thal; 2342 (US): papy – Liesner RL 1106 (P): thal; 17379 (US): hook – Lindeman JC 27 (Z): cren – Lombardi JA 4576 (BHCB): volu – Lopes MS & Pietrobom MRS 550 (HUEFS, INPA): volu.
- Maas PJM & Maas H 443 (INPA): hook – Maguire B & Fanshawe DB 32359 (US): hook – Maguire B & Politi L 28766 (K, US): hook – Maguire B et al. 41477 (US): hook – Marcano CV et al. 967 (P): papy; 1027 (P): papy – Marie Ed s.n. code P00398445 (P): cren – Martius 59 (LE): volu; code 01042391 (LE) volu – Matos FB & Santos RR 1547 (NY): volu – Matos FB et al. 1366 (NY): volu – Maxon WR 512 (US): thal; 4893 (US): thal – Mazziero FFF & Soller A 648 (NY): volu – McDaniel S 11758 (USM): hook – McDaniel S & Rimachi MY 16912 (USM): hook; 26631 (USM): hook – McDowell & Gopaul D 3630 (CAY, US): hook – Mexia Y 6276 (K, US, Z): papy; 7175 (US): papy; 8426 (K, US, USM): papy – Meyer G 245 (Z): hook – Miers J 177 (K): volu; 180 (K): volu – Moran R 3344 (AAU, MO): papy – Moran R & Vásquez 3672 (USM): hook – Moran R et al. 6034 (AAU, TUR): amaz – Moritz 109 (K, P, US): cren – Mostacero J & Castillo R 259 (US): cren – Murillo MT 1582 (AAU, P): hook – Mutchnick P et al. 240 (CAY, US): hook. Navarrete H 1257 (AAU): amaz; 1497 (AAU): amaz; 1509 (AAU): amaz – Nee M 7899 (US): thal; 9756 (AAU, US): papy; 42973 (INPA, K, NY, SP, US): hook – Nee M & Smith D 11112 (AAU): thal; 11117 (AAU): thal – Neil D et al. 6406 (AAU, US): papy – Niño SM 367 (US): cren – Nobrega GA 520 (UEC): volu – Nuñez P et al. 21025 (USM): amaz.
- Øllgaard B & Navarrete H 1308 (AAU): papy; 1309 1/2 (AAU): volu; 1309 2/2 (AAU): papy; 1488 (AAU): papy; 1907 (AAU): papy; 2395 1/3 (AAU): papy; 2395 2/3, 3/3 (AAU): amaz; 105457 (AAU): papy.
- Pace MR et al. 174 (SPF): volu – Palacios W 2672 (Z): thal; 2952 (AAU, Z): papy – Palacios W et al. 9803 (AAU): papy – Pedraza-Peñalosa P et al. 2074 (NY): thal – Perdiz RdeO et al. 952 (SPF): volu – Père Duss 1700 (NY): cren; 1901 (NY): cren; 4160 (US): cren – Perea J et al. 3902 (AAU, US): amaz – Peterson PM 8576 (US): papy – Philcox D et al. 3051 (K, P): papy – Phillipson WR & Idrobo JM 1838 (US): thal – Phillipson WR et al. 2264 (US): papy – Pietrobom da Silva MR 1753 (SPF): volu; 4243 (INPA): volu; 5425 (INPA): volu – Pietrobom da Silva MR & Santiago ACP 4690 (INPA): volu; 4788 (INPA): volu; 4859 (INPA): volu; 4885 (INPA): volu; 5076 (INPA): volu – Pietrobom da Silva MR et al. 5622 (INPA): volu – Pipoly J 5182 (MO): thal – Pipoly J et al. 16670 (AAU): thal; 18466 1/2 (K): papy; 18466 2/2 (K): thal – Pittier H 1173 (US): papy; 1701 (US): thal; 1836 (US, Z): papy; 5624 (US): thal – Pokorny Fr (AAU): cren – Poulsen AD 8326 (TUR): amaz; 78407 (TUR): amaz; 78431 (TUR): amaz; 78524 (TUR): amaz; 79081 (TUR): amaz; 79103 (TUR): amaz; 79210 (TUR): amaz; 79270 (TUR): amaz; 79413 (TUR): amaz; 79488 (TUR): amaz; 79505 (TUR): amaz; 79569 (TUR): amaz; 79620 (TUR): amaz; 79799 (TUR): amaz; 79986: papy; 79989 (TUR): amaz; 80042 (TUR): amaz; 80078a (TUR): papy; 80078b (TUR): amaz; 80106 (AAU): papy; 80143 (AAU): amaz; 80326 (TUR): amaz; 80460 (AAU): papy; 80515 (TUR): amaz; 80545 (TUR): papy; 80662 (TUR): amaz; 80802 (AAU): amaz – Prado J & Costa MAS 575 (INPA, SP): hook – Prado J & Labiak PH 749 (US): volu – Prado J et al. 956 (INPA, NY): volu; 1821 (TUR): hook; 1863 (NY, SP, TUR): hook – Prance GT et al. 9963 (K, US): papy; 13525 (INPA, K, NY, US): papy; 21612 (NY): papy – Proctor G 97 (US): cren; 20130 (US): cren. Quelal C et al. 546 (AAU): papy – Questel A 1968 (P, US): cren – Questel A? 2662 (P): cren.
