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Pagamea Aubl. (Rubiaceae), from species to processes, building the bridge

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How long
Do works endure? As long
As they are not completed.
Since as long as they demand effort
They do not decay.

Inviting further work
Repaying participation
Their being lasts as long as
They invite and reward.

Useful works
Require people
Artistic works
Have room for art
Wise works
Require wisdom
Those devised for completeness
Show gaps
The long-lasting
Are always about to crumble
Those planned on a really big scale
Are unfinished.

Still imperfect
Like a wall waiting for ivy
(It was once unfinished
Long ago, before the ivy came; bare)

Still short lived
Like a machine that is used
But not good enough
But gives the promise of a better model
Work for endurance must
Be built like
A machine full of shortcomings.
...

from “About the Way to Construct Enduring Works”
B. Brecht

ABSTRACT

Species delimitation have a great impact in scientific, environmental and other human activities, and is fundamental for understanding evolution. Plant species are usually delimited based on morphology and rarely species concepts are stated and analysis of variation made explicit. Botanists do see species as “segments of evolutionary lineages”, but reproductive isolation is rarely addressed. Yet, reproductive isolation is necessary for understanding species, because speciation is the process of acquiring reproductive barriers. Almost any lineage will have species at different stages of isolation, and a single type of data will be insufficient for species delimitation. In plants, other biological processes such as hybridization, selfing and apomixis, make our search for species more challenging. If one focus on sympatry, reproductive isolation can be inferred, even if species are then defined only locally. If in a single locality putative species are distinct, then they must be reproductively isolated. Here, I first combine molecular phylogenetics (chloroplast and ITS), multivariate analyses of morphology, and sympatry for inferring reproductive isolation and delimiting species in *Pagamea*, a plant lineage from Tropical South America. I then used phylogenetic estimates of relationships to gain insights into the tempo and mode of speciation in this lineage. The results suggest 29 species in *Pagamea*. These include monophyletic and paraphyletic species, sympatric but cryptic species, and species that can be recognized only in a local sense. The ITS phylogeny best describes patterns of morphological, ecological and geographical variation, and the chloroplast shows a pattern consistent with the differential sorting of ancestral polymorphisms. *Pagamea* started diversifying ~ 10 million year ago and all speciation events took place before the Pleistocene (>1.5 million years). Data exploration suggests peripatric speciation as the predominant mode in *Pagamea*, in agreement with the island-like distribution of its specific habitat (white-sand systems). *Pagamea* diversified along environmental gradients related to both flooding and altitude, with altitudinal shifts being phylogenetically more conserved than shifts for flooding levels. Eight new species of *Pagamea* are recognized and novel species circumscriptions are made. Hypothesis of species and intraspecific patterns of variation are also made explicit, and several interesting evolutionary scenarios emerge.

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CHAPTER 1

Combining phylogenetics, phenetics and the sympatry criterion for delimiting species in *Pagamea* Aubl. (Rubiaceae)

INTRODUCTION

Most species concepts agree that, in sexually reproducing organisms, species may be recognized as discrete, reproductively isolated groups occurring in sympatry (Coyne and Orr 2004). Coyne and Orr's (2004) version of the Biological Species Concept (Mayr 1942) focuses on "substantial" reproductive isolation and sympatry and is perhaps the best suited for the practice of species delimitation. The focus on reproductive isolation is important because speciation is the continuous process of acquiring reproductive barriers. This process of differentiation may be initiated in different ways, and we may recognize different "kinds" of species as speciation proceed (see de Queiroz 1998). Ultimately, reproductive isolation is required for species to be independent evolutionary lineages. Allowing flexibility in the reproductive isolation criterium ("substantial") is a practical necessity, precisely because in any group we study species may be in different stages of differentiation. Furthermore, the search for reproductive barriers will allow understanding of speciation. From a practical perspective, sympatry is central for the recognition of species (Coyne and Orr 2004). If in a single locality species are kept distinct, then they must somehow be reproductively isolated. The so called "ring-species" are the best example of the importance of sympatry: a lineage may comprise two reproductively isolated species in the region where they are sympatric, but these are interconnected by gene flow through a series of allopatric or parapatric populations (Irwin et al. 2001a, 2001b, 2005).

Plant species are generally delimited mainly on the basis of morphology (MacDade 1995), but there is rarely any explicit analysis of morphological variation (Rieseberg et al. 2006). Furthermore, reproductive isolation between such clusters is rarely addressed (MacDade 1995; Rieseberg et al. 2006). The use of statistical procedures for the identification of morphological clusters are also rare (Coyne and Orr 2004), despite their potential for species delimitation, particularly when used in a nested geographical fashion (e.g. Coronado 2003). These approaches have usually been applied to the understanding of problematic groups, such as species complexes and hybrids (Henderson 2006), or for confirming the existence of *a priori* defined groups using techniques such as discriminant analysis (Rieseberg et al. 2006). Few studies of tropical plants have used phenetic analyses to understand species (but see Henderson 2005; Poulsen and Nordal 2005), and these usually fail to address the issue of reproductive isolation by taking into consideration the sympatry criterion. Morphologically distinct groups at a particular site may merge in morphological space when samples are taken from different localities. Species delimitation may be biased by human neurological processes (Mishler and Donoghue 1982; Ridley 1996), which may result in both over- or under-differentiation, depending on the circumstances (Stevens 1996, Rieseberg et al. 2006), especially when species differences are based on few characters. By failing to make explicit the existence of phenotypic groups and the inference of reproductive isolation, the nature (biological reality) of species remains elusive in many plant groups.

