Newly discovered diversity in the tropical fern genus *Metaxya* based on morphology and molecular phylogenetic analyses

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Summary. For a long time, the genus *Metaxya* was treated as monotypic with a single species, *Metaxya rostrata*. A second species, *M. lanosa*, was described in 2001 on the basis of morphological features and *rbcL* gene sequences with a suggestion that the genus may contain even more species. We have now systematically compared morphological traits in a large number of *Metaxya* specimens collected in tropical America. We have also carried out phylogenetic analyses of 32 *Metaxya* and 5 outgroup specimens based on four markers of the plastid genome (*rbcL, matK, and rps4* genes, and *trnG-trnR* intergenic spacer). Based on the morphological variation among the *Metaxya* specimens, we accept six distinct species, three of which we describe as new in this paper. Molecular phylogenetic analyses resolved five distinct clades. Four of these corresponded with the morphologically delineated species (*M. contamanensis* sp. nov., *M. elongata* sp. nov., *M. lanosa*, and *M. parkeri*). The fifth clade contained all the individuals of the remaining two species, of which *Metaxya rostrata* was rendered paraphyletic by *M. scalaris* sp. nov. being nested within it. Since *M. scalaris* was resolved as monophyletic, and the two are clearly distinguishable morphologically, we consider them true species despite the incomplete genetic differentiation.

Key Words: Metaxyaceae, Neotropics, new species, systematics, taxonomic revision.

Introduction

Metaxya is widely distributed in tropical America, from southern Mexico and some Caribbean islands in the north to the Guianas and coastal Brazil in the east and to Bolivia in the south (Tryon & Tryon 1982). Although individuals of *Metaxya* have a creeping rhizome (Lucansky 1974, 1982) rather than an erect trunk, it had already been associated with tree ferns for a long time (Tryon 1970; Lucansky 1982; Kramer & Green 1990) before molecular data confirmed the relationship (Hasebe 1994).

The phylogenetic position of *Metaxya* inside the tree fern clade has varied among studies according to the analytical method used. Parsimony analyses have resolved *Metaxya* as the sister of the remaining tree ferns, while maximum likelihood (ML) and Bayesian analyses have positioned it as the sister of Dicksoniaceae (Korall *et al*. 2006a; Lehtonen 2011). This variation in results has been attributed to the difficulties in establishing the relationships among very long branches, such as that leading to *Metaxya* (long-branch attraction; Korall *et al*. 2006a, see also Bergsten 2005).

The first legitimate name for what is now considered *Metaxya rostrata* (Kunth) C.Presl was *Aspidium rostratum* Kunth (1815), which was transferred to the genus *Metaxya* by Presl (1836). Hooker & Greville (1831) described a related species, which they named *Polypodium parkeri*. This species had already been recognised but not formally described by Charles S. Parker, who thought that it belonged to the genus *Trichopteris* (Hooker & Greville 1831).

For a while, two species were accepted within *Metaxya* (*M. rostrata* and *M. parkeri*; Smith 1842). However, little more than a decade after its description, opinions on the status of *M. parkeri* changed and it began to be considered conspecific with *M.*

rostrata (Hooker 1846; Smith 1866; Hooker & Baker 1874). Hooker (1846) considered *Polypodium rostratum* (=*Metaxya rostrata*) and *Polypodium parkeri* (=*Metaxya parkeri*) as synonyms, but inofficially recognised a new variety, *polycarpa*. This variety has not been described or recognised by other workers, so *Metaxya* was treated as monotypic for more than a century (e.g. Bower 1926; Morton 1959; Roy & Holttum 1965; Tryon 1970; Lucansky 1974; Tryon & Tryon 1982; Kramer & Green 1990; Qiu *et al.* 1995). The situation changed in 2001, when *M. lanosa* A.R.Sm. & Tuomisto was described (Smith *et al*. 2001). Although Smith *et al.* (2001) only described one new species, they observed that the morphological and genetical variation that remained within *M. rostrata* was substantial and suggested that the genus may contain even more species.

We have now compiled a dataset that is much larger than the one that was available to Smith *et al*. (2001). We use these data to test the proposition that the genus contains more than two species, to study the phylogenic relationships within *Metaxya*, and to assess the distribution of the Amazonian species along edaphic gradients.

Materials and methods

Morphological studies

We made observations on morphological variation in *Metaxya* on the basis of 61 herbarium specimens deposited at TUR (all herbarium acronyms according to Thiers, continuosly updated), which contained a total of 67 fertile leaves. Measurements of the external parts of the specimens (leaves, pinnae, petioles, petiolules, hairs), were taken with a ruler and a caliper and using a stereoscope when necessary. We also observed the number of lateral pinnae, lamina texture, pinna margins, pinna shape, presence of hairs in different parts of the plant, and the distribution of sori.

Additionally, we studied specimens deposited at K, SP and US, as well as more than 600 digital images of specimens deposited at AAU, B, CAY, COL, GH, HUEFS, INPA, K, MO, NY, P, UC and Z. These were used to verify the ranges of and variation in the observed characters when possible. The terminology used to describe the morphological features of the plants follows Lellinger (2002).

Molecular studies

Laboratory procedures

For many of the specimens deposited at TUR, material for molecular analyses had been dried separately using silica gel in order to ensure DNA quality (Chase & Hills 1991). For other specimens, material for DNA extraction was provided by colleagues (Table 1).

Total genomic DNA was extracted from 32 *Metaxya* and five outgroup specimens (Table 1) with E.Z.N.A. SP Plant DNA Kit (Omega Bio-tek, Doraville, Georgia) following the protocol for dry samples. Polymerase chain reaction (PCR) amplifications were performed using the PuReTaq Ready-To-Go (PCR) Beads (Amersham Bio-sciences, Piscataway, New Jersey). Four plastid markers, *matK*, *rbcL*, and *rps4* genes and *trnG-trnR* intergenic spacer were amplified using PCR. In every PCR tube, we added 25 μl of ddH_2O, 1 μl of each primer, and 5 μl of the template resulting approximately in 32 μl of solution. The PCR programs and primers used are detailed in Table 2. PCR results were purified and sequenced by Macrogen Inc. (Seoul, South Korea / Amsterdam, the Netherlands). Voucher information and GenBank accession codes are listed in Table 1 and final data matrices and the resulting trees are available in TreeBASE (study number TB2:S17345).

Phylogenetic analyses

The sequence reads were verified by comparing forward and reverse sequence chromatograms, edited when necessary and compiled with PhyDE version 1.0 (Müller *et al.* 2010). At first, we tested data congruence by running independent analyses for each of the plastid markers using RAxML version 7.0.3 (Stamatakis 2006). Since these trees did not show conflicting clades with high bootstrap support, we concatenated all the sequence data for further analyses using SequenceMatrix (Meier *et al.* 2006).

Phylogenetic trees were inferred for the combined dataset with parsimony, ML and Bayesian methods. For the ML and Bayesian analyses we produced multiple sequence alignments with the default parameters in MAFFT version 7.149 (Katoh & Standley 2013). For ML analysis we used the parallel Pthreads-version of RAxML 7.0.3 (Stamatakis 2006; Ott *et al.* 2007). The default GTR+G model was used to run 1,000 runs. Bootstrap support values were obtained by running 1,000 bootstrap replicates in RAxML and summarizing the results with DendroPy (Sukumaran & Holder 2010). Bayesian inference was performed using MrBayes version 3.2.3 (Ronquist *et al.* 2012) in a supercomputer cluster at Finnish IT Center for Science. The evolutionary model was set to GTR+G and a default flat Dirichlet prior distribution. Four chains of 5,000,000 generations were run and every 1000th generation was sampled. The first 25% of trees were discarded as burn-in and a 50% majority-rule consensus tree was calculated from the remaining trees.

In addition, we evaluated the sensitivity of our results for alternative sequence alignments under the parsimony optimality criterion by performing a sensitivity analysis (Wheeler 1995). For this we used direct optimization (Wheeler 1996) as implemented in the computer program POY 5.1.1 (Wheeler *et al*. 2015). Six different parameter combinations with varying indel opening (0 or 3), transversion (1 or 2) and transition (1 or 2) costs were applied, while keeping the indel extension cost always at 1. Optimal topologies were searched under each parameter combination by subjecting 200 random addition starting trees to heuristic search alternating subtree pruning and regrafting (SPR) and tree bisection and reconnection (TBR) swapping algorithms. In addition to the most optimal trees, also suboptimal trees within 5% of the lowest cost were evaluated during the swapping. Results from these analyses were pooled together as sensitivity plots with the program Cladescan (Sanders 2010).

Observations on geographical distribution and ecology

Information on the distribution of *Metaxya* along edaphic gradients was obtained from data collected for more general studies on fern ecology in Amazonia. All study sites were in non-inundated old-growth forests. A large part of the field work was carried out in the 1990's, when *Metaxya* was thought to be both monotypic and easy to identify in the field. The splitting of *M. rostrata* makes those field identifications incomplete, so here we use only data corresponding to either individuals that we have seen as voucher specimens, or data collected so recently that we consider their species identifications accurate. Details about the field procedures and selection of the study sites in Colombia, Ecuador, Peru and northern Brazil can be found in Tuomisto *et al.* (2003a,b, 2014) and Higgins *et al.* (2011). More recent unpublished data collected using the same procedures are also available from western Brazil and French Guiana. To characterise edaphic gradients, a few (usually three) soil samples were collected at each site. Each soil sample consisted of five subsamples of surface soil (top 5 cm of the mineral soil) collected within an area of 5 m by 5 m and mixed. In most cases, sampling of both soils and ferns was done within 500-m-long line transects (Tuomisto

2003a, 2014; Higgins 2011). Some data came from transects that were originally more than 20 km long (Tuomisto *et al*. 2003b and unpublished data), and in these cases the data from soil samples collected within 500 m of a given *Metaxya* observation were used. The soil samples were dried at room temperature and stored in plastic bags until they were analyzed at MTT Agrifood Research Finland (Jokioinen, Finland). Here we focus on the concentration of exchangeable bases (Ca, Mg, K and Na) and aluminium as extracted in 1 M ammonium acetate at pH 7. For more details on soil sampling and analysis procedures, see Tuomisto *et al*. (2003a).

Information on geographical distributions of each *Metaxya* species was extracted both from the ecological datasets and from the labels of the available herbarium specimens.

Results

Morphology

On the basis of morphological features (Table 3) we classified the studied *Metaxya* specimens into six groups, which are here treated as true species. We recognise all three *Metaxya* species that have been described previously (*M. lanosa, M. parkeri* and *M. rostrata*), as well as three new species to be formally described below (*M. contamanensis* sp. nov., *M. elongata* sp. nov., *M. scalaris* sp. nov.).

Morphologically, the most clearly distinct species is *Metaxya lanosa*, which is characterised by coriaceous lamina texture, clearly cartilaginous pinna margins and a dense (but easily abraded) cover of reddish brown to orange-brown woolly hairs on the petioles and rachises. The next thickest lamina texture is that of *M. contamanensis* and then that of *M. scalaris*. In comparison, the lamina texture of *M. elongata* is thin and herbaceous, with the remaining species being intermediate.

In comparison with the other species, *M. lanosa* and *M. rostrata* have relatively few pinnae (2 – 7 to a side when fertile). The other species generally have more than 7 pinnae on each side of the rachis (up to 16), although *M. parkeri* can occasionally have as few as 4. In absolute terms, *M. lanosa* and *M. rostrata* tend to have the broadest pinnae (4.0 – 6.5 cm) and *M. contamanensis* and *M. elongata* the narrowest (2.5 – 3.5 cm). In terms of pinna shape, the broadest pinnae are those of *M. lanosa*, (about 5 times as long as wide) and the narrowest those of *M. elongata* (about 9 – 10 times as long as wide). In the other species, pinnae length-width ratio is intermediate. Pinna apices are cuspidate to caudate in *M. rostrata* and *M. lanosa*. Both species can have entire pinna apices, but in general the apices are irregularly and coarsely dentate in *M. rostrata*, and with a few sharp but shallow serrations in *M. lanosa*. Pinna apices of *M. scalaris* and *M. parkeri* are mostly caudate to attenuate. These species differ in that the apex margins are dentate with step-like teeth to coarsely dentate-serrate in *M. scalaris*, but serrate (rarely slightly dentate) in *M. parkeri*. Pinna apices of *M. contamanensis* are caudate to attenuate and often asymmetric, with almost entire to irregularly and shallowly serrate margins. Finally, pinna apices in *M. elongata* are long-attenuate to caudate and symmetric, with finely and regularly serrate margins (Fig. 1).

The arrangement of sori is a useful diagnostic character for fertile specimens (Fig. 2). In most species, two or three sori are borne on the same vein, but in *M. scalaris* there is usually only one and in *M. rostrata* there are three or four. *Metaxya scalaris* is further characterised by having most sori arranged in a single dense line touching the midvein, and a second but more incomplete line of sori a few millimeters further towards the pinna margin (sometimes there are additional scattered sori in the basal part of the pinna). *Metaxya rostrata* can also have a line of sori touching the midvein, but most of its sori are scattered widely over the abaxial surface of the pinna. *Metaxya parkeri* and *M. contamanensis* may have some sori touching the midvein, but these do not form such a clear and dense line as in *M. scalaris*. In *M. lanosa* and *M. elongata*, there is always a sterile space of some mm between the midvein and the nearest sori. *Metaxya parkeri* is the only species with wide variation in soral arrangement. In most of the specimens that we have sequenced, the sori are scattered over the entire surface of the lamina except near the midvein, but in two specimens, the sori are concentrated to one line a short distance from the midvein. Additionally, we have also seen specimens that have many sori touching the midvein. This suggests that *M. parkeri* as circumscribed here may be a species complex. However, we have not found other morphological characters to obviously correlate with the soral arrangement types, and therefore leave the question open until genetic data become available to sort it out.

Molecular phylogenetics

Trees from ML, Bayesian and parsimony analyses were consistent with each other in grouping the sampled individuals into five clades (Fig. 3). One of the clades contained all specimens identified as *M. contamanensis* and its sister clade contained all specimens of *M. elongata*. The single sequenced specimen of *M. lanosa* formed the third clade. The fourth clade consisted of all specimens of *M. parkeri*. The fifth clade consisted of a monophyletic *M. scalaris* that was embedded within a paraphyletic *M. rostrata*.

Metaxya contamanensis and *M. elongata* were resolved as highly supported sisters in all analyses (Fig. 3). *Metaxya lanosa* was resolved as sister of either *M. parkeri* (ML with bootstrap support <50) or the *rostrata+scalaris* clade (Bayesian analysis with a posterior probability of 0.5), or the *elongata+contamanensis+rostrata+scalaris* clade (under five parameter combinations in POY). The deepest split was either between *elongata+contamanensis* and the rest (ML) or between *M. parkeri* and the rest (five POY parameter combinations), or it remained unresolved (Bayesian analysis and one POY parameter combination).