- Raynal A & Tirel C 18572 (P): hybr – Redden KM et al. 1867 (US): hook; 5812 (US): hook – Reveal JL & Duke JA 4929 (US): thal – Ribeiro JELS et al. 1025 (INPA, US): hook; 1454 (INPA, SP): hook – Riedel L 96 (LE): volu; code 01042383 (LE) volu; code 01042393 (LE): volu; code 01042394 (LE): volu; Riedel? code 01042387 (LE): volu – Rimachi MY 4008 (USM): hook; 8034 (US, USM): hook – Rinnert CH 1208 (FURB): volu – Robles R 2198 (AAU, US): papy – Rodríguez L 4257 (P): cren – Rodríguez W et al. 7001 (NY): amaz; 7337 (NY): papy; 7098 (NY): papy; 7475 (NY): hook; 8212 (NY): amaz – Rojas R & Ortiz G 5312 (USM): papy – Rosa NA & Cardoso O 3227 (INPA): papy – Rosa NA & Pires JM 3988 (INPA, NY): volu – Rosenstock E & Wacket L 192 (K, US): volu – Rothrock A 318 (MO): papy – Rowlee WW & Rowlee HE 57 (NY, US): papy – Rueda R 8780 (US): papy.
- Saiki Y CR-36 (Z): papy; CR-38 (Z): papy; CR-52 (Z): papy – Salinas N et al. 6787 (USM): papy – Salino A 402 (AAU, BHCB, UEC): papy; 934 (BHCB, UEC): volu; 2841 (BHCB): volu; 11013 (BHCB): volu; 1339 (UEC): volu; 1807 (BHCB): volu – Salino A et al. 1502 (BHCB, UEC): volu; 5317 (BHCB): volu; 6198 (BHCB): volu; 8740 (BHCB): volu; 11013 (BHC): volu; 11220 (BHCB): volu; 13024 (BHCB): volu; 13803 (BHCB): volu; 14313 (BHCB):

- volu; 15317 (BHCB): papy; 15868 (BHCB): papy – Sampaio LCQMP & Garcia RJF 246 (SPF): volu – Sandeman C 5868 (K): papy – Sanín D et al. 5168 (NY): papy – Sanjuan P & Pietrobom MR 398 (SP): hook; 543 (SP): hook – Sastre C 3012 (P): hook – Scamman E 6033 (US): papy; 7718 (US): papy – Schmitt JL et al. 106 (FURB): volu; 308 (FURB, UFSC): volu; 435 (FURB): volu; 1192 (FURB): volu – Schneider H 454 (Z): papy – Schnell R 8483 (P): volu; 8643 (P): volu – Schomburgk 1140 (K): papy – Schultes RE & Cabrera I 15410 (US): hook; 15992 (US): hook; 17449 (US): hook – Schunke C 40 (US): papy; A185 (US): papy – Schunke J 5541 (US): amaz; 7019 (US, USM): amaz; 14105 (K, Z): amaz – Schwacke CAW 574 (P, US): hook; 4110 (P): hook; code P01419538 (P): hook – Scolnik R et al. 19An437 (US): papy – Sehnem A 3080 (US): volu – Seifriz W 71 (US): thal – Sellow code K000902260 (K): volu; code 01042385 (LE) volu; code 691586 (US): volu – Silva JM & Campos AR 4315 (HUEFS): volu – Sirén A et al. 12 (QCA, TUR): papy; 58 (QCA, TUR): papy; 64 (QCA, TUR): papy; 79 (QCA): papy; 117 (QCA): papy; 225 (QCA): papy; 657 (QCA, TUR): amaz; 1850 (QCA, TUR): amaz; 2023 (QCA, TUR): amaz; 2268 (QCA): amaz – Skutch AF 2166 (US): papy – Smith A 48/251 (US): papy – Smith DN 4141 (USM): papy; 5118 (USM): papy – Smith JD 6872 (US): papy; 6873 (US): papy – Sothers CA & da Silva CA 1009 (INPA, SP): hook – Soukup J 5019 (US): papy – Sparre B 13121 (AAU): amaz; 18058 (P): thal – Spruce R 189 (US): hook; 1263 (K, NY, P): hook; 2800 (K, P): hook; code 02617976 (NY): hook; code P00347472 (P): hook; code P00347473 (P): hook; code P00347474 (P): hook; code P00347475 (P): hook; code P00347476 (P): hook; code P00347477 (P): hook – Standley PC 27540 (US): thal; 27546 (US): thal; 33861 (US): papy; 36912 (US): papy; 37256a (US): papy; & Torres RR 50985 (US): papy – Stehlé H 640 (P, US): cren; 1215 (P, US): cren – Steinbach J 9411 (K, Z): papy – Stergios B 10526 (AAU): hook – Stevens WD & Krukoff BA 4959 (AAU): papy – Stevenson DW et al. 792 (INPA, NY): hook; 815 (INPA, NY): hook – Steyermark JA 52667 (US): papy; 54204 (US): papy – Stival-Santos A et al. 1123 (FLOR, FURB): volu; 1227 (FURB): volu; 2121 (FURB): volu; 2848 (FURB): volu – Stork HE 502 (US): papy; 1327 (US): papy; 2649 (US): papy; 3064 (US): papy – Suominen L et al. 6 (TUR): papy; 7 (TUR): papy; 10 (TUR): papy; 23 (TUR): papy; 39 (TUR): papy; 41 (TUR): papy; 69 (TUR): papy; 91 (TUR): amaz; 152 (TUR): amaz; 176 (TUR): amaz; 219 (TUR): amaz; 233 (TUR): amaz; 285 (TUR): amaz; 286 (TUR): papy; 382 (TUR): papy; 406 (TUR): amaz; 408 (TUR): papy.