Molecular data, generally in the form of DNA sequences, have permitted new approaches for species delimitation, especially when combined with other kinds of data (e.g., Hardig *et al*. 2000; Matos and Schaal 2000; McGowen *et al*. 2001; Borba *et al.* 2002; Lefebure et al. 2006). Pons et al. (2006) combined a birth model of lineage diversification with coalescent theory to determine with DNA sequences the transition point between species- (phylogenetic) and population- (tokogenetic) level evolutionary processes. However, despite its attractiveness, such an approach depends on large datasets which may be limiting when studying large clades from poorly collected regions. Moreover, finding genetic variation in species-level studies of plants has not been easy (but see Shaw et al. 2005; Hughes et al. 2006), and plant species are known to hybridize, requiring different genetic markers to understand boundaries between them, or lack thereof. It is also unlikely, given the continuous nature of evolution, that a single kind of data will suffice for species delimitation, or that researches will not have to make qualitative judgments when delimiting species (Sites and Marshall 2004). However, phylogenetic data may help in identifying species boundaries, even when sampling is not extensive. The observation of phylogenetically unrelated clades in sympatry may indicate reproductive isolation, even in the absence of phenotypic differences (i.e. cryptic species). This may be more complicated in plants, given the potential for hybridization, but if one combines markers with different modes of inheritance (chloroplast and nuclear genes), sympatry of clades that are unrelated according to both these makers may support the hypothesis of reproductive isolation. On the other hand, incongruence between markers may help understand, or at least identify, cases when hybridization may have occurred (e.g., Soltis et al. 1996; Hardig et al. 2000). There is great potential, currently poorly explored, to recognize species by combining phylogenetics with phenetics in an explicit geographical context (see also Grant 2003).

Pagamea Aubl. is a clade of edaphically specialized species that occurs only in white-sand (sandstone) habitats throughout tropical South America. It is sister to the paleotropical *Gaertnera* Lam., a relationship supported by morphology (both have sheathing stipules and a secondarily superior ovary), wood anatomy, pollen (Jansen *et al.* 1996, Igersheim *et al.* 1994), and more recently by molecular data (Andersson and Rova 1999, Bremer and Manen 2000, Malcomber 2002). The divergence between *Gaertnera* and *Pagamea* is estimated to have occurred in the Miocene (~ 10 my ago), since which time *Gaertnera* has undergone rapid radiation (Malcomber 2002). Molecular data support the monophyly of *Gaertnera* (Malcomber 2002), but the monophyly of *Pagamea* has previously been merely inferred because of its geographical isolation, since there are no obvious morphological apomorphies supporting it, and molecular data were still lacking.

Species of *Pagamea* are found only in scrublands and low forests characteristic of oligotrophic (sandy) and usually temporarily flooded substrates, which have island-like distributions throughout tropical South America (Berry *et al.* 1995; Huber 1995; Kubitzki 1990; Prance 1996; Steyermark 1986). Previous studies have recognized 24 species (Taylor 1996; Steyermark 1974), but there are 32 specific and 13 infra-specific names for specimens of this genus. Most recognized species are from the lowlands, but the genus is also found at high altitudes (up to 2500 m.a.s.l.) in both the Guayana Shield and the Andes in Peru and Ecuador. Morphological variation in *Pagamea* is mostly quantitative and overlapping, which makes it essential to use statistical procedures to understand morphological grouping. *Pagamea* has been well studied only for the Venezuelan Guayana region (Steyermark 1974; Vicentini and Steyermark 2004). Even then, species seem to be poorly delimited and too many have been recognized; most of the high-altitude species are endemic and isolated on separate tepuis. Steyermark (1965, 1974) also described several 'varieties' and even 'forms' within two widespread lowland species. Not only are species poorly delimited in *Pagamea,* but the question of their reproductive isolation has not been addressed.

Here, I present phylogenetic hypotheses for *Pagamea* using both nuclear (*ITS*) and chloroplast (*rps16* intron and *rpl20-rps12* spacer) markers. I first assess support and congruence among these datasets. I then analyze the morphological variation in the context of individual and combined phylogenetic hypotheses, to understand the morphological similarities and distinctions between and among clades. Decisions on species limits are then made in the context of phylogenetic and phenetic patterns that are analyzed in a geographical context.

METHODS

Sampling

Herbarium specimens of *Pagamea* were initially sorted into morphotypes (see also Morphological analyses). Subsequent fieldwork was directed towards collecting leaf material of as many morphotypes as possible, and attempting to cover the whole geographical range of the genus. Preference for inclusion in the molecular dataset was given to individuals from morphotypes that were found in sympatry, but to test for species monophyly, whenever possible, individuals from the extreme of the geographical range of morphotype were selected for inclusion. Samples for morphotypes endemic to the Venezuelan Guayana and from a few other localities were extracted from herbarium material.

DNA extraction, PCR & sequencing

DNA was extracted from silica-gel dried leaf material or from herbarium material. Total DNA was extracted using a mini-scale CTAB protocol (Doyle and Doyle, 1987), with addition of 2-3 % polyvinylpyrrolidone (PVP). High concentration extracts were obtained only when leaf material was grinded using FastPrep® (BIO 101® Systems, Qbiogene, Inc., Vista, California, USA). DNA extractions from herbarium specimens never yielded high quality extractions.