The clade formed by individuals of *M. scalaris* within *M. rostrata* was only supported by one base substitution in the *trnG-trnR* intergenic spacer. The genetic differentiation was much larger between the other species, but still only a fraction of the very long branch separating *Metaxya* from other tree ferns (Fig. 3).

Ecology and distribution

Three of the six *Metaxya* species appear to have rather restricted geographical distributions (Map 1): *M. contamanensis* (near the Andes in Peruvian and Bolivian Amazonia), *M. elongata* (Central America and the coastal regions of Colombia) and *M. scalaris* (the Guianas and adjacent Brazil).

Metaxya lanosa is relatively widely distributed in the northern parts of Amazonia, as it is known from Brazil, Colombia, Guyana, Peru and Venezuela. However, this species can be considered an edaphic specialist. According to herbarium labels and our own observations, it grows in white sand forests (known as varillal in Peru and campinarana in Brazil), which have extremely nutrient-poor sandy soils, and on sandstone boulders. In this respect, *M. lanosa* differs from all the other *Metaxya*, which grow in more typical rain forests on more fine-grained soil.

Metaxya rostrata and especially *M. parkeri* are broadly distributed across the Amazon basin. In western Amazonia, these two species have often been seen growing in the same sites (Fig.4). Both species also have a wide range along the soil cation concentration gradient, the main difference being that *M. rostrata* seems to be, in general, more concentrated to those sites with a high aluminium:cation concentration ratio (Fig. 4). The ranges of *M. parkeri* and *M. scalaris* overlap in northern Amazonia and the Guianas, but *M. rostrata* seems to be more restricted to the western parts of the Amazon basin.

Discussion

For quite some time, we have informally recognised two sympatric forms of *Metaxya* in western Amazonia, the 'broad' form (with few broad pinnae) and the 'narrow' form (with many narrow pinnae). These forms were also mentioned by Smith *et al*. (2001). However, both the shape and the number of pinnae vary to the extent that the distinction between the two did not become clear-cut until we realised that also the pinna apices were different: irregularly and coarsely dentate-serrate in the 'broad' form, vs. sharply serrate (the serration often extending a long distance down the margin) in the 'narrow' form. These diagnostic characters made it possible to divide the specimens into two clearly separated groups. Here we have shown that they are also genetically distinct: all phylogenetic analyses based on DNA sequence data resolved them into separate clades. This strongly indicates lack of gene flow between the two forms in spite of sympatry, which suggests that they represent distinct evolutionary lineages and supports their recognition at the species level. Although the type specimen of *M. rostrata* (*Bonpland & von Humboldt* 966 at B!) only consists of two pinnae, we are relatively confident that our 'broad' form corresponds to this species. We associate the 'narrow' form with *M. parkeri*, although in this case the situation is more complicated.

We attach the name *Metaxya parkeri* to the specimen 00021875 at GH!, which matches the illustration of the species provided in Hooker and Greville (1831) better than does any of the other historical specimens that we have seen. In addition, its label text corresponds with what is said in the original protologue. This specimen is not a perfect match for our 'narrow' form, because its sori are closer to the midvein and not scattered, but the serrations of the pinna apices and margins are similar. We have opted to treat our 'narrow' form as conspecific with *M. parkeri*, because there is gradual variation between the extremes in the morphological characteristics, especially in soral arrangement. When genetic data from specimens that fully match the type of *M. parkeri* become available, the validity of this decision can be tested.

At present, we accept six morphologically defined species in *Metaxya*. Our molecular phylogenetic results support only five of them, but the two that are not well differentiated genetically (*M. rostrata* and *M. scalaris*) are clearly distinct morphologically. In particular, they differ in the distribution of sori and in the shape of the pinna apex. Geographically the two overlap in the Manaus region (N Brazil), but mostly *M. rostrata* is found in western Amazonia and *M. scalaris* in the Guianas.

The *Metaxya contamanensis*+*elongata* clade was strongly supported by all phylogenetic analyses, as was the distinction between the two. In addition, *M. contamanensis* and *M. elongata* differ morphologically in the size, shape and texture of pinnae, and they also occupy geographically disjunct areas. The branches leading to these two species are shorter than branches leading to *M. lanosa*, *M. parkeri* or *M. rostrata*+*scalaris*, but still indicate much greater genetic differentiation than is observed within any of the six species.

When Smith *et al*. (2001) described *Metaxya lanosa*, they reported greater phylogenetic difference between *M. rostrata* specimens from Costa Rica and Ecuador (0.63% sequence divergence in *rbcL* gene) than between either one of these and *M. lanosa* from Peru (0.32% sequence divergence). It is now evident that none of their

DNA sequences actually represented *M. rostrata*, but instead they had sampled *M. parkeri* in Ecuador and *M. elongata* in Costa Rica.

Metaxya lanosa was represented by only one specimen in our genetic analyses, because the other specimens we extracted failed to yield DNA. Even this specimen failed for the *matK* and *rbcL* sequences, which may explain why its phylogenetic position varied between the analyses. Given that *Metaxya lanosa* is so distinct morphologically, we have no doubt about its status as a true species. In addition, it is the only species of the genus that grows in white sand forests, which makes it also ecologically distinct.

The root node varied between the analyses: ML and parsimony analyses disagreed in rooting, and the Bayesian analysis left it unresolved. This may result from different sequence alignments in parsimony and model-based analyses, or from different use of gaps in these analyses (informative in parsimony, non-informative in ML). The problem may also be an indication of long-branch attraction, i.e. caused by the long genetic distance to the outgroup. Correct rooting is an essential prerequisite for making biogeographical and other evolutionary conclusions, so more data are needed to verify the provisional ML based rooting presented here.

Taxonomic treatment

Metaxya Presl, Tent. Pterid. 59. 1836.

Genus description

Terrestrial. *Rhizome* short-creeping, branched, dorsiventral, solenostelic, 0.8 – 2 cm in diam.; apex densely hairy; hairs 3 – 10 mm long, consisting of 6 – 17 cells, yellowish to dark brown. *Leaves* monomorphic, up to 2.5 (– 3.6) m long. Petioles abaxially terete throughout, adaxially sulcated or sometimes terete at the very base, with one omega-shaped vascular bundle, glabrous or with brown hairs up to 14 mm in length, easily abraded but most persistent at the base. Laminae once pinnate with conform terminal pinna, herbaceous to coriaceous, glabrous on the adaxial side, sparse occurrence of erect or appressed hairs (less than 1 mm long, with 2 – 3 cells) on the abaxial side, branched hairs (0.5 – 3 mm long) along the midvein. Lateral pinnae alternate in the apical part of the lamina, subalternate to opposite in the basal part; stalked, sessile or decurrent; narrow-elliptic, narrow-lanceolate, narrow-oblanceolate, oblong-elliptic or oblong-lanceolate, 5 – 10 times as long as wide; apex caudate, cuspidate or attenuate, with entire, dentate or serrate margin. Rachises and midvein adaxially sulcated, abaxially rounded. Veins evident, simple or bifurcated near the base, parallel, free. *Sori* abaxially on the veins, one to several borne on the same vein; globular (rarely oval), exindusiate, densely covered by filiform paraphyses. Sporangia maturing simultaneously, with a short stalk. Spores 64 per sporangium, trilete, 45 – 90 µm). Chromosome number n=94 – 96 (Roy & Holttum 1965).

Juveniles of all *Metaxya* species have deeply lobed pinnae (Roy & Holttum 1965; Tuomisto & Groot 1995).

Identification key to species

1a. Lamina texture stiff and coriaceous; pinna margins clearly cartilaginous; pinnae oblong and about 5 times as long as wide: ***M. lanosa***

1b. Lamina texture chartaceous to herbaceous; pinna margins not cartilaginous or only slightly so; pinnae narrowly elliptic, lanceolate or oblanceolate and (5 –) 6 – 12 times as long as wide: 2

2a. Lateral pinnae 2 – 7 to a side, 4.0 – 6.0 cm wide; pinna apices cuspidate to caudate with margins irregularly and coarsely dentate to almost entire with few teeth: ***M. rostrata***

2b. Lateral pinnae (4 –)7 – 16 to a side, 2.4 – 4.5 (– 5.5) cm wide; pinna apices caudate to long-attenuate with serrate, dentate or almost entire margins: 3

3a. Lateral pinnae mostly broadest above the middle; pinna apices caudate to caudate-attenuate with step-like profile due to round-dentate (rarely dentate-serrate) margin; each vein usually with a single sorus (rarely 2 – 3), most of these forming a dense line touching the midvein: ***M. scalaris***

3b. Lateral pinnae parallel-sided or broadest at or below the middle; pinna apices long-attenuate to caudate with almost entire to serrate (rarely dentate) margin; each vein with 1 – 3 (– 4) sori that do not touch the midvein (or if so, only in the basal part of the pinna): 4

4a. Lamina texture chartaceous, margin slightly cartilaginous; pinna apices often asymmetric (falcate), almost entire with a few shallow serrations: ***M. contamanensis***

4b. Lamina texture herbaceous, margin not cartilaginous; pinna apices symmetric, serrate: 5.

5a. Pinnae long and narrow, usually more than 9 times as long as wide; pinna apices long-attenuate with finely and regularly serrate margin; pinna margin becomes entire soon below the attenuate apex; sori usually 1 – 2 per vein, arranged in a narrow band some distance away from the midvein: ***M. elongata***

5b. Pinnae variable, usually less than 9 times as long as wide; pinna apices attenuate to caudate with slightly irregularly serrate (rarely dentate) margin; pinna margin serrate beyond the apex, sometimes all the way to base of pinna; sori usually 2 – 3 per vein, arrangement variable (widely scattered over the entire lamina except near the midvein or concentrated near the midvein but not touching it or in a narrow band some distance away from the midvein): ***M. parkeri***

Metaxya contamanensis *Tuomisto & G.G.Cárdenas* **sp. nov.**

Type: Peru, Loreto Dept., Contamana, 07 July 2002, *Tuomisto, Cárdenas & Christenhusz* 13877 (holotype USM!; isotypes AMAZ!, K!, TUR!, UC!).

Leaves up to 1.5 (– 3.6) m long, petiole 51 – 59 cm long, shorter than to almost as long as the lamina, lamina 56 – 90 cm long. Pinnae 7 – 13 to a side, basal pinnae with petiolule 0.4 – 1.2 cm long, uppermost lateral pinna with small petiolule or decurrent basiscopically, attached to rachis by up to 3 mm; lateral pinnae narrow-lanceolate to narrow-elliptic, up to 20.0 – 28.6 (– 35.0) cm long and 2.5 – 3.5 cm wide, usually falcate; terminal pinna narrow-lanceolate, 16.0 – 24.0 cm long and 2.4 – 3.4 cm wide; pinna texture chartaceous, margin paler than the rest of the lamina, slightly cartilaginous; pinna base oblique; pinna apex caudate to attenuate, often asymmetric, almost entire, with a few irregular and shallow serrations. *Sori* (1 –)2(– 3) per vein, irregularly scattered up to 2/3 of the way from the midvein towards the margin and 3/4 (– 4/5) of the way from the base towards the apex of the pinna. Figs. 5A, 6.

RECOGNITION. *Metaxya contamanensis* is characterized by narrow-lanceolate to narrow-elliptic, often clearly falcate pinnae that have chartaceous lamina texture, slightly cartilaginous margins and asymmetric caudate to attenuate apices with a few irregular and shallow serrations. It has woolly, easily abraded hairs on the petiole and rachis that resemble those of *Metaxya lanosa*, but that species has oblong-lanceolate to oblong-elliptic pinnae that are coriaceous (rather than chartaceous) and clearly more cartilaginous at the margins. *Metaxya elongata* has narrower and longer pinnae that are parallel-sided with regularly and finely serrate apices and a more herbaceous texture. *Metaxya parkeri* is not only serrate at the pinna apices but usually also along the pinna margins. *Metaxya rostrata* has cuspidate to caudate apices (rather than caudate to attenuate) that are coarsely and irregularly dentate, and *M. scalaris* has narrow-elliptic to narrow-oblaneolate pinnae with caudate to caudate-attenuate apices that have step-like coarse dentations. *Metaxya contamanensis* has mostly 2 sori per vein scattered over the abaxial surface of pinnae. In *Metaxya elongata* the sori form a distinct line a few millimeters away from the midvein and *Metaxya scalaris* usually has just one sorus per vein (and this touches the midvein).

DISTRIBUTION. *Metaxya contamanensis* is known from a narrow zone along the eastern foothills of the Andes in Amazonian Peru and Bolivia.

SPECIMENS EXAMINED. BOLIVIA. Cochabamba Dept.: Sinahota, 17°05’S, 65°14’W, 306 m, 5 June 2009, *Weigelt, Normann & Perez* 90150 (TUR!, UC); La Paz Dept.: Challana River Region, 700 m, *Cárdenas* 1267 (UC, US!); Larecaja, Tuiri, Río Mapiri, 490 – 750 m, 12 – 30 Sept. 1939, *Krukoff* 10959 (K!, MO, UC, US!); Mapiri, 610 m [2000 feet], 30 March – 9 April 1926, *Tate* 425 (UC, US!). **PERU**. Amazonas Dept.: Bagua, 450 – 600 m, 5 Sept. 1962, *Wurdack* 1872 (US!); Cuzco Dept.: La Convención, 11°41’S, 73°00’W, 350 m, 18 April 1998, *Nuñez, Beltran, Nauray, Acurio, de la Colina, Llerena & Salas* 21646 (CUZ, US!, USM); Loreto Dept.: Vicinity of Aguaytia, along Rio Aguaytia, 3 Oct. 1972, *Croat* 20966 (MO, US!); Balsapuerto (low Rio Huallaga basin), 350 – 550 m, 29 Aug. 1929, *Killip & Smith* 28521 (US!); Ucayali, 40 km NNE (air distance) of Contamana at the Ucayali river, near the village Canchahuaya, 7°00’S, 75°06’W, 200 – 300 m, 07 July 2002, *Tuomisto, Cárdenas & Christenhusz* 13877 (holotype USM!; isotypes AMAZ!, K!, TUR!, UC!); Ucayali, 30 km N (air distance) of Contamana at the Ucayali river, 8-9 km E-SE of the village Canelos, 7°06’S, 75°02’W, 300 – 400 m, 9 July 2002, *Tuomisto, Cárdenas & Christenhusz* 13891 (AMAZ!, TUR!, USM); Ucayali, 18-19 km NE of Contamana, 6 – 7 km E of the end of the Contamana - Aguas Calientes road, 7°14’S, 74°53’W, 600 – 700 m, 13 July 2002, *Tuomisto, Cárdenas & Christenhusz* 13918 (AMAZ, TUR!, USM); Ucayali, 17 – 18 km NNE of Contamana beyond the end of the Contamana – Aguas Calientes road, 7°11’S, 74°57’W, 250 – 350 m, 14 July 2002, *Tuomisto, Cárdenas & Christenhusz* 13934 (AMAZ, TUR!, USM); San Martín Dept. [Huánuco Dept.]: Tingo María, 625 – 1100 m, 30 Oct. 1949 – 19 Feb. 1950, *Allard* 20727 (US!); Tingo María, 625 – 1100 m, 30 Oct. 1949 – 19 Feb. 1950, *Allard* 20812 (US!); San Martín Dept.: San Martín, Cascades in Río Shilcayo, near Tarapoto, 6°27’S, 76°20’W, 649 m, 30 July 2002, *Christenhusz, Cárdenas & Huatangare* 1930 (AMAZ, NY!, TUR!, USM); Mariscal Cáceres, 500 – 700 m, 12 March 1979, *Gentry, Schunke & Aronson* 25602 (MO, US!); Mariscal Cáceres, Campanilla, 15 Oct. 1969, *Schunke* 3524 (US!); Tocache Nuevo, Isla de Pucunuchu, 03 April 1971, *Schunke* 4783 (INPA!, K!, MO, US!); Tocache Nuevo, Palo Blanco, 700 – 800 m, 19 Dec. 1972, *Schunke* 5748 (K!, US!).