- Teixeira LOA 208 (INPA, NY): hook – Testo W 215 (AAU): papy – Thomas WW et al. 10717 (NY): volu – Tonduz A 9468 (US, Z): papy; 12774 (US): papy – Torres RR 60 (US): papy – Tosta A 56 (INPA): volu – Tostain O et al. 1664 (P): hybr – Tryon RM & Tryon AF 5178 (US, USM): hook – Tuomisto H & Aguilar 15159 (PMA, TUR): thal; 15160 (TUR): papy; 15162 (TUR): thal – Tuomisto H & Oré I 8827 (TUR, USM): amaz – Tuomisto H & Ruokolainen K 11410 (TUR): amaz; 11675 (TUR): papy – Tuomisto H et al. 2432 (TUR): hook; 2668 (TUR): amaz; 3097 (AAU, TUR): amaz; 4119 (TUR): amaz; 4133 (TUR): amaz; 4140 (TUR): amaz; 4197 (TUR): amaz; 4198 (TUR): amaz; 4199 (TUR): amaz; 4402 (TUR): amaz; 4771 (AAU, TUR): hook; 4773 (TUR): hook; 5252 (TUR): amaz; 5257 (TUR, USM): amaz; 5759 (TUR): amaz; 5761 (AAU, TUR): amaz; 6493 (TUR, USM): amaz; 6494 (TUR, USM): amaz; 6618 (AAU, TUR): amaz; 7165 (TUR): amaz; 7183 (TUR): amaz; 7701 (TUR): amaz; 7717 (TUR): amaz; 7880 (AAU, TUR): hook; 8077 (TUR, USM): amaz; 8098 (TUR, USM): amaz; 8172 (TUR, USM): amaz; 8730 (TUR, USM): amaz; 9311 (TUR, USM): amaz; 9384 (TUR, USM): amaz; 9652 (TUR): amaz; 10003 (TUR): amaz; 10083 (TUR): hook; 10542 (TUR): amaz; 10985 (TUR, USM): amaz; 10149 (AMAZ, TUR): hook; 11252 (AAU, AMAZ, TUR, UC, USM): hook; 12029 (TUR): hook; 12034 (TUR): amaz; 12082 (TUR): hook; 12270 (TUR): amaz; 12322 (AAU, NY, TUR): hook; 12379 (TUR): hook; 12677 (AMAZ, TUR, USM): hook; 12785 (AMAZ, TUR, USM): hook; 13007 (TUR): amaz; 13588 (TUR): papy; 13601 (TUR): amaz; 13907 (AAU, TUR): amaz; 14108 (TUR): amaz; 14123 (AMAZ, TUR, UC, USM): hook; 14142 (TUR): amaz; 14417 (TUR): amaz; 14441 (TUR): papy; 14450 (AMAZ, TUR): hook; 14499 (TUR): amaz; 14562 (TUR): amaz; 14771 (TUR): hook; 14956 (AMAZ, TUR): hook; 15141 (PMA, TUR): thal; 15144 (TUR): thal; 15145 (TUR): papy; 15291 (TUR): hook; 15436 (AAU, INPA, SP, TUR): hook; 15651 (TUR): cren; 15787 (TUR): hybr; 16010 (SP, TUR): amaz; 16070 (TUR): hook; 16118 (SP, TUR): amaz; 16550 (SP, TUR): amaz; 16902 (SP, TUR): hook; 16904 (TUR): amaz – Tyson EL & Nee M 7338 (AAU): thal.
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- Webster GL et al. 9285 (US): cren – Wercklé C code 575347 (US): papy; code 575348 (US): papy – Werling L & Leth-Nissen S 428A (AAU): thal; 428B (AAU): thal – Whitefoord C & Eddy A 357 (US): thal; 3965 (US): cren – Williams LI 14824 (US): hook – Williams RS 511 (US): thal; 1147 (US): papy; 1295 (US): amaz – Windisch PG 1391 (AAU): papy; 2210 (AAU): papy – Windisch PG et al. 4875 (AAU): volu; 4881 (AAU): volu; 7709 (INPA): papy – Wurdack JJ 1893 (US, USM): amaz.
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