25 µl PCR reactions contained: 2.5 µl of 10X reaction buffer, 2.5 µl of 25mM $MgCl_2$, 1.5 µl dNTP (10 mM solution), 1.5 µl of each primer (10 mM solutions), 1.5 µl BSA, 1.5 µl of undiluted DNA extraction (20-80 ng/µl ; or 0.25 of undiluted PCR product in the case of nested PCRs, see below) and 0.25 µl of *Taq* polymerase (Promega, Madison, Wisconsin, USA). For the nuclear ITS regions 0.5 µl of 100% dimethyl sulfoxide (DMSO) was added to the reaction (see Buckler *et al*. 1997). The reactions were initially denatured for 2 min at 95° C, followed by 34-39 cycles of 30 sec at 95° C, 1 min at 55-62° C (according to primer Tm) and 90 sec at 72°C, with a final 10 min extension at 72° C. All primers designed for this study were selected using PrimaClade (Gadberry *et al*. 2005).

Two non-coding regions of the chloroplast were amplified. The first intron of the ribosomal protein S16 gene, *rps16_intron1* was amplified using primers rps16Exon1R (5' GTG GTA GAA AGC AAC GTG CGA CTT-3') and rps16Exon2F (5' TCG GGAT CGA ACA TCA ATT GCA AC-3') from Oxelman (1997). The *rpl20-rps12* intergenic spacer was amplified using primers rpl20F (5' TTT GTT CTA CGT CTC CGA GC 3') and 5'rps12R (5' GTC GAG GAA CAT GTA CTA GG 3') from Hamilton (1999). For samples with poor quality DNA I used a nested PCR approach for both markers. Nested primers rps16-nestedF (5' TCC ATT GTG GAT TCT TTC TTT TAT C 3'), rps16-nestedR (5' AGT TTT MTC CTC GTA CGG CTC 3'), rpl20-nestedF (5' CCC CGT CTA ATY CTA GTC RTTG 3') and rpl20-nestedR (5' TAG GGK GTA TGC GCG

ACTC 3') were designed based on an alignment containing sequences of two species of *Pagamea* and and two of *Gaertnera*.

Several putative low copy nuclear genes were surveyed for variation in pilot studies: *G3pdh* (Olsen 1999), *Tpi* (Strand et al. 1997), *PepC_small* (Malcomber 2002), *Met* (Chiang et al. 2002). However, for most of these markers there was either low variation or amplification was problematic. Additional putative low copy nuclear genes were amplified with primers designed to target intron-rich regions of Conserved Ortholog Regions (COS, http://www.sgn.cornell.edu/markers/cos_markers.pl) using Solanaceae and *Arabidopsis* sequences (*Arabidopsis* sequences from TAIR http://www.arabidopsis.org/). Unfortunately none of the 12 markers that were tested had sufficient variation or, if variable, they did not represent single copy genes (list of intron-rich markers are available at http://www.umsl.edu/services/kellogg/links.html). Therefore, to obtain a nuclear estimate of phylogeny, the entire ITS1 - 5.8S gene -ITS2 region was amplified. Despite possible problems related to its large number of copies and lack of concerted evolution (Alvarez and Wendel 2003), ITS is still one of the most variable and widely used nuclear markers for species-level studies of plants. A pilot study using primers itsleu1 (5'-GTC CAC TGA ACC TTA TCA TTT AG-3') and its4 (5'-TCC TTC CGC TTA TTG ATA TG C-3'; see Malcomber 2002), revealed the presence of pseudo-copies of ITS, i.e. clones that were clearly not under concerted evolution since they predated the split between *Pagamea and Gaertnera*. Thus the following approach was taken to amplify the ITS region. The pilot dataset, including sequences of *Pagamea* and *Gaertnera* (Malcomber 2002), were aligned using BlastAlign 1.1 (Belshaw and Katzourakis 2005). This program identifies conserved regions among sequences by blasting all sequences against each other and producing an output alignment in which only the conserved regions are included. While the 5.8S gene was present in all sequences in the output file of BlastAlign, the entire ITS1 and ITS2 regions were missing for some *Pagamea* clones. These were considered pseudogenes and were excluded. These clones had different sequences at the 5' end of ITS1 and the 3' end of ITS2. The clones for which BlastAlign kept ITS1 and ITS2 were used to design new primers, and included sequences of both *Gaertnera* and *Pagamea*. All subsequent sequencing were performed using specific primers itspag1F (5' CTG CGG AAG GAT CAT TGT C 3') and itspag4R (5' GTA ATC CCG CCT GAC CTG G 3').

PCR products for all gene regions were purified using the QIAquick Gel extraction kit (Qiagen, Valencia, California, USA). Purified PCR fragments were cloned using pGEM-T vectors (Promega Corp.). The chloroplast markers were also cloned because of the presence of homopolymeric regions in both markers, which made direct sequencing difficult. For the chloroplast, only a single clone per PCR product was sequenced. For the nuclear regions from 2-5 clones per PCR were sequenced to investigate the possibility of paralogy. Plasmid DNA was cleaned using the QIAprep Spin Miniprep Kit (Qiagen, Valencia, California, USA).