HABITAT. Amazonian terra firme rain forest close to the Andes; alt. 200 – 800 (– 1100) m.

CONSERVATION STATUS. Least Concern (LC) according to IUCN (2001) red list criteria. Although there is no information on its population size, the species has a reasonably wide distribution range in a mainly forested area.

ETYMOLOGY. The species is named after the Contamana region, where it was first discovered.

NOTES. *Metaxya contamanensis* is characterised by a combination of narrow-lanceolate pinna shape, asymmetric and almost entire pinna apices (some shallow serrations may be present), chartaceous lamina texture and slightly cartilaginous pinna margins. Although *M. parkeri* and *M. elongata* can also have lanceolate pinna shape, their pinna apices are symmetric and obviously serrate, and they have clearly thinner pinnae with non-cartilaginous margin.

Metaxya elongata *Tuomisto & G.G.Cárdenas* **sp. nov.**

Type: Costa Rica, Heredia Prov., Sarapiquí. La Selva Biological Station, 11 June 2002, *Jones & Olivas* 480 (holotype TUR!; isotypes CR, LSCR, USJ).

Leaves up to 1.9 m long, petiole 67 – 96.5 cm long, about the same length as the lamina, lamina 66 – 97 cm long. Pinnae 11 – 16 to a side, basal pinnae with petiolule 0.7 – 1.4 cm long, uppermost lateral pinna decurrent basiscopically, attached to rachis by up to 1 cm; lateral pinnae narrow-lanceolate to narrow-elliptic, sometimes slightly falcate, up to 25 – 37.3 cm long and 2.8 – 3.2 cm wide; terminal pinna narrow-lanceolate, 20.5 – 34.3 cm long and 2.6 – 3.1 cm wide; margin paler than the rest of the lamina, slightly undulated; pinna base slightly oblique; pinna apex long-attenuate to caudate, regularly and finely serrate. *Sori* 1 – 2(– 3) per vein, the ones nearest to the midvein forming an irregular line about 1 – 4 mm away, the ones farthest being up to 9 mm away from the midvein, generally closer to the midvein in the basal part of the pinna than in the apical part, restricted to the basal 2/3 of the pinna. Figs. 5B, 7.

RECOGNITION. *Metaxya elongata* is characterised by a large number (> 10 on each side) of thin-textured pinnae, these being long, narrow, generally parallel-sided and with long-attenuate regularly and finely serrate apices. Furthermore, the relatively few sori per vein are concentrated to a zone that is closer to the midvein than to the pinna margin. *Metaxya lanosa* and *M. rostrata* have fewer (< 7 on each side) and broader pinnae with a thicker texture, and their sori are more widely scattered.

Metaxya contamanensis differs in having chartaceous pinnae that are more clearly lanceolate (rather than parallel-sided) and apices that are often falcate and have only a few shallow serrations. *Metaxya scalaris* has slightly chartaceous pinnae whose apices are mostly coarsely dentate with a step-like shape, and sori concentrated into a dense line touching the midvein. *Metaxya parkeri* margins are generally serrate to far below the apex and the serrations are coarser than those of *M. elongata.* The sori of *M. parkeri* are often (but not always) much more widely scattered than are those of *M. elongata*.

DISTRIBUTION. *Metaxya elongata* occurs in Central America and the Pacific and Caribbean coasts of Colombia.

SPECIMENS EXAMINED. BRITISH HONDURAS [BELIZE]. Toledo Dist.: Big Creek, March 1929, *Schipp* 89 (K!, MO, Z!). **COLOMBIA**. Antioquia Dept.: Anorí, 7°16’N, 75°03’W, 700 m, 11 Nov. 2003, *Rodriguez, Colorado & Rúa* 4271 (COL!, MO); Bolivar Dept.: Achi, 8°20’N, 74°30’W, 20 – 80 m, 6 July 1987, *Callejas, Betancur, Roldán & Martínez* 4392-A (COL!); Cauca Dept.: Guapí, Parque Nacional Natural Gorgona, 9 Sept. 1987, *Lozano & Rangel* 5733 (COL!); Chocó Dept.: 100 m, 19 Nov. 1976, *Forero* 778 (COL!, MO); 4°42’N, 76°55’W, ca. 20 m, 4 April 1979, *Forero, Jaramillo, Espinoza & Palacios* 4545 (COL!, MO); Parque Nacional Natural de Los Katios, 60 m, 15 June 1976, *León* 77 (COL!); Santander del Norte Dept. [Norte de Santander]: 9°9 – 10’N, 72°50’W, 40 – 50 m, 15 – 20 May 1965, *García-Barriga & Lozano* 18309 (COL!); Valle del Cauca Dept.: Pacific Coast, 0 – 5 m, 17 May 1944, *Cuatrecasas* 17729 (US!); Buenaventura, Pacific Coast, 0 – 10 m, 5 – 10 Oct. 1922, *Killip* 11945 (US!). **COSTA RICA**. Limón Prov.: Talamanca, 200 m, April 1895, *Pittier* 9470 (P!); Heredia Prov.: Sarapiquí, La Selva Biological Station, 10°26’N, 84°1’W, 50 – 150 m, 11 June 2002, *Jones & Olivas* 480 (holotype TUR!;

isotypes CR, LSCR, USJ); Puntarenas Prov.: 8°43’N, 83°36’W, Canton de Osa, 400 m, 23 Nov. 1993, *Herrera, Vargas & Ruiz* 6653 (K!); 22 July 1978, *Kress* 78 – 1012 (F!); *Pittier* 3543 (Z); San José Prov.: Cerro Turrubares, Puriscal, 250 m, April 1912, *Jiménez* 611(P!). **GUATEMALA**. 1862, *Godman* s.n. (Herbarium Hookerianum in K!). **HONDURAS**. Atlantida Dept.: Campamento Quebrada Grande, 15°42’N, 86°51’W, 80 – 150 m, 9 May 1993, *Liesner* 26111 (MO!); vicinity of La Ceiba, 12 July 1938, *Yuncker, Koepper & Wagner* 8406 (K!, MO). **PANAMA**. Chiriqui Prov.: 1886, *Hart* (K!); Colón Prov.: PN San Lorenzo, 9°17’N, 79°58’W, 183 m, 18 April 2008, *Jones* 1030 (MO, PMA, STRI, TUR!); Santa Rita ridge, 200 – 250 m, 13 Feb. 1974, *Nee & Hale* 9681 (F!, MO); Santa Rita, 9°21’N, 79°44’W, 400 m, *Tuomisto, Portugal, Condit & Aguilar* 15143 (PMA!, TUR!); Panama Prov.: PN Soberania, 9°10’N, 79°45’W, 215 m, 28 Jan. 2008, *Jones, Mandl & Mitre* 687 (PMA, STRI, TUR!); PN Soberanía, 9°12’N, 79°46’W, 254 m, 9 Feb. 2008, *Jones, Mandl & Mitre* 762 (MO, PMA, STRI, TUR!); PN Soberanía, 9°10’N, 79°44’W, 187 m, 07 Feb. 2008, *Jones, Mandl & Mitre* 948 (PMA, STRI, TUR!); La Laguna, 9°5’N, 79°47’W, 80 m, 15 May 2008, *Jones* 1093 (PMA, STRI, TUR!); Juan Díaz, 50 m, 30 Sept. 1917, *Killip* 2530 (P!); Chiman, 12 Dec. 1967, *Lewis, Correa, Dressler, Oliver, Ridgway & Robyns* 3276 (COL!, UC). **VENEZUELA**. *Liesner* 10530 (MO, UC!). Zulia State: Rio de Oro, 9.3°N, 72.47°W, 26 – 28 June 1980, *Davidse, Gonzalez & Leon* 18604 (MO, UC!).

HABITAT. Tropical rain forest; alt. 0 – 700 m.

CONSERVATION STATUS. Least Concern (LC) according to IUCN (2001) red list criteria. The species is widely distributed and apparently abundant.

ETYMOLOGY. *Metaxya elongata* is named for the length of the pinnae which are among the longest in the genus.

NOTES. *Metaxya elongata* is morphologically clearly distinct from all the other species of *Metaxya*, but some forms of *M. parkeri* come relatively close in pinna shape, apex serration and distribution of sori. However, in most cases the serrations in the margin of *M. parkeri* are coarser and continue much further down along the pinna margins, and often the sori are either more concentrated along the midvein or more scattered over the pinnae than in *M. elongata*. Genetic data from Colombia and the Caribbean islands would help in defining the exact limit between the two species.

Metaxya lanosa *A.R.Sm. & Tuomisto* (Smith *et al.* 2001: 480 – 482).

Type: Peru. Loreto Dept., Maynas, Experimental Station “El Dorado” of INIA, km 25 along the road Iquitos-Nauta, 3°57’05”S, 73°24’31”W, 100 – 200 m, 24 Sept. 1998, *Tuomisto & Ruokolainen* 13054 (holotype USM!; isotypes AMAZ!, TUR!, UC!).

Leaves up to 1.5 – 2.5 m long, 59 – 68 cm long, petiole as long as or longer than the lamina, lamina 44.5 – 49.5 cm long. Pinnae 4 – 10 to a side, basal pinnae with a petiolule up to 2 cm long, uppermost lateral pinna with a short petiolule or slightly decurrent; lateral pinnae oblong-lanceolate to oblong-elliptic, up to 31 cm long and 6.5 cm wide; terminal pinna up to 20.7 cm long and 4.5 cm wide; pinna texture coriaceous, margin paler than the rest of the lamina and clearly cartilaginous; pinna base oblique; pinna apex cuspidate to caudate, sometimes slightly falcate, entire or with a few sharp but shallowly serration that do not incise beyond the cartilaginous margin. *Sori* (1 –)2 – 3(– 4) per vein, irregularly scattered, restricted to the basal 2/3 of the pinna. Figs. 5C, 8.

DISTRIBUTION. *Metaxya lanosa* occurs in northern Amazonia and the Guianas (Brazil, Colombia, Guyana, Peru and Venezuela).

SPECIMENS EXAMINED. BRAZIL. Amazonas State: Rio Negro, road from São Gabriel da Cachoeira to Cucuí, lower slopes of Sierra do Padre, 1°24'S, 66°38'W, 250 m, 27 Nov. 1987, *Stevenson & Ramos* 1082 (INPA!). **COLOMBIA**. Guainía Dept.: Corregimiento de Caño Colorado, 2°09'N, 68°14'W, 300 m, 20 Oct. 2009, *Cárdenas, Castaño & Aguirre-Santoro* 24397 (NY!); Río Caquetá, alrededores de Araracuara, 10 – 22 Nov. 1982, *Idrobo, Mahecha, Carbono, Orozco, Ortega, Pabon, Ramos, Ruiz & Vidal* 11410 (COL!); Vaupés Dept.: Río Kananarí, Cerro Isibukuri, 250 – 700 m, 4 Aug. 1951, *Schultes & Cabrera* 13333 (COL!). **GUYANA**. Cuyuni-Mazaruni Region: 5°14'N, 60°30'W, 488 m, 28 June 2004, *Clarke, Perry, Tripp, Stern & Gittens* 12153 (US!); Maipuri Falls, Karowrieng River, 5°41'N, 60°14'W, 650 – 770 m, 17 Dec. 1989, *Gillespie & Smart* 2747 (CAY!, INPA!, MO); Pakaraima Mts., Mt. Membaru, 5°57'N, 60°33 – 34'W, 550 – 600 m, 12 Nov. 1979, *Maas & Westra* 4338 (K!, Z!); 5°41'N, 60°12'W, 605 m, 25 Jan. 2004, *Redden, Perry & Williams* 1544 (US!). **PERU**. Loreto Dept.: Maynas, Reserva Nacional Allpahuayo-Mishana. 3°57'S, 73°26'W, 110 m, 8 Dec. 2000, *Cárdenas, Vargas & Mesones* 513 (AMAZ!); Maynas, Experimental Station "El Dorado" of INIA, km 25 along the road Iquitos-Nauta, 3°57'S, 73°25'W, 100 – 200 m, 24 Sept. 1998, *Tuomisto & Ruokolainen* 13054 (holotype AMAZ!; isotype TUR!, UC!, USM!). **VENEZUELA**. Territorio Federal Amazonas [Amazonas State]: Río Negro, 0°50'N, 66°10'W, 140 m, 5 Feb. 1984, *Liesner* 15643 (INPA!, MO, Z!); Río Negro, 0°51'N, 66°10'W, 150 – 200 m, 1 March 1984, *Liesner* 16332 (MO, Z!); Amazonas State: Base of Piedra de Cucui, 1°24'N, 67°44'W, 100 – 200 m, 28 Oct. 1987, *Stevenson, Maas, Rodríguez & Ramos* 843 (INPA!, MO).

HABITAT. Terra firme tropical forest, on white sand soils, also reported from sandstone boulders; alt. 100 – 700 m.

CONSERVATION STATUS. Least Concern (LC) according to IUCN (2001) red list criteria. The species is widely distributed and abundant in its habitats, although the habitats themselves are patchily distributed.