Sequencing reactions were conducted either in house using BigDye and analyzed on ABI 377 automated DNA sequencer (both from Applied Biosystems, Foster

City, CA, USA), or plasmid products were sent for sequencing at Macrogen Inc. (Seoul, Korea). For cloned material double stranded sequences were obtained using plasmid primers T7 and SP6. For some accessions of both chloroplast markers it was necessary to use internal primers to obtain double stranded sequences. Internal primers used for the *rps16* intron1 were 364F (5'-CGGGAATCAATCGTTCGTAAG-3') and 653R (5'-GGTTTCGATTCCTTCGGTGC-3'), and for the *rpl20-rps12* intergenic spacer were 441F (5' TAGTTCATCCTTTTTGGCTC-3') and 572R (5'-GGGTCAACTACTCAGGTAATTTTC-3'). Double stranded sequences (> 80% overlap) were then assembled using Seqman version 4.00 (DNASTAR Inc., Madison, WI)

Alignment

Alignments were initially performed using Clustal W (Thompson *et al*. 1994) and then manipulated using Se-Al v2.0a11 (Rambaut 1996). In the ITS there was one C+indel-rich region where alignment was ambiguous. This region comprising 10 to 19 base pairs was excluded. Both chloroplast markers had also regions consisting of motifs or homopolymeric repeats of variable length that were impossible to align and were also excluded.

Phylogenetic analyses

The individual and combined datasets were analyzed using maximum parsimony (MP), maximum likelihood (ML) and Bayesian approaches. Analyses were implemented using PAUP* 4.0b10 (Swofford 2003) and MrBayes 3.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003), and were run on a Beowulf-class cluster computer at the University of Missouri-Saint Louis. The ITS dataset was analyzed with gaps always treated as missing data. For both chloroplast markers, MP analyses were performed both, by treating gaps as missing data and by including the unambiguously aligned indels as single binary characters. Unless otherwise specified, MP analyses were heuristic searches with constant characters excluded, 1000 random sequence additions, TBR branch swapping, and MAXTREES set to 10.000 trees. Support for branches from MP analyses was assessed with bootstrapping (1000 replicates) with the same conditions except that MAXTREEs was set to 500. Maximum likelihood analyses consisted of heuristic searches with TBR branch swapping, random sequence addition, and support was assessed with bootstrapping (100 replicates). The model of nucleotide substitution was selected for each DNA partition using the AIC criterion with Modeltest 3.04 (Posada and Crandall 1998). The best fit model for both chloroplast partitions was the TrN+G, whereas for the TIM+G model was the best fit for the ITS partition. Bayesian analyses consisted of 2 parallel runs, each with 4 simultaneous chains. The model of evolution for Bayesian analyses was selected with MrModeltest 2.01 (Nylander 2004). The GTR+G model as the best fit model for all partitions. Markov chains were run for

Table 1. Description of characters used in multivariate analyses.

Label	Type	Description
LEAFLEN	mm	Average leaf length
LEAFWID	mm	Average leaf width
PETIOLEN	mm	Average petiole length
VENADENS	ratio	Average venation density (number of secondary veins/lamina length)
DOMADENS	ratio	Average domatia densisty (number of domatia)/(number of veins)
LFSHAPE1	ratio	Average (lamina length to maximum width)/ (lamina length)
LFSHAPE2	ratio	Average (lamina width)/(lamina length)
LFSHAPE3	ratio	Average (petiole length)/(leaf length)
REVPROP	ratio	Average (revolute size/leaf width)
INFLPEDU	mm	Average inflorescence peduncle length
INFLLEN	mm	Average inflorescence total length
INFLBRAN	mm	Average inflorescence 1st branch length
INFLSH1	ratio	Average inflorescence (peduncle length)/(total length)
INFLSH2	ratio	Average inflorescence (1st branch length)/(main axis length)
INFLSH3	ratio	Average inflorescence (main axis 1st internode length)/(main axis length)
INFLSH4	ratio	Average (1st branch 1st internode length)/ (1st branch length)
INFLNO1	count	Average number of nodes on main axis
INFLNO2	count	Average number of nodes on 1st lateral branch
NFLOWERS	count	Average number of flowers per inflorescence
CALYXLOB	mm	Average length of flower calyx lobes
CALYXTUB	mm	Average length of flower calyx tube
CALYXRAT	ratio	Average (calyx lobes length)/ (calyx tube length)
PETIPUB	score	Principal Coordinate Analyses scores on a single axis representing the correlation of two ranks describing petiole indumentum (density and length)
PUBABAX	score	Principal Coordinate Analyses scores on a single axis representing the correlation of six ranks describing indumentum abaxially (density and length on lamina, veins and midrib)
PUBADAX	score	Principal Coordinate Analyses scores on a single axis representing the correlation of six ranks describing indumentum adaxially (density and length on lamina, veins and midrib)
INFLPUB	score	Principal Coordinate Analyses scores on a single axis representing the correlation of two ranks describing inflorescence peduncle indumentum (density and length)
CALXYPUB	score	Principal Coordinate Analyses scores on a single axis representing the correlation of two ranks describing indumentum inside the calyx tube (density and length)
OVARYPUB	score	Principal Coordinate Analyses scores on a single axis representing the correlation of two ranks describing indumentum on ovary (density and length)

10,000,000 generations, with sampling every 1000 generations. *Burnin* was determined by stationarity of all parameters in the output of MrBayes. After the *burnin* trees were removed, results of two independent runs were combined and summarized in a majority rule consensus tree with the frequency of nodes as their posterior probability.

Data and topological congruence

Congruence between partitions and datasets were tested by the incongruence length difference test (ILD; Farris *et al*., 1994), with constant characters excluded and the following heuristic search options: 1000 replicates with random addition sequence, TBR branch swapping, MAXTREES set to 5000. Topological differences were tested for significance in likelihood scores by the SH (Shimodaira and Hasegawa 1999) and AU tests (Shimodaira 2002) as implemented in the program CONSEL (Shimodaira and Hasegawa 2001). Topological constraints (e.g. monophyly of clones, clades) were tested by comparing trees from analyses enforcing the constraint with unconstrained trees; the trees were the strict-consensus MP tree and the best tree from ML analyses.

Morphological analyses

Morphological data were obtained from specimens from nineteen herbaria (NY, MO, K, US, F, P, INPA, SP, VEN, TFVA, COL, BM, PORT, AMAZ, SP, HALCB, CEPEC, COAH, QCNE; see Holmgren and Holmgren 1998 for abbreviations). Twenty eight characters were measured from 901 specimens (of the 1700 available). Specimens were selected to cover the geographical distribution of predefined morphotypes. Thirty seven morphotypes had been initially delimited by sorting all specimens into groups based on general overall similarity. In addition, specimens that could not be clearly assigned to a particular morphotype were selected for inclusion. The selected characters were mostly measurements and ratios describing both the size and shape of leaves, inflorescences and flowers (Table 1). Six characters described the indumentum on leaves and inflorescences. For these characters, I initially coded observations on several parts of the leaves (veins, lamina, petiole and for each of these separately abaxially and adaxially) using relative ranks for both the size (i.e. minute, medium, long) and density (i.e. glabrous, sparse, dense) of hairs coverage. These semi-quantitative descriptors (ranks) were then reduced to single variables using Principal Coordinate Analysis (PCoA) and a distance matrix calculated using the Manhattan distance coefficient, $d[jk] = sum(abs(x[ij] - x[ik])$ (Legendre and Legendre 1998). These reduced variables were then used in the final morphological data matrix with the measurements and ratios. This was done to convert semiquantitative observations on indumentum into few quantitative variables.

In order to identify morphological clusters, I used Non-Metric Multidimensional Scaling (NMDS; Kruskal 1964), which attempts to optimize the position of samples in a reduced space (the number of dimensions of choice) so that they best represent the morphological distances among samples. Distance matrices were calculated using the Gower coefficient, i.e. *d[jk] = sum (abs(x[ij]-x[ik])/(max(x[i])-min(x[i])* (Gower 1971), because the variables were of mixed types: ratios, measurements in mm, and the indumentum PCoA scores. Not only is Principal Component Analysis (PCA) inappropriate in such circumstances (Legendre and Legendre 1998), but the data also clearly violate the assumptions of univariate and multivariate normality. Although deviations from normality may not be a problem in reasonably unskewed distributions (Legendre and Legendre 1998, p. 411; Tabachnick and Fidell 1996), transformations failed to normalize most of the variables used in this study, many of which had strongly skewed distributions. There is no reason to expect normality in a sample including mixed species. Discriminant Analyses (DA), were used, in at least one case, to predict group membership of samples for which only vegetative characters were available. This was done using vegetative characters only. Multivariate analyses were implemented in R (Becker et al. 1988) using several packages, mainly Vegan (Oksanen et al. 2006), Ade4 (Chessel et al. 2006) and Labdsv (Roberts 2006), all available at http://cran.r-project.org. The orthonormal decomposition of variance method of Ollier et al. (2006) was used to test for phylogenetic dependence of continuous variables across the phylogenetic trees. This method consists of first transforming the topology of a phylogenetic tree into a series of vectors of numeric values. This is done by defining all nodes in the tree as dummy variables and coding all descendant tips and nodes as 1's and all other tips and nodes as 0's. These variables are then ranked according to the complexity of the subtree they originate, by measuring the number of permutations (*np*) of tips and nodes that preserve the topological structure of the subtree stemming from each node. The greater the number of permutations the more complex the subtree, and this value is used in ranking the vectors. These vectors are not linearly independent, and this was obtained thereafter by suppressing for each node the dummy variable corresponding to the direct descendant with lowest *np* value. The set of linearly independent vectors are then orthogonolized, so constituting the orthonormal basis of the topology (see Ollier et al. 2006 for details). No branch length information is considered. The orthonormal vectors are linear combinations of the original dummy variables and are orthogonal, and thus uncorrelated with each other. In fully bifurcating trees, the orthormal vectors represent the comparisons between the sister clades of each node, from root to tips, with one daughter clade having positive scores in this axis, and the other negative ones. The amount of variance in a quantitative trait explained by each node in the tree is then accessed by correlations of the trait vector with the orthonormal vectors representing the topology (see also Giannini 2003).

Ollier et al. (2006) also propose four test statistics to diagnose both the intensity and nature of phylogenetic dependence of the quantitative trait being tested: (1) R2Max, which is expected to peak (100% of variance explained) when a unique vector, representing a single node on the tree, accounts for most of the variance in the variable; (2) Dmax, which is derived from the cumulative orthogram, the cumulative variance decomposition from root to tips (not shown here), and which tests for “diffuse phylogenetic dependence”, i.e. when variance in a trait is partitioned among several nodes; (3) SCE, which tests the "average local variation of the orthogram values"; and (4), the SkR2k statistic, which indicates whether the variance distribution is skewed towards the root (negative values) or the tip (positive values) of the phylogenetic tree (see Ollier et al. 2006 for details about these statistics). Tests were performed by 999 permutations as implemented in the package Ade4 in R.