ETYMOLOGY. The name refers to the abundance of long wool-like hairs on the petioles and rachises of this species.

NOTES. *Metaxya lanosa* is unique in that its leaves are thick and coriaceous with distinctly cartilaginous margins, and its petioles and rachises are covered in long woolly hair (although this is easily abraded). *Metaxya contamanensis* is the only other species in the genus to approach this lamina texture, but its pinnae are narrow-elliptic to narrow-lanceolate (rather than oblong-elliptic to oblong-lanceolate). The laminae of *Metaxya scalaris* are relatively stiff, but this species has narrow-oblanceolate to narrow-elliptic pinnae and its apices are coarsely dentate (rather than almost entire or with a few sharp but shallow serrations). Pinna apices also differentiate *M. lanosa* from *M. parkeri* and *M. elongata*, which have clearly serrate pinna apices, and from *M. rostrata*, which has irregularly and coarsely dentate apices. In addition, *M. elongata* has many more pinnae (11 – 16 vs 4 – 6 per side) and these are clearly narrower (2.8 – 3.2 cm vs 4.0 – 6.5 cm).

Metaxya parkeri *(Hook. & Grev.) J.Sm.* (Smith 1842: 668).

Lectotype (designated here): Guianas. Creek near River Mazaronie, May 1824, *Parker* s. n. GH! [GH00021875].

Polypodium parkeri Hook. & Grev. (Hooker & Greville 1831: 232).

Leaves up to 2.5 m long, petiole 60 – 130 cm long, longer than the lamina, lamina 36.5 – 94.5 cm long. Pinnae 4 – 16 to a side, basal pinnae with petiolule 0.4 – 1.8 cm long, uppermost lateral pinna sessile, with small petiolule or decurrent basiscopically, attached to rachis by up to 0.6 cm; lateral pinnae narrow-lanceolate to narrow-elliptic, oblong-elliptic, 18.5 – 37 cm long and 2.4 – 4.5 cm wide; terminal pinna lanceolate (to elliptic), 13 – 34 cm long and 2.4 – 5.4 cm wide; pinna texture herbaceous; pinna margin slightly paler than the rest of the lamina, serrate at least in the apical part of the pinna but sometimes all the way to the base; pinna base oblique; pinna apex long-attenuate to caudate, serrate or rarely dentate, sometimes slightly falcate. *Sori* (1 –)2 – 3(– 4) per vein, arrangement varying from concentrated near the midvein to irregularly scattered over most of the pinna surface. Figs. 5D, 9.

DISTRIBUTION. *Metaxya parkeri* is the most widespread species in the genus. It is known from Amazonia (Bolivia, Brazil, Colombia, Ecuador, Peru, Venezuela), the Guianas, some Caribbean islands (Guadeloupe, Trinidad) and the Atlantic coast of Brazil (Bahia).

SPECIMENS EXAMINED. BOLIVIA. Beni Dept.: Ballivian, Pilón Lajas Rurrenabaque La vertiente, río Beni, 14°28’S, 67°34’W, 220 m, 17 Nov. 1999, *De Boer* 1311 (UC). Cochabamba Dept.: Carrasco, 17°23’S, 64°23’W, 630 m, 20 Sept. 1997, *Acebey* 685 (UC); La Paz Dept.: 12°53’S, 68°53’W, 170 m, 21 June 2004, *Gonzales* 3739 (UC); Santa Cruz Dept.: Velasco, Parque Nacional Noel Kempff M, 13°54’S, 60°48’W, 650 m, 18 May 1994, *Arroyo* 713 (UC). **BRAZIL**. Acre State: Estr. BR 364 (Cruzeiro do Sul-Rio Branco), 15 Sept. 1985, *Jangoux, Campbell, Coelho, Frame, Menezes, Richardson, dos Santos & Rosas* 85-043 (NY!); Vicinity of Periquito, Rio Juruá-Mirim, 19 May 1971, *Maas, Kubitzki, Steward, Ramos, Pinheiro & Lima* P13150 (NY!); Amazonas State: Estrada do Tibirrá (Piçarreira), 0.21°S, 65.02°W, 29 Sept. 1999, *Freitas* 671 (SP!); Reserva Florestal Ducke, Manaus-Itacoatiara km 26, 2°53’S, 59°58’W, 3 July 1993, *Ribeiro, Ramos, Santana & Souza* 992 (INPA!, SP!); Autazes, 3°34’S, 59°31’W, 20 – 40 m, 13 Jan. 2008, *Tuomisto,* *Zuquim, Ruokolainen & de Souza* 15238 (INPA!, SP!, TUR!, UC!); Novo Airão, Km 15 of the Novo Airão-Manacapuru road, 2°45'S, 60°56'W, 40 – 80 m, 18 Jan. 2008, *Tuomisto, Zuquim, Ruokolainen & de Souza* 15293 (INPA!, SP!, TUR!); Presidente Figueiredo, km 140 of the Manaus-Boa Vista road, 1°49'S, 60°9'W, 80 – 120 m, 13 Feb. 2008, *Tuomisto, Zuquim, Ruokolainen & de Souza* 15743 (SP!, TUR!, Z!); Itamarati, ca. 9 km west from the village of Boca do Xeruá, Jurua River, 6°03'S, 67°55'W, 100 m, 4 April 2012, *Tuomisto, Moulatlet, Ruokolainen, Emilio & Figueiredo* 16079 (SP!, TUR!); Itamarati, ca. 5 km north-west from the town of Itamarati, Jurua River, 6°24'S, 68°17'W, 120 – 150 m, 8 April 2012, *Tuomisto, Moulatlet, Ruokolainen, Emilio & Figueiredo* 16127 (SP!, TUR!); Itamarati, ca. 2.5 km north from the village of Cubiu, Río Juruá, 6°27'S, 68°39'W, 120 – 140 m, *Tuomisto, Moulatlet, Ruokolainen, Emilio & Figueiredo* 16184 (NY!, SP!, TUR!); Borba, Campina da Catuquira, 4°54'S, 61°06'W, 30 m, 14 July 2007, *Viana, Maruenza, Nascimento, Cohn-Haft & Adeney* 3133 (SP!); Bahia State: Municipio de Una, near REBIO Una, 13 Jan. 2000, *Barradas-Paciencia* 432 (SP!); Maranhão State: Municipio Carolina, 13 April 1983, *Silva, Taylor, Rosa, Silva, Oliveira, Rosário & Santos* 1085 (INPA!, US!); Mato Grosso State: Expedition Base Camp: 12°49'S, 51°46'W, 22 Oct. 1968, *Harley, Souza & Ferreira* 10756 (K!, NY!, P!); Município de Barra do Garças, 15°44'S, 52°24'W, 24 Aug. 2003, *Athayde et al.* 1434 (SP!); Rio Aripunã, road from Nucleo Pioneiro de Humboldt to new airport, 10°12'S, 59°21'W, 23 Oct. 1973, *Berg, Steward, Ramos, Monteiro & Lima* P19847 (K!, MO, NY!, US!); 4 km N of the base camp of the expedition (base camp 12°54'S, 51°52'W), 11 June 1968, *Ratter, de Santos & Souza* 1709 (K!, US!); Município de Aripuanã, 4 km de Aripuanã, 10°05'S, 59°22'W, 9 Oct. 1996, *Windisch* 8583 (SP!); Município Vera, about 5 km from BR 163, 13°07'S, 56°01'W, 6 Oct. 1997, *Windisch* 8834 (SP!); Pará

State: Itaituba, 5°06’S, 57°05’W, 1 Dec. 2009, *Zuquim & Costa* 1011 (INPA!); Piaui State: Município Caracol, Parna, Serra das Confusões, 9°13’S, 43°29’W, 510 m, 23 Jan. 2006, *Sousa, Barros, Vieira, Oliveira, Marques & Silva* 571 (HUEFS!); Roraima State: SEMA Ecological Reserve, Ilha do Maracá, 3°43’N, 62°41’W, 22 May 1987, *Milliken & Bowles* 249 (INPA!, K!, SP!); Rondônia State: Guajara Mirim, ca. 32 km SE of Guajara Mirim, ca. 10°57’S, 65°04’W, 175 m, 23 April 1987, *Nee* 34811 (K!, MO, SP!); Porto Velho, Módulo Caiçara, 9°27’S, 64°48’W, 90 m, 22 Aug. 2012, *Pereira-Silva et al.* 16351 (INPA!, NY!, RON!); 3 – 4 km SW of Mutumparaná on railroad to Abunã, 2 July 1968, *Prance, Phileox, Forero, Coelho, Ramos & Farias* 5439 (INPA!, K!, US!); 8 km NE of Porto Velho, 9 Nov. 1968, *Prance, Rodrigues, Ramos & Farias* 8272 (MO, P!, US!); T.F. de Rondônia [Rondônia State]: a 13 km de Vilhena, 12°45’S, 60°10’W, 2 Nov. 1979, *Vieira, Petersen, Nelson, Ramos & Mota* 861 (INPA!, US!). **COLOMBIA**. Amazonas Dept.: Río Igara-Parana (affl. Río Putumayo), 5 June 1974, *Sastre* 3126 (COL!, P!, US!); Río Miritiparaná, Caño Guacayá, 0°30’S, 70°40’W, 2 – 8 March 1952, *Schultes & Cabrera* 15743 (COL!, US!); Amazonas or Vaupés Dept.: Río Apaporis, 250 m, 25 – 26 Aug. 1952, *García-Barriga* 14244 (COL!, US!); Río Apaporis, ca. 250 m, 13 June 1951, *Schultes & Cabrera* 12489 (US!); Boyacá Dept.: Santa María alrededores, 4°45’N, 73°18’W, 850 m, 28 March 2001, *Murillo & estudiantes Sist. Vegetal I/2001* 2901 (COL!); Caquetá Dept.: Sierra de Chiribiquete, 1°20’N, 71°57’W, 21 Nov. 1992, *Cardiel & Pedrol* 4693 (COL!); Intendencia del Caquetá [Caquetá Dept.]: cabeceras del Río Mesay, desembocadura del Río San Jorge al Río Cuñaré, 1 – 6 March 1980, *Pabón* 966 (COL!); Vaupes Dept.: Rio Kananari, Cerro Isibukuri, 0°15’N, 70°35’W, 23 – 25 Jan. 1952, *Schultes & Cabrera* 15065 (COL!, US!); Río Piraparaná (tributary of Río Apaporis), between 0°15’S, 70°30’W and 0°25’N, 70°30’W, 6 Sept. 1952, *Schultes &*

Cabrera 17215 (COL!, US!); Río Vaupés, 14 – 24 May 1953, *Schultes & Cabrera* 19321 (US!). **ECUADOR**. Napo Prov.: Cuyabeno, 0°0'2"S, 76°12 – 15'W, 200 m, 6 Nov. 1987, *Hekker & Hekking* 10109 (Z!); Orellana Prov.: Yasuni National Park, 0°40'S, 76°28'W, 200 – 300 m, 22 April 1997, *Tuomisto, Markkanen & Ruokolainen* 10834 (QCA, QCNE, TUR!); Pastaza Prov.: Río Bobonaza, below Montalvo (Limón), 2°7'S, 76°55'W, 300 m, 17 July 1980, *Øllgaard, Asanza, Brandbyge, Roth & Sperling* 34498 (AAU!, MO); Oil exploration camp Chichirota, on the Río Bobonaza, 2°22'S, 76°40'W, c. 300 m, 26 July 1980, *Øllgaard, Asanza, Brandbyge, Roth & Sperling* 35240 (AAU!, MO); Sucumbios Prov.: Reserva Faunística Cuyabeno, 0°00'S, 76°12'W, 265 m, 11 April – 10 June 1988, *Poulsen* 80951 (AAU!, MO, TUR!). **GUADELOUPE**. 1862, *L'Herminier* 175 (K!, P!); *L'Herminier*, NY01864633 (NY!). **GUIANAS**. *Hostmann* 1080: K000640370, P00625600 (K!, P!); Creek near River Mazaronie, May 1824, *Parker* s. n. GH00021875 (lectotype GH!). **GUYANA**. Cuyuni-Mazaruni Region: 5°46'N, 60°15'W, 600 m, 20 May 1992, *Hoffman, Kelloff, Gharbarran & Sprague* 1744 (CAY!); 5°32'N, 60°07'W, 650 – 750 m, 22 Feb. 1987, *Pipoly, Gharbarran & Samuels* 10532 (CAY!); Potaro-Siparuni Region: Iwokrama Rainforest Reserve, 4°10'N, 59°03'W, 200 m, 20 May 1995, *Ehringhaus* 125 (CAY!, MO, US!); 4°50'N, 59°58'W, 650 m, 18 Jan. 1993, *Henkel, Chin & Ryan* 874 (CAY!); 5°06'N, 59°58'W, 625 m, 19 Oct. 1994, *Mutchnick, Henkel & Williams* 74 (K!); Upper Takutu-Upper Essequibo Region: Essequibo River, 1°39'N, 58°37'W, 250 m, 30 March 1994, *Henkel, Williams & James* 5371 (CAY!, US!); Rupununi District, Kuyuwini Landing, 2°10'N, 59°15'W, 200 m, 10 Feb. 1991, *Jansen-Jacobs, ter Welle, Gopaul & James* 2541 (K!, P!, US!, Z!); 2°5'N, 59°15'W, 150 – 250 m, 16 Oct. 1992, *Jansen-Jacobs, ter Welle, Sipman & James* 2965 (CAY!, K!, P!, US!, Z!); Rupununi Savanna, 1°60'N, 59°34'W, 290 m, 9 Sept.