Geography and sympatry

Geographical coordinates were obtained for all specimens of *Pagamea,* either directly from label information or from online gazetteer databases. Although the coordinates of gazetteer localities may not reflect the exact site where the plants were collected, corrections were made whenever possible by taking into consideration additional information from specimen labels (e.g. river names), and by searching for the white-sand savannas and forests at nearby locations using satellite images (Landsat images from https://zulu.ssc.nasa.gov/mrsid), in which these habitats are clearly seen.

The geographical relationships between clades were estimated using geographical distances between collecting localities rather than gross overlap in ranges. To estimate the geographical relationships between A and B (i.e. any two groups of data), I first calculated all distances (in km) between each A and its closest B (a vector of the minimum distances from A to B), and then estimated the proportion of such distances that were found within different distance classes. This is a very crude measure of geographical relationship between groups of samples. However, it may better reflect the actual geographical proximity of the samples of two groups than range overlap, and appears particularly important when collecting efforts are scarce and strongly biased as in the Amazon region (Nelson et al. 1990; Prance et al. 2000). The proportion of samples between two groups within different distance classes can be plotted as pie plots in a pairwise matrix, providing a helpful depiction of the actual distances between samples of two groups, whether species, clades or any other grouping (see Fig. 10; calculations and plots were implemented with a script in R using package *gmt* (Magnusson 2005) to calculate the distances in km from latitude and longitude data; available upon request to the author). The combination of such plots with maps of the range overlap between groups allows, for this kind of unevenly distributed data, a better understanding of their geographical relationships.

RESULTS

Phylogenetic analyses

All sampled molecular markers showed low levels of genetic variation and, consequently, the trees from individual phylogenetic analyses had low resolution. The two chloroplast markers, *rps16* intron1 and *rpl20-rps12* intergenic spacer, were sequenced for 151-153 samples from to 31 of the 37 morphotypes. Both markers were extremely variable in length (Table 2). Some of this length variation was caused by three regions of homopolymeric repeats, two in the *rpl20-rps12* spacer (one corresponding to

Table 2. Descriptions of molecular datasets

	rpl20-rps12	**rps16**	**ITS**
Number of samples (clones)	151	153	97 (194)
Number of morphotypes included	31/37	31/37	29/37
Aligned matrix bp	906	1331	700
Sequence length variation outgroup (*Gaertnera*)	790-796	834-862	614-615
Sequence length variation ingroup (*Pagamea*)	777-819	812-934	521-643
N binary coded indels	17	38	0
N parsimony-informative substitutions	64	71	248
N parsimony-informative total characters	81	110	235
N parsimony-informative characters (*Pagamea*)	49	69	185
Pairwise distance (*Pagamea*); min (avg) max	0.0 (3.6) 10.9%	0.0 (2.5) 9.7%	0.0 (3.5) 15.3%
Pairwise distance including indels (*Pagamea*)	0.0 (5.7) 14.7%	0.0 (5.7) 16.2%	0.0 (6.1) 26.4%

a SSR noted by Weising 1999) and one in the *rps16* intron1. These regions could not be properly aligned for the whole dataset and were excluded from all analyses. Analyses of the entire chloroplast dataset yielded a more resolved phylogenetic hypothesis than did analyses of any individual dataset. The inclusion of binary coded indels as characters also increased resolution and support and did not change the topology. For the chloroplast regions, I present only the results of the analyses of the entire dataset, because both markers were congruent, both when analyzed separately and when binary coded indels from each gene were included (ILD test, P=0.258). However, variation is still low and few clades are strongly supported by the chloroplast data alone (Fig. 1).

Fewer individuals were sampled for ITS (Table 2), but representatives for all but two of the 31 morphotypes in the chloroplast dataset were included. Clones from the same accessions in the ITS dataset formed monophyletic groups in the strict consensus of a MP analysis (tree not shown), with the exception of four clones that formed clades with other accessions of the same morphotype. Constraining the monophyly of all ITS clones