1997, *Jansen-Jacobs, Lilwah, Raghoenandan, Scheplitz & Vermeer* 5435 (K!, P!). **PERU**. Loreto Dept.: Datén del Marañón, Andoas, Near to Sungachi, 110 m, 28 July 2003, *Cárdenas & Vormisto* 1501 (TUR!, AMAZ!); Maynas, 4°17'S, 73°27'W, 200 m, 27 July 2002, *Christenhusz & Vargas* 1913 (AMAZ, GOET, TUR!); Maynas, Nanay River, ca. 150 m, 10 Jan. 1976, *Gentry, Ayala & Revilla* 15823 (MO, US!); Maynas, Explorama/ACEER reserve, 5 – 15 km E of the mouth of Quebrada Sucusari at lower Napo, 3°15'S, 72°50'W, 100 – 200 m, 23 Jan. 1995, *Tuomisto, Ruokolainen, Aguilar & Sarmiento* 7769 (AMAZ, KSP, TUR!, UC); Loreto, Río Pucacuro, 3°3'S, 75°6'W, 100 – 200 m, 15 Jan. 2005, *Tuomisto, Cárdenas, Higgins & Ruokolainen* 14155 (AMAZ, TUR!, UC, USM); Loreto, Río Tigre, 2°60'S, 75°22'W, 100 – 200 m, *Tuomisto, Cárdenas, Higgins & Ruokolainen* 14561 (AMAZ, TUR!, USM); Loreto [Pucallpa] Dept.: Bosque Nacional Alexander von Humboldt, 7 Sept. 1980, *Maas, Cobb & Grothe* 4506 (Z!); Madre de Dios Dept.: Manu, Río Madre de Dios, S of the river at Mirador Chico, 12°34'S, 70°29'W, 250 – 350 m, 31 Oct. 1998, *Tuomisto, Ruokolainen & Zegarra* 13576 (CUZ, TUR!, USM). **SURINAME**. Nickerie Dist.: Upper Maratakka, 4 Feb. 1915, *Gonggrijp & Stahel* 913 (P!). **TRINIDAD**. Tunapuna-Piarco Region: Aripo Road, 3–4 mile posts, 15 May 1927, *Broadway* s.n. (Z!); Arima Valley, 250 – 350 m, 10 March 1956, *Smith* 10090 (US!). **VENEZUELA**. Lower Orinoco, 1896, *Rusby & Squires* 123 (K! MO, US!, Z!); Amazonas State, slope of Cerro Aracamuni, 23 Oct. 1987, *Liesner & Carnevali* 22361 (MO, UC!); Territorio Federal Amazonas [Amazonas State], Cerro Aratitiyope, 2°10'N, 65°34'W, 990 – 1670 m, 24 – 28 Feb. 1984, *Steyermark, Berry & Delascio* 130251 (MO, UC!, US!); Bolivar State, 9 – 14 April 1999, *Duno de Stefano & Stauffer* 859 (UC!); 4°23'N, 61°38'W, 520 m, 21 Oct. 1985, *Liesner & Holst* 18879 (MO, US!); P.N Canaima, Rio Cucurital, 28 March 2000, *Riina & Duno*

1078 (UC!); Dist. Piar, Rio Aparaman, 21 April 1986, *Holst & Liesner* 2656 (UC!); Carabobo State, 22 – 23 June 1991, *Diaz & Jimenez* 463 (UC!).

HABITAT. Terra firme tropical rain forest; alt. 20 – 750 (– 1670) m.

CONSERVATION STATUS. Least Concern (LC) according to IUCN (2001) red list criteria. The species is widely distributed and abundant.

ETYMOLOGY. This species was named in honour of Charles S. Parker, who first recognised it as a new species.

NOTES. *Metaxya parkeri* is unique in that the serration of the pinna margins is not limited to the pinna apex, but usually extends down at least a quarter of the length of the pinna and sometimes until the base. The type of pinna apex easily distinguishes *M. parkeri* from *M. contamanensis* and *M. lanosa*, whose apices are almost entire, and *M. rostrata*, whose apices are irregularly and coarsely dentate. Most *M. scalaris* have characteristic coarsely and bluntly dentate apices, but some have serrations resembling those of *M. parkeri*. However, in *M. scalaris* the serrations are restricted to the apical part of the pinna (rather than continuing towards the pinna base). The same is true for the apical serrations of *Metaxya elongata*, which are also finer and more regular than those of *M. parkeri*.

In other characteristics of the pinnae, *Metaxya parkeri* as circumscribed here is variable enough to overlap with the other *Metaxya* species: the number of pinnae ranges from 4 to 16 per side, lateral pinna width from 2.4 to 4.5 cm, and pinna apex shape from long-attenuate to caudate. In addition, its sori can be either concentrated near the midvein (resembling the soral distribution of *M. scalaris*), at a small distance from the midvein (as in *M. elongata*), or widely scattered over most of the abaxial surface of the pinnae, except for the immediate vicinity of the midvein (as in *M.*

lanosa). In general, those specimens that have their sori near the midvein have narrower pinnae than the specimens with scattered sori.

In their description of *Metaxya parkeri*, Hooker and Greville (1831) made reference to the form with more concentrated sori: "The sori originate in two series near the lower part of the lateral veins; one series placed very near to the midvein, the other at some distance from it, and much more irregular in the disposition of its sori. Between these two series, and a little beyond the outer one, other sori are indiscriminately scattered". In 1846, Hooker considered *M. parkeri* conspecific with *M. rostrata*, but at the same time informally recognised var. *polycarpa*. The specimen he cited as var. *polycarpa* (*Hostmann* 1080: K000640369!, K000640370!, P00625600!, P00625601!) represents the form of *M. parkeri* with scattered sori (note: the pinna apex fragment in the envelope attached to K000640369 belongs to *M. scalaris*). Specimens of *M. parkeri* that have sori close to the midvein were also cited under *M. rostrata* (e.g., *Schomburgk* 18: K000640367!; *Schomburgk* 313: K000640365!). This set is heterogeneous, however. Reference is made to a Parker specimen, probably the one mentioned in the protologue of *M. parkeri*, which has sori near to the midvein. In addition, the set includes specimens we have identified as *M. scalaris* (*Schomburgk* 313: K000640366!, P00625300!), as well as Central American specimens that probably represent *M. elongata* (*Skinner* s.n. and *Cuming* 1126). We have not seen all the specimens, and therefore do not know if *M. rostrata* s.s. was included as well.

Our genetic data come mostly from the form of *M. parkeri* with scattered sori, but two specimens represent the form with sori close to the midvein. Unfortunately, we do not have genetic data from the form that includes the type specimen. Despite variation in soral arrangement, all our material was placed in the same clade, and this is genetically distinct from *M. scalaris*. Because the morphological variation among the forms of *M. parkeri* appears continuous, we have opted for a broad circumscription of *M. parkeri* until more genetic data become available to sort out the complex.

Metaxya rostrata *(Kunth) C.Presl* (Presl 1836: 60). Type: Venezuela, Javita, May 1800, *Bonpland & von Humboldt* 966, (B!) [B -W 19691 -01 0].

Polypodium rostratum Humb. & Bonpl. ex Willd. (Willdenow 1810: 193 – 194), **nom. illegit.** Later homonym of *Polypodium rostratum* Burm.f. (Burman 1768: 235).

Aspidium rostratum Kunth (1815: 12 – 13).

Polypodium humboldtii Poir. (Poiret 1816: 497), **nom. illegit**. Superfluous replacement name for *Polypodium rostratum* Humb. & Bonpl. ex Willd.

Alsophila rostrata (Kunth) Mart. (Martius 1828 – 1834: 64).

Amphidesmium rostratum (Kunth) J. Sm. in Bentham (1842: 201), **nom. nud.** The generic name *Amphidesmium* is a nomen nudum (Morton 1959) making this combination invalid.

Alsophila blechnoides Hook. (Hooker 1846: 35), **nom. illegit.** The name is superfluos because the type of *Aspidium rostratum* was included in the original protologue.

Leaves up to 2.3 m long, petiole 49 – 134 cm long, as long as or longer than the lamina, lamina 41 – 106 cm long. Pinnae 2 – 7 to a side, basal pinnae with a petiolule up to 1.1 cm long, uppermost lateral pinna sessile or decurrent basiscopically, attached to rachis by up to 1.3 cm; lateral pinnae oblong-elliptic to narrow-lanceolate, up to 21.6 – 43 cm long and 4 – 6 cm wide; terminal pinna 29 – 40.5 cm long and 4 – 6.2 cm wide; pinna texture herbaceous, margin paler than the rest of the lamina; pinna base oblique; pinna apex cuspidate to caudate, irregularly and coarsely dentate to almost entire with few teeth, sometimes slightly falcate. *Sori* (1 –)3 – 4(– 6) per vein, irregularly scattered over most of the abaxial surface of the lamina. Figs. 5E, 10.

DISTRIBUTION. *Metaxya rostrata* occurs in western to central Amazonia (Brazil, Colombia, Peru and Venezuela).

SPECIMENS EXAMINED. BRAZIL. Amazonas State: Rio Javari, behind Palmeiras army post, 5°8’S, 72°49’W, 1 Aug. 1973, *Lleras, Steward, Ongley, Coelho, Ramos & Lima* P16982 (INPA!, K!, MO, US!); Reserva Florestal Ducke, 2°53’S, 59°58’W, 14 March 1995, *Prado, Costa, Freitas & Nascimento* 577 (INPA!, K!, SP!, US!); Reserva Florestal Ducke, 2°53’S, 59°58’W, 1 Nov. 1994, *Ribeiro, Assunçao & Pereira* 1468 (INPA!, SP!); Presidente Figueiredo, 1°44’S, 59°17’W, 80 – 130 m, 05 Feb. 2008, *Tuomisto, Zuquim, Prado, Ruokolainen & de Souza* 15627 (TUR!, SP!, INPA!, NY!); Carauari, ca. 3 km north-east from the village of Novo Horizonte, Río Juruá, 5°02’S, 67°08’W, 90 m, 27 March 2012, *Tuomisto, Moulatlet, Ruokolainen, Emilio & Figueiredo* 15864 (SP!, TUR!); ca. 7 km north from the town of Itamarati, Río Juruá, 6°23’S, 68°16’W, 90 m, 10 April 2012, *Tuomisto, Moulatlet, Ruokolainen, Emilio & Figueiredo* 16136 (INPA!, SP!, TUR!); Itamarati, ca. 5 km north-west from the village of Nova Olinda, Jurua River, 6°26’S, 68°32’W, 120 – 140 m, 14 April 2012, *Tuomisto, Moulatlet, Ruokolainen, Emilio & Figueiredo* 16174 (SP!, TUR!, Z!); Eirunepé, ca. 3.5 km west from the village of Deixa Falar, Río Juruá, 6°41’S, 70°21’W, 160 – 180 m, 03 May 2012, *Tuomisto, Moulatlet, Ruokolainen, Emilio & Figueiredo* 16570 (SP!, TUR!, UC!). **COLOMBIA**. Amazonas Dept.: Río Caquetá, W of Río Metá and 4 km N of its confluence with Caquetá, 0°54’S, 71°37’W, 150 – 250 m, *Tuomisto, Ruokolainen & Duque* 12033 (COAH!, TUR!); Vaupés Dept.: Río Vaupes, 320 m, 7 – 8 Nov. 1952, *Humbert & Fernandez* 27270 (K!, P!, US!). **PERU**. Loreto Dept.: Rio Tigre, San Jacinto, 2°28’S, 75°47’W, 175 – 205 m, 10 June 1993, *Beltran & Foster* 523 (F!); Maynas, Estación Biológica Quebrada Blanco, 4°21'S, 73°09'W, 110 m, 18 Sept. 2010, *Cárdenas, Hartikainen & Cariajano* 1787 (AMAZ!, TUR!); Maynas, Mishana, 3°50'S, 73°30'W, 140 m, 18 Nov. 1981, *Ruiz & Murphy* 180 (K!, MO); Maynas, between the roads Ex Petroleros and Bello Horizonte, km 38 – 40 of the road Iquitos-Nauta, 4°4'S, 73°28'W, 100 – 200 m, 2 Aug. 1992, *Tuomisto, Ruokolainen, Sarmiento & Järvinen* 7117 (AMAZ, SP!, TUR!, USM, Z); Maynas, San Gerardo, km 13 of the road Iquitos-Nauta, 3°55'S, 73°22'W, 100 – 200 m, 14 Jan. 1995, *Tuomisto & Ruokolainen* 7232 (AMAZ, NY, SP!, TUR!, USM); Loreto, Río Pucacuro, 3°17'S, 74°59'W, 100 – 200 m, 13 Jan. 2005, *Tuomisto, Cárdenas, Higgins & Ruokolainen* 14117 (AAU, AMAZ, TUR!, UC, USM); Loreto, Río Tigre, 3°09'S, 75°17'W, 100 – 200 m, 23 Jan. 2005, *Tuomisto, Cárdenas, Higgins & Ruokolainen* 14527 (AMAZ, P!, TUR!, USM, Z!). **VENEZUELA**. Territorio Federal Amazonas [Amazonas State], Atures, May 1989, *Foldats & Velazco* 9542 (UC!); Amazonas State: Javita, May 1800, *Bonpland & von Humboldt* 966 (B!); Yavita, 128 m, 27 Jan. 1942, *Williams* 14012 (US!); Yavita, 128 m, 29 Jan. 1942, *Williams* 14057 (US!).

HABITAT. Terra firme rain forest; alt. 80 – 320 m.

CONSERVATION STATUS. Least Concern (LC) according to IUCN (2001) red list criteria. The species is widely distributed and apparently abundant.

ETYMOLOGY. Rostrata means "*provided with a long beak*" (Stearn 2004).

NOTES. *Metaxya rostrata* is characterized by having few pinnae (2 – 7 on each side) that are broad (4 – 6 cm) and have cuspidate to caudate pinna apices that are irregularly and coarsely dentate to almost entire with few teeth. Sori are scattered over most of the abaxial surface of the lamina, also along the midvein. *Metaxya lanosa* is most similar in general appearance, but has much thicker lamina texture and conspicuously cartilaginous margins. *Metaxya parkeri* differs clearly in having serrate pinna margins. The pinnae are generally much narrower, and there are more of them, in *M. contamanensis*, *M. elongata* and *M. scalaris*. In addition, *M. contamanensis* has narrow-lanceolate to narrow elliptic (rather than oblong-elliptic to narrow-oblanceolate) pinnae, and pinna apices are serrate in *M. elongata* and coarsely but regularly dentate in a step-wise manner in *M. scalaris* (rather than irregularly dentate).

After the segregation of the five other species of *Metaxya*, the distribution of *M. rostrata* s.s. has become limited from almost all Neotropics to the western and central parts of Amazonia.

Metaxya scalaris *Tuomisto & G.G.Cárdenas* **sp. nov.**

Type: French Guiana. Commune Roura. Réserve Naturelle Volontaire Trésor, 4°36’N, 52°16’W, 200 – 267 m, 20 Feb. 2003, *Christenhusz & Bollendorff* 2418 (holotype mounted on three sheets TUR-576502!, TUR-576503!, TUR-576504!; isotypes CAY, E).

Leaves up to 2 m long, petiole 46 – 112 cm long, as long as or longer than the lamina, lamina 45.5 – 87 cm long. Pinnae 7 – 14 to a side, basal pinnae with petiolule 0.5 – 1.1 cm long, uppermost lateral pinna decurrent basiscopically, attached to the rachis by up to 1.2 cm; lateral pinnae narrow-elliptic to narrow-oblanceolate, up to 19.5 – 26.7 cm long and 2.4 – 5.5 cm wide; terminal pinna 15 – 25 cm long and 2.2 – 3.5 cm wide; pinna texture slightly chartaceous, margin the same color as the rest of the lamina or slightly paler, entire but slightly undulating; pinna base oblique; pinna apex caudate to caudate-attenuate, dentate with a step-like profile to coarsely dentate-serrate, sometimes slightly falcate. *Sori* 1 (2 – 3) per vein, most of them in a dense line immediately next to the midvein, with few scattered less regularly 2 – 3 mm from the midvein, restricted to the basal 3/4 of the pinna. Figs. 5F, 11.

RECOGNITION. *Metaxya scalaris* is characterised by coarsely dentate pinna apices that have a step-like profile, by most of its sori being concentrated to one dense line along each side of the midvein, by narrow-elliptic to narrow-oblanceolate pinnae and by a relatively stiff lamina texture. In the other species, pinna apices are either serrate (*M. elongata*, *M. parkeri*) almost entire (*M. contamanensis*, *M. lanosa*) or irregularly dentate (*M. rostrata*). The other species also have either a sterile space without any sori along the midvein (*M. contamanensis*, *M. elongata*, *M. lanosa*, most *M. parkeri*) or, in *M. rostrata*, the sori along the midvein are a minority and most sori are scattered widely across the lamina and often more than 2 sori are borne on the same vein (rather than just 1). *Metaxya contamanensis* has a similar lamina texture than *M. scalaris*, whereas texture in *M. lanosa* is clearly thicker and in the other species clearly more herbaceous. *Metaxya lanosa* and *M. rostrata* have fewer pinnae (up to 7 on each side) than *M. scalaris* (7 – 14 on each side). *Metaxya scalaris* shares with *M. rostrata* the tendency towards narrow-oblanceolate pinnae, whereas pinnae in the other species are broadest at or below the middle.

DISTRIBUTION. *Metaxya scalaris* is found in the Guianas (French Guiana, Guyana, Suriname) and adjacent Brazil and Venezuela.

SPECIMENS EXAMINED. BRAZIL. Amazonas State: Rio Preto da Eva, 22 Jan. 2008, *Prado, Tuomisto, Ruokolainen, Zuquim & de Souza* 1806 (TUR!); Presidente Figueiredo, na margen da Rodovia AM-240, Presidente Figueiredo–Cachoeirinha, 2 Feb. 2008, *Prado, Tuomisto, Ruokolainen, Zuquim & de Souza* 1870 (SP!); Pará State: Tumuc Humac, 380 m, 1 Aug. 1972, *de Granville* 1065 (CAY!, P!, Z!); Brazil, State of Pará, Acará, 30 m, 18 July 1931, *Mexia* 5932 (MO, US!, Z!); Banks of Rio

Muirapiranga, 2°33 – 50'S, 50°38 – 50'W, 8 Oct. 1965, *Prance, Pennington & Silva* 1561 (K!, SP!, US!); Ilha de Marajó, Rio Anajás, 1°00'S, 50°10'W, 25 Oct. 1987, *Beck, Rabelo, Hennen & Siriacu* 197 (INPA!). **FRENCH GUIANA**. Cayenne Dist.: Commune Roura, Réserve Naturelle Volontaire Trésor, km 17 along Route Départementale 6, 4°36'N, 52°16'W, 200 – 267 m, 20 Feb. 2003, *Christenhusz & Bollendorff* 2418 (holotype TUR! 576502, 576503; isotypes CAY, E); Sur l'Orapu, 20 May 1977, *Cremers* 4822 (CAY!, P!, US!, Z!); 500 m, 29 Aug. 1980, *de Granville* 3676 (P!, Z!); Montagne de la Trinité, 350 m, 10 Jan. 1984, *de Granville, Berg, Jansen-Jacobs & van Setten 5823* (K!, Z!); Montagne de la Trinité, *de Granville, Berg, Jansen-Jacobs & Van Setten* 6256 (P!, US!, Z!); Mont Saint-Marcel, zone Sud-est du massif-, 2°23'N, 53°00'W, 300 m, 23 July 2002, *de Granville, Aliker, Sarthou* 15432 (B, CAY, P!, US!); Réserve Naturelle Nationale des Nouragues, 4°05'N, 52°40'W, 120 m, 3 Nov. 2013, *Lehtonen, Antonelli, Zizka, Bacon & Santamaria* 800 (CAY!, TUR!); National road RN2: km 122, 4°11'N, 52°08'W, 100 m, 15 Nov. 2013, *Lehtonen & Geniez* 844 (CAY!, TUR!); km 132, 4°08'N, 52°05'W, 70 m, 17 Nov. 2013, *Lehtonen & Geniez* 884 (CAY!, TUR!); km 173, 3°57'N, 51°52'W, 50 – 70 m, 21 Nov. 2013, *Lehtonen & Geniez* 945 (CAY!, TUR!); Mt. Grand Matoury, 4°52'N, 52°25'W, 255 m, 19 March 1985, *Skog, Feuillet, de Granville & Gradstein* 5649 (P!, US!). **GUYANA**. Cuyuni-Mazaruni Region: Pakaraima Mtns., 6°05'N, 60°21'W, 350 m, 31 July 1992, *Hoffman & Marco* 2241 (US!); Isseneru Creek, 6°26'N, 60°20'W, 99 m, 30 Nov. 2006, *Redden, Perry, Benjamin, Singh & Wilkie* 4930 (K!, US!); Potaro-Siparuni Region: Iwokrama Rainforet Reserve, Essequibo River, 4°26'N, 58°29'W, 70 – 80 m, 6 Oct. 1995, *Clarke* 374 (CAY!, MO, US!); Kurupukari village, 4°27'N, 58°47'W, 150 m, 19 May 1995, *Ehringhaus* 83 (CAY!, MO, US!); Siparuni River, 4°45'N, 59°01'W, 50 m, 26 April 1992, *Hoffman Pennington & Gharbarran*

1455 (K!, MO, P!); Upper Takutu-Upper Essequibo Region: Kanuku Mts., 3°21'N, 59°29' W, 140 – 320 m, 26 Nov. 1987, *Jansen-Jacobs, ter Welle, Görts-van Rijn & Ek* 1280 (CAY!, P!, Z!); Slopes of Mt. Makarapan, 3°59'N, 58°57'W, 250 m, 18 Sept. 1988, *Maas, Koek-N, Lall, ter Welle & Westra* 7524 (CAY!, K!, MO, Z!); Upper Demerara-Berbice Region, 5°20'N, 58°40'W, 150 – 200 m, 3 June 1986, *Pipoly* 7512 (CAY!, P!). **SURINAME**. Brokopondo Dist.: Brownsberg Nature Park, 4°57'N, 55°11'W, 400 – 500 m, 5 Mar. 2003, *Christenhusz & Bollendorff* 2559 (TUR!); Marowijne Dist. Lely Mots., 4.16°N, 54.44°W, 650 – 670 m, 21 Nov. 2004, *Jansen-Jacobs, Ramharakh, Haripersaud, et al*. 6640 (P!); Sipaliwini Dist.: Tafelberg, trail from Caiman camp to tepui summit, 3°53'N, 56°10'W, 855 m, 19 Aug. 2013, *Aguirre-Santoro & Michelangeli* 1881 (NY!); Saut Paloulou Icholi – Basin du haut-Maroni, 2°42'N, 54°16'W, 150 m, 9 Sept. 1994, *de Granville* 12534 (CAY!, P!, US!); Kappelsavanna, 15 Feb. 1961, *Kramer, Hekking & Tryon* 5651 (P!, US!). **VENEZUELA**. Bolivar State, Región de Canaima, 6°16'N, 62°46'W, 17 Feb. 1964, *Agostini* 332 (K!).

HABITAT. Terra firme tropical rain forest; alt. 50 – 500 m.

CONSERVATION STATUS. Least Concern (LC) according to IUCN (2001) red list criteria. The species is widely distributed and abundant.

ETYMOLOGY. *Metaxya scalaris* is named after the coarsely dentate pinna apices, which have a profile resembling steps of stairs.

NOTES. The typical *M. scalaris* is easy to recognise by the combination of step-like dentations in pinna apices and the sori being mostly arranged in one line along the midvein. However, there is gradual variation in both of these characteristics towards the condition seen in *M. parkeri* (serrate pinna apices and more widely scattered sori). As a result, we have seen many specimens that are intermediate between the two. It is possible that the two hybridise, in which case the gradual variation could be indication of a hybrid swarm. We are confident that at least two species are involved, because our molecular data indicate that typical *M. scalaris* is genetically distinct from the *M. parkeri* we have sequenced, and these do not even have a sister relationship. We have opted to circumscribe *M. scalaris* relatively narrowly to keep it morphologically uniform, which has rendered *M. parkeri* rather variable. More data are needed to clarify the limit between these two species.

Acknowledgments

We thank K, SP, US and Z for access to their physical collections, COL, NY, UC and Z for scanning specimens on request and the following herbaria for online access to their collections: AAU, B, CAY, COL, GH, HUEFS, INPA, K, MO, NY, P, SP and UC. We thank Jefferson Prado, Robbin C. Moran, Michael Kessler, Alan R. Smith and Michel Boudrie for information on additional specimens, Alan R. Smith, Maarten Christenhusz, Rafaël Govaerts and Irina Belyaeva for comments on nomenclature and taxonomic literature, Nelly Llerena for making the illustrations, Mirkka Jones for linguistic comments, Mikael Kukkonen for scanning specimens and Servicios de biodiversidad (http://serviciosdebiodiversidad.com/web/) for support.

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Figure legends.

Map 1. Geographical distribution of *Metaxya* species.

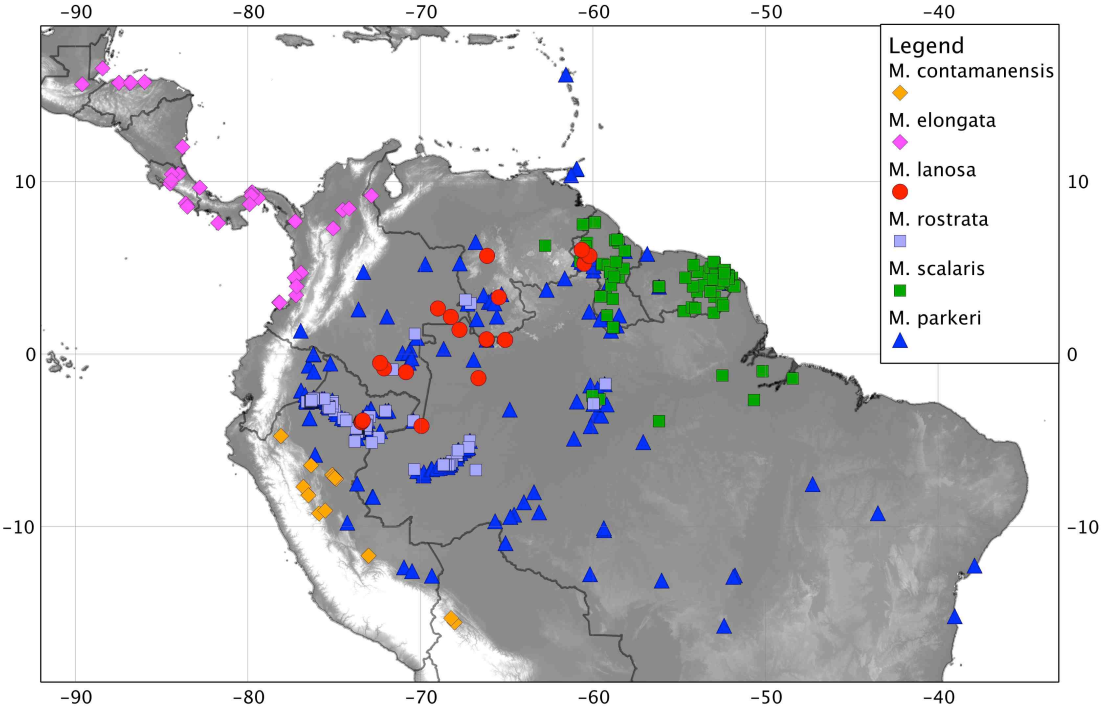


Fig. 1. Pinna apex of the six *Metaxya* species. A *Metaxya contamanensis*, B *Metaxya elongata*, C *Metaxya lanosa*, D *Metaxya parkeri*, E1 *Metaxya rostrata* (almost entire), E2 *Metaxya rostrata* (irregularly and coarsely dentate), F *Metaxya scalaris*. Scale bar = 1 cm.

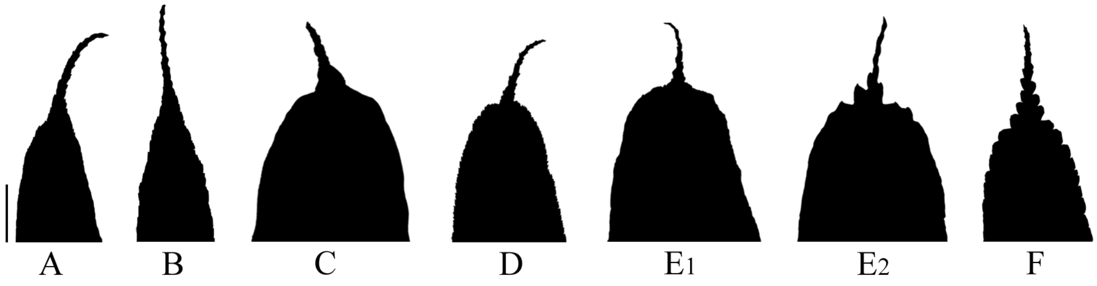


Fig. 2. Medial part of a pinna of the six *Metaxya* species showing soral arrangement. A. *Metaxya contamanensis*, B *Metaxya elongata*, C *Metaxya lanosa*, D1 *Metaxya parkeri* ('broad'), D2 *Metaxya parkeri* ('narrow'), E *Metaxya rostrata*, F *Metaxya scalaris*. Scale bar = 1 cm.

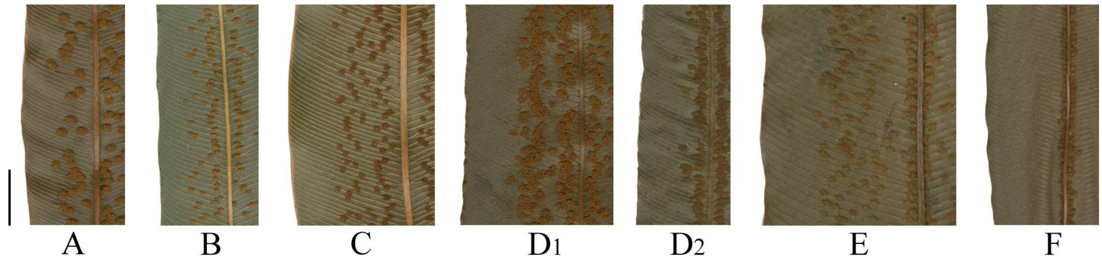


Fig. 3. Maximum likelihood phylogram of combined *Metaxya* data. The small grey tree shows the original proportions of the phylogram, the large tree focuses on the crown groups. Numbers above the nodes are ML bootstrap support / Bayesian posterior probabilities. The results from POY sensitivity analyses are illustrated as sensitivity boxes; black box indicates that the node was present in the most parsimonious tree obtained under the corresponding parameter values, white box indicates that the node was not present.