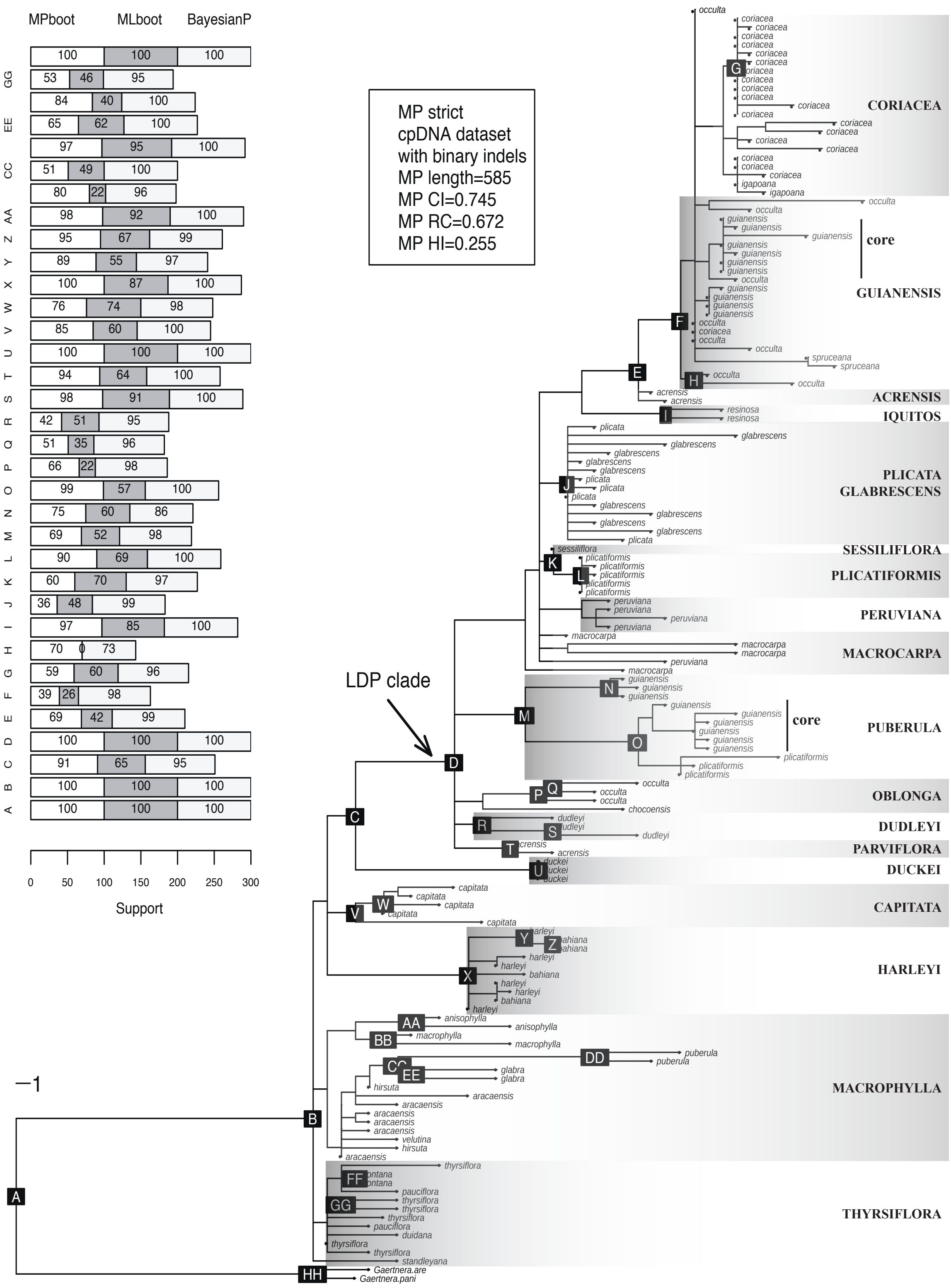


Fig. 1. MP strict consensus tree for the combined chloroplast markers (*rps16* intron1 and *rpl20-rps12* inter genic spacer), binary coded indels included. Support shown only for nodes with at least 70% bootstrap for either MP or ML analyses, or with 95% Bayesian posterior probability.