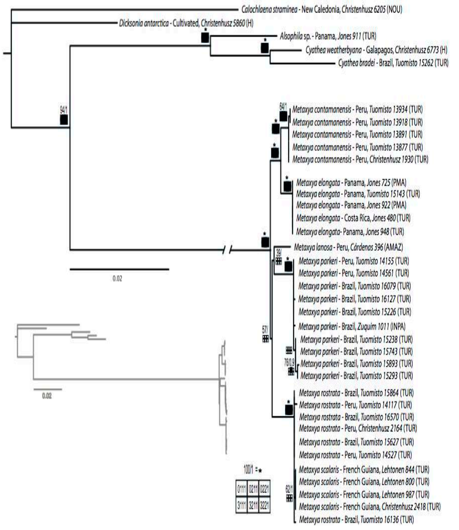


Fig. 4. Distribution of four Amazonian *Metaxya* species along gradients of soil cation and aluminium concentration.

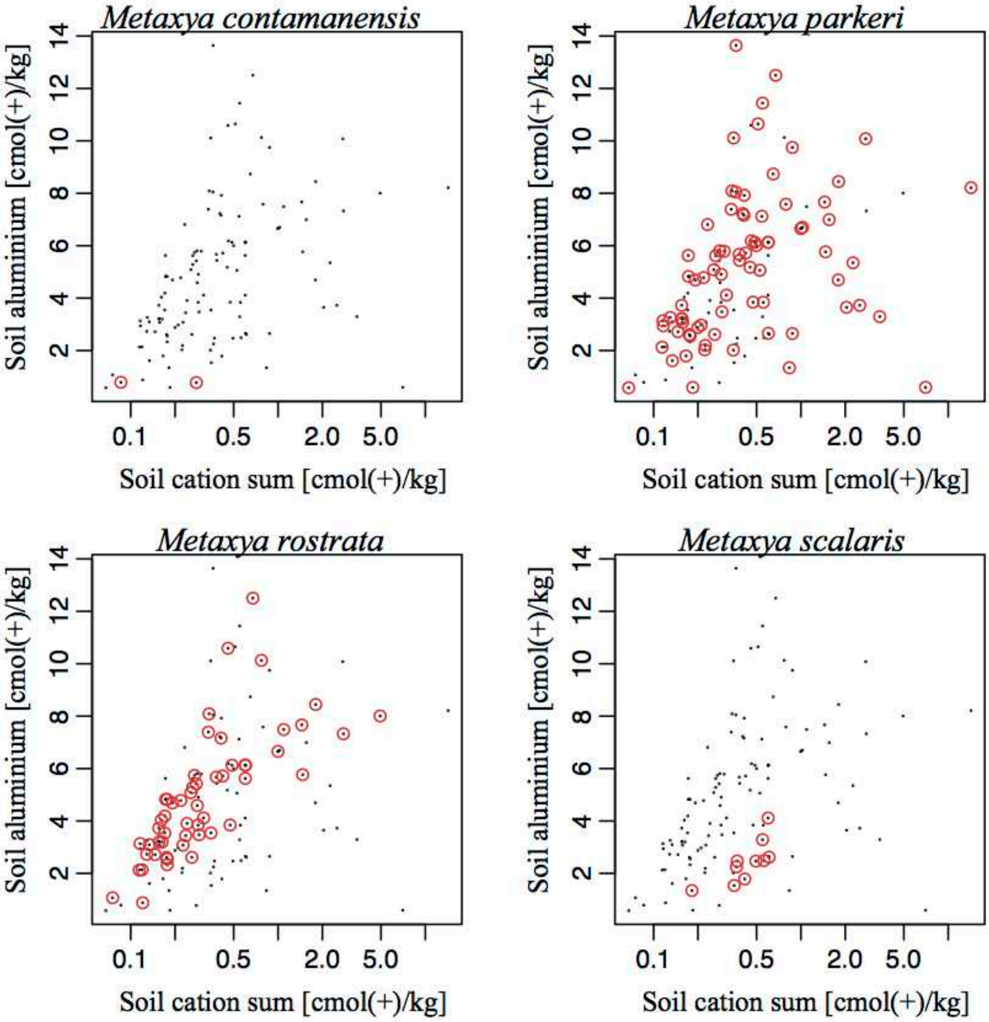


Fig. 5. *Metaxya* species in the field. A. *Metaxya contamanensis*, B *Metaxya elongata*, C *Metaxya lanosa*, D *Metaxya parkeri*, E *Metaxya rostrata*, F *Metaxya scalaris*. PHOTOS A – E: HANNA TUOMISTO, F: SAMULI LEHTONEN.

Fig. 6. *Metaxya contamanensis*. A adult, B1-B3 juveniles, C pinna apex. Drawn by Nelly Llerena.

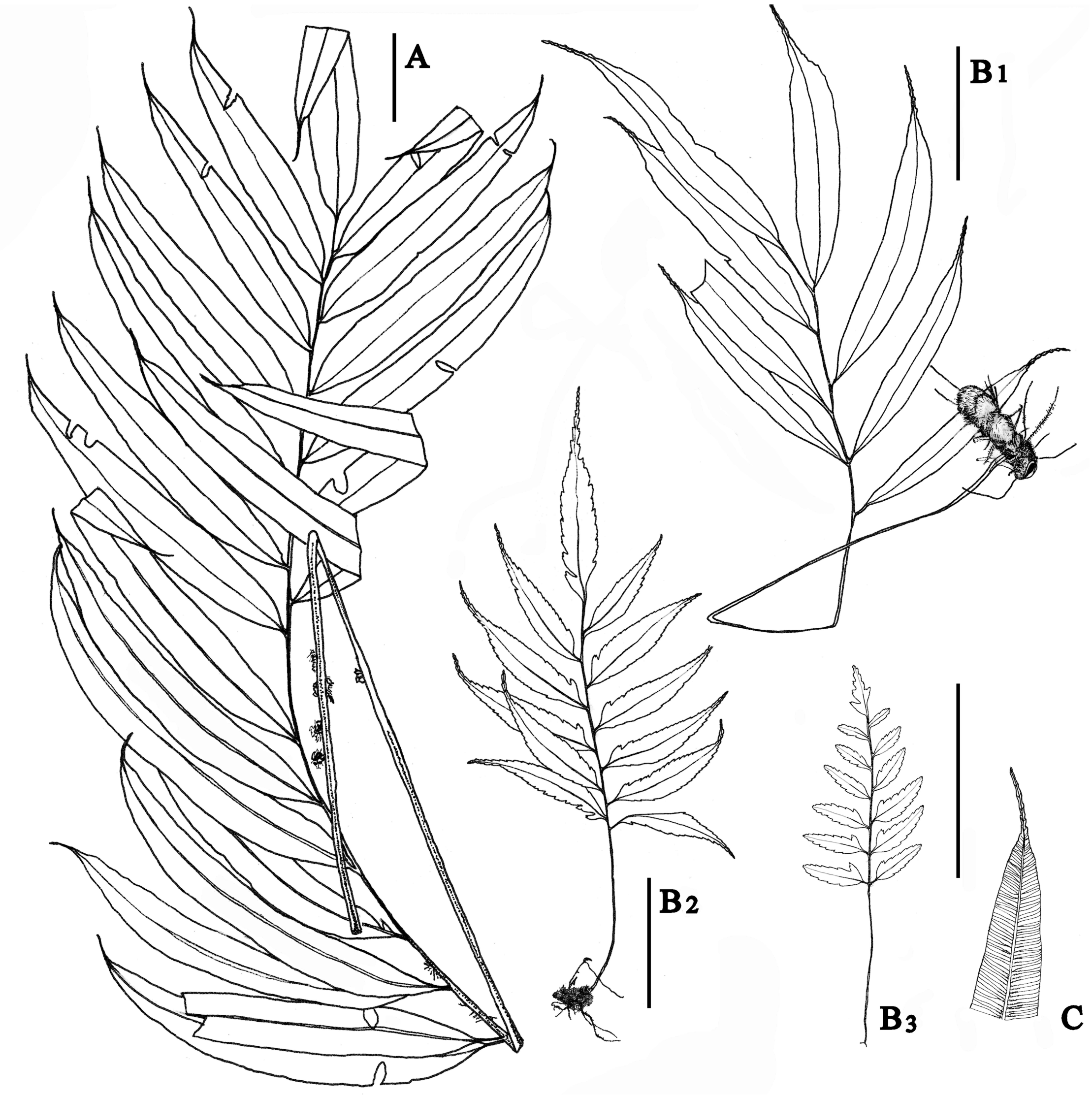


Fig. 7. *Metaxya elongata*. A adult, B1-B2 juveniles, C pinna apex. Drawn by Nelly Llerena.

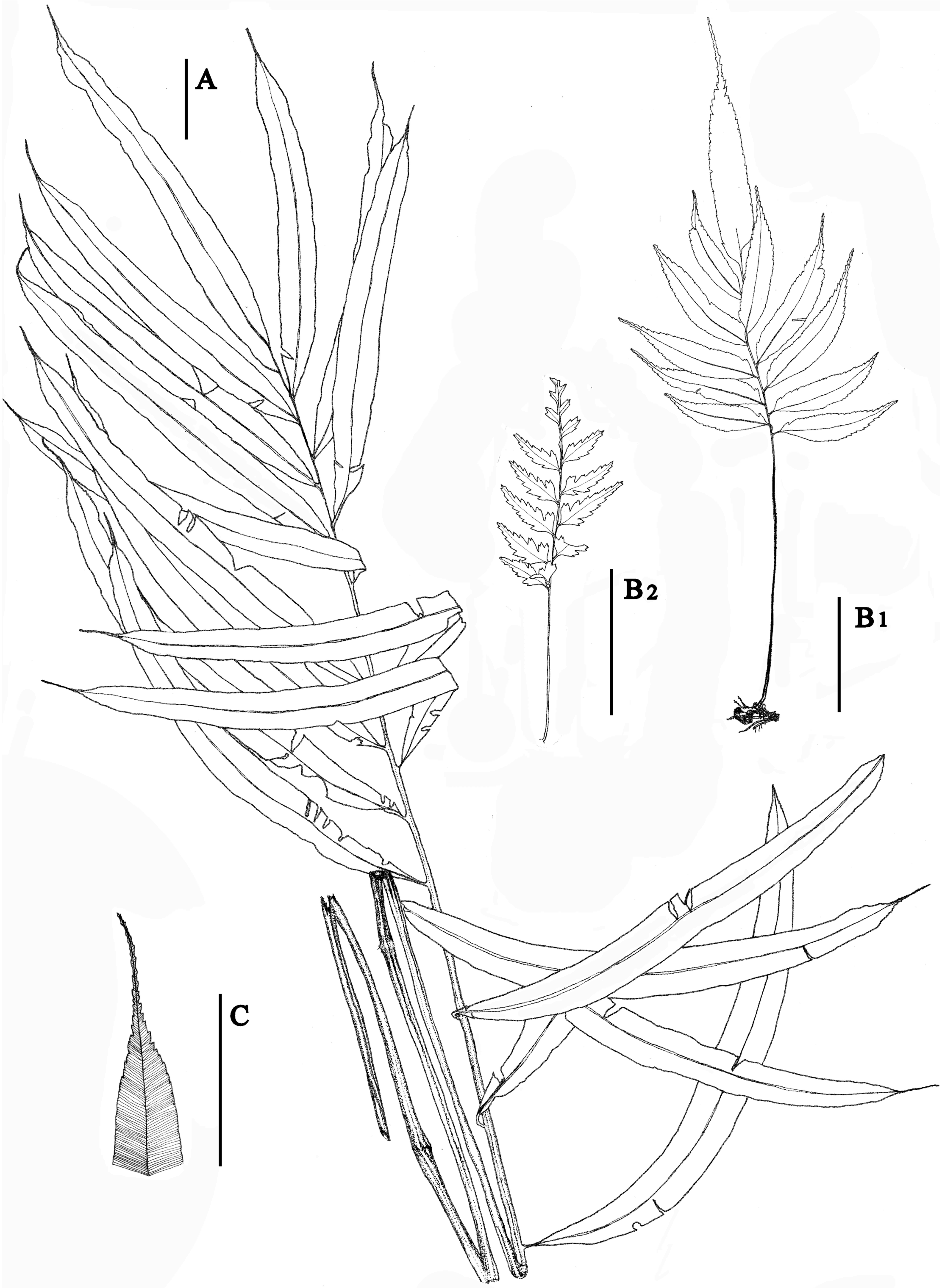


Fig. 8. *Metaxya lanosa*. A adult, B1-B2 juveniles, C pinna apex. Drawn by Nelly Llerena.

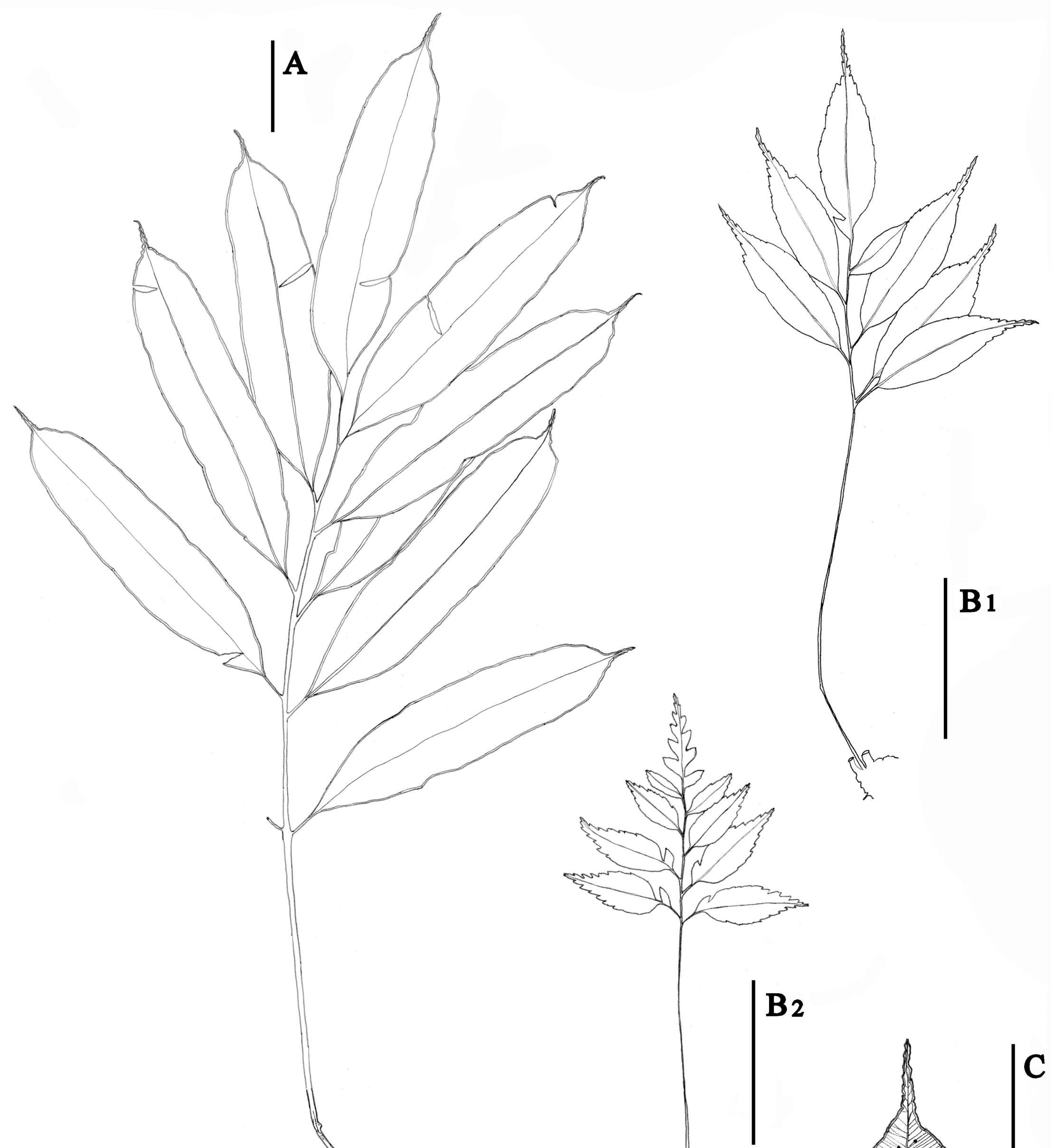


Fig. 9. *Metaxya parkeri*. A adult, B1-B2 juveniles, C pinna apex. Drawn by Nelly Llerena.

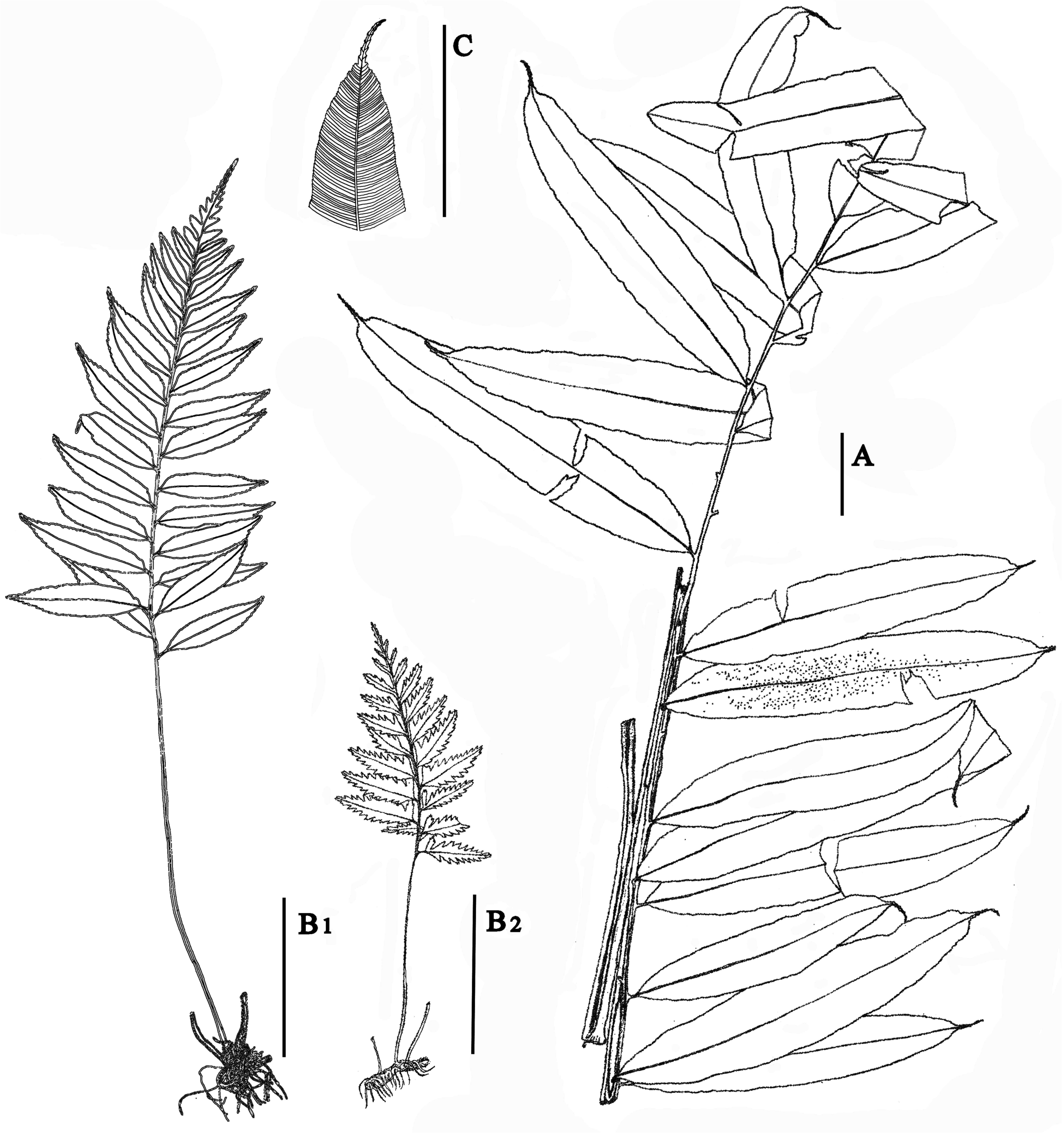


Fig. 10. *Metaxya rostrata*. A adult, B1-B2 juveniles, C pinna apex. Drawn by Nelly Llerena.

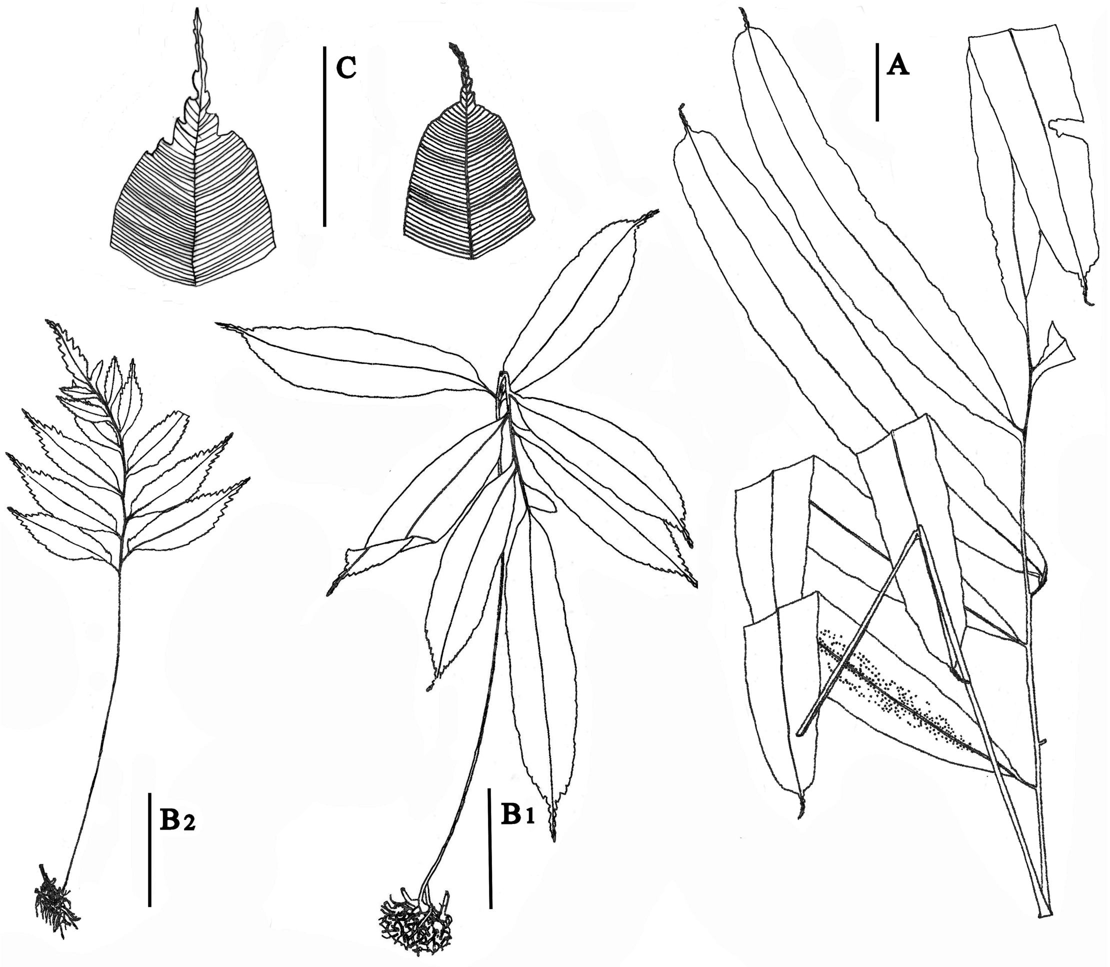
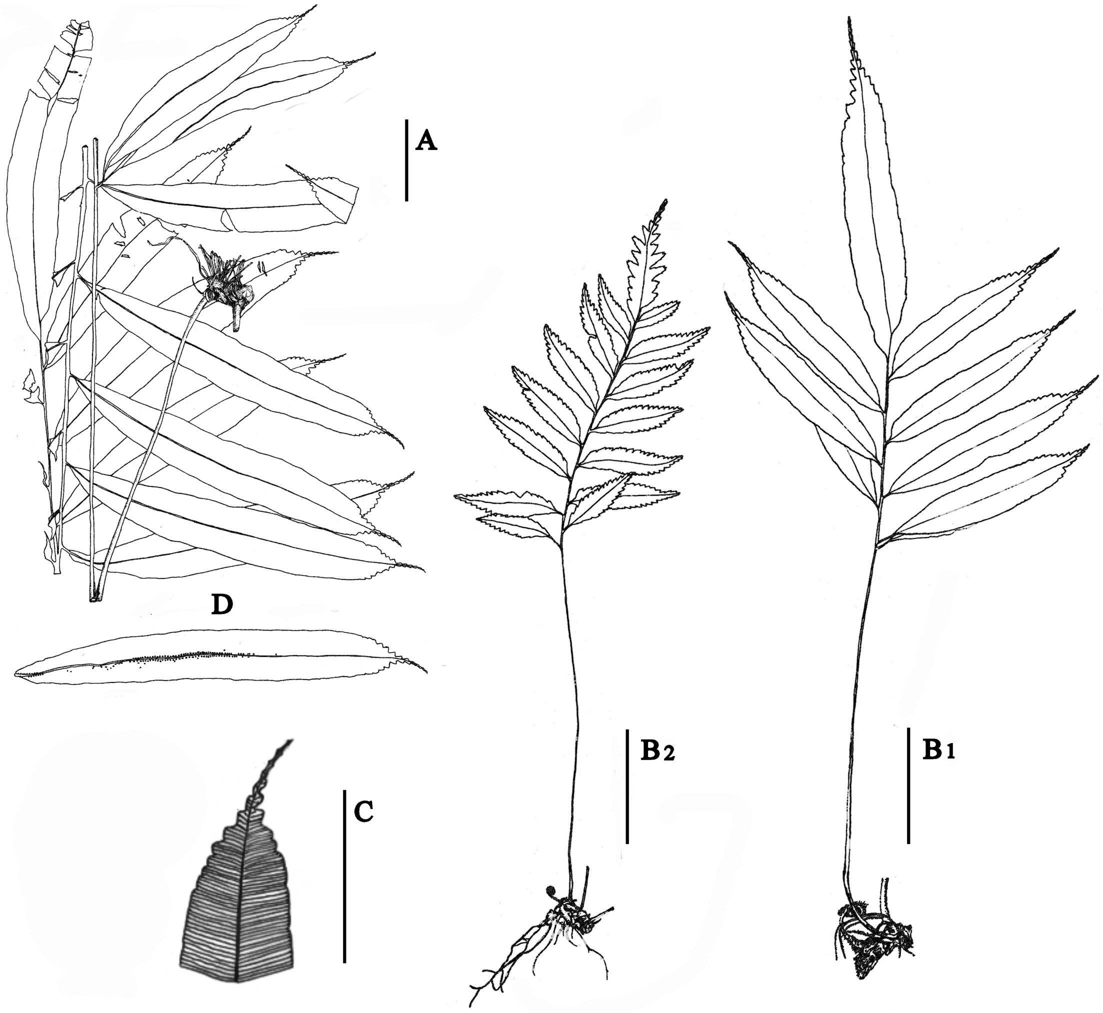


Fig. 11. *Metaxya scalaris*. A adult, B1-B2 juveniles, C pinna apex, D fertile pinna.

Drawn by Nelly Llerena.



KEW BULLETIN (2016) 71: 49
DOI 10.1007/S12225-016-9661-6

ISSN: 0075-5974 (print)
ISSN: 1874-933X (electronic)

Erratum to: Newly discovered diversity in the tropical fern genus *Metaxya* based on morphology and molecular phylogenetic analyses

Glenda G. Cárdenas[1], **Hanna Tuomisto**[1] **& Samuli Lehtonen**[1]

Erratum to: KEW BULLETIN (2016) 71: 5
DOI 10.1007/S12225–016–9618–9

The original version of this article unfortunately contains an error in Fig. 5 whereby the caption mismatches the images. The correct version of the caption is presented below:

Fig. 5. *Metaxya* species in the field. **A** *M. lanosa*; **B** *M. elongata*; **C** *M. rostrata*; **D** *M. parkeri*; **E** *M. contamanensis*; **F** *M. scalaris*. PHOTOS: **A – E** HANNA TUOMISTO, **F** SAMULI LEHTONEN.

Accepted for publication 12 August 2016.

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