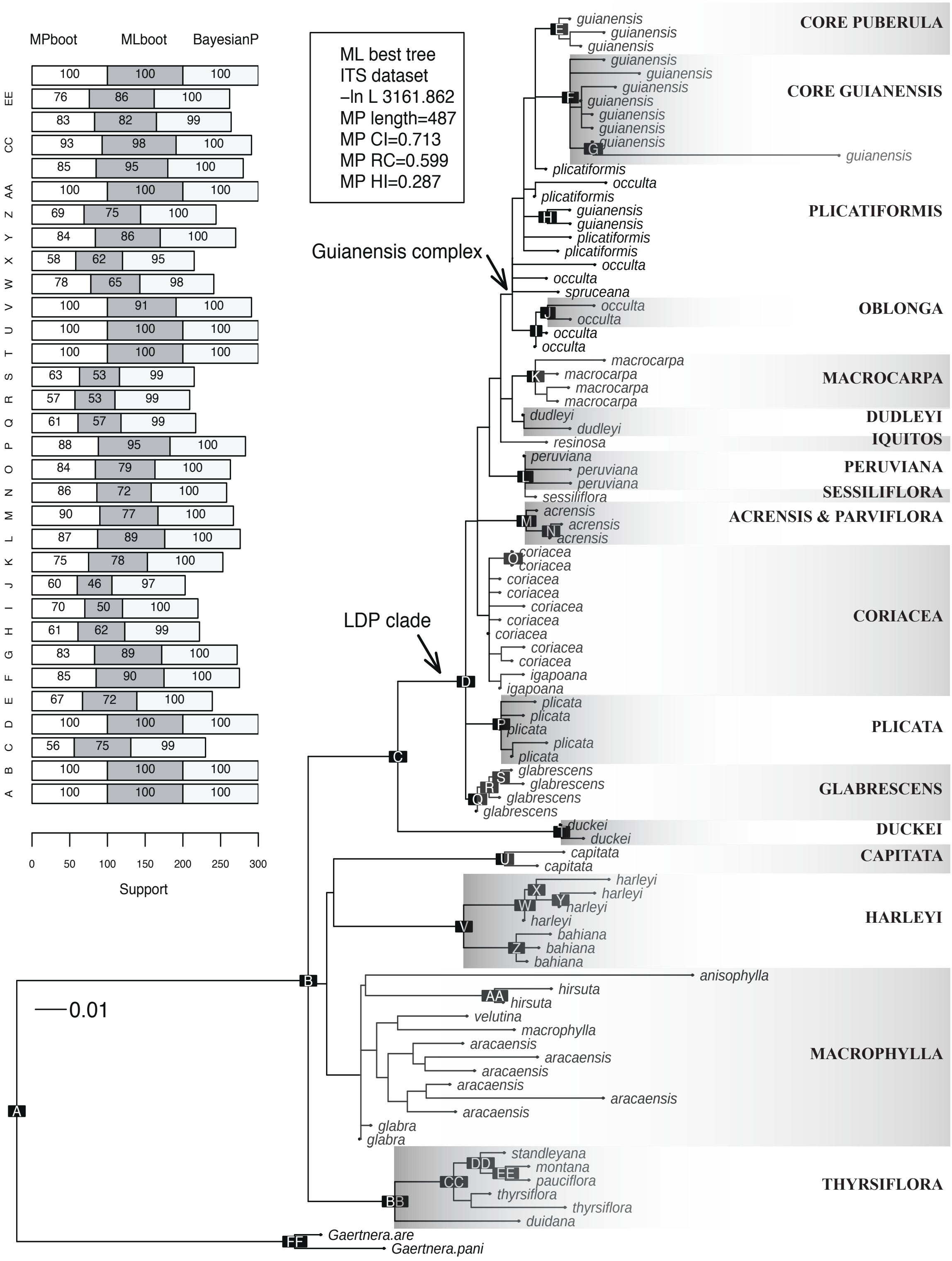


Fig. 2. ML best tree for the ITS dataset. Nodes indicated with at least 70% bootstrap (for either MP or ML analyses) or with 95% Bayesian posterior probability. *Gaertnera* and the Guianensis sample from French Guiana (with a very long branch) are from GeneBank (Malcomber 2002). Inclusion or exclusion of this accession did not change the phylogenetic results.

did not result in significantly longer trees (Templeton test, difference in length 3 steps; N=39, P=0.943).

The ITS and chloroplast datasets were incongruent according to the ILD test (P<0.001). Comparison of both the ITS and cpDNA trees indicated that the incongruence was localized (Fig. 1, 2), and involved only the position of some clades within the sister-group to Duckei[1], a clade that I will refer to as the Late Diverging *Pagamea* (LDP; Fig. 1, 2). Only two deep nodes ("C" and "D") in the combined tree (Fig. 3; indels excluded) are well supported. Both these nodes place the Duckei clade as sister to the LDP clade, and are also supported in the ITS and chloroplast data individual analyses (Fig. 1, 2). The LDP+Duckei clade forms a near-polytomy with four other well-supported clades in the combined tree: Harleyi, Thyrsiflora, Macrophylla and Capitata (Fig. 3). Macrophylla has support only in the combined tree. Relationships among these clades are poorly supported in both individual and combined analyses.

The precise position of the root within *Pagamea* is uncertain, with different positions being found depending on the method of analysis and inclusion or exclusion of indels. The Harleyi clade is supported as sister to the rest of *Pagamea* according to both chloroplast (77% bootstrap in ML) and ITS (Bayesian analyses, 96% PP), but this relationship is not retrieved by ML analyses of both ITS and combined datasets

[1] The following conventions are used throughout the text regarding names of groups, clades and species: (a) clades are upper case and regular font (e.g. Duckei) and refer, unless otherwise specified, to clades supported in Fig. 3; (b) clades within Clades or morphological groups within Clades are uninomial, lower case, italics (e.g. *hirsuta*); and, (c) species, as recognized by this study, are binomials (e.g. *P. hirsuta*).

(Fig. 2, 3). The MP strict consensus from an analysis with POY (Wheeler et al. 2002) using Fixed State Optimization (Wheeler 1999) for the combined dataset (with only one LDP representative, as in Fig. 4), and including also the indel-rich regions (four of the chloroplast and one of the ITS) excluded in all other analyses, places Macrophylla+Thyrsiflora as sister to the rest of the genus, a topology congruent with that of the ML combined tree (Fig. 3). The indel-rich regions included represent an addition of 133-297 bp in the data matrix (N=29). The bootstrapping method implemented in POY (-jackboot option) gives 100% values for all the nodes in this tree, an obvious overestimation driven by the indels. This topology is supported by a ~60 bp long insert in the *rps16* intron of Capitata+Harleyi+Duckei+LDP (arrow in Fig. 3), which is absent in the Thyrsiflora and Macrophylla clades and in *Gaertnera*. This insert is part of an indel-rich region with high "A" content (> 70%). Despite this correlation, the differences in rooting are not significant, according to both the individual and combined datasets (SH and AU tests, P ~ 0.5).

Within the LDP clade, analyses of the combined cpDNA+ITS datasets (no indels) indicate 13 major clades, of which all but Guianensis are well supported as monophyletic (Fig. 3), although Acrensis and Iquitos are represented by only single accessions. Iquitos is a well supported clade in the chloroplast tree (Fig. 1), and two accessions of Acrensis in this tree, despite low resolution, are not rejected as monophyletic. The chloroplast tree has a very similar topology to the combined tree, but has lower resolution. The ITS data rejected the combined ML topology for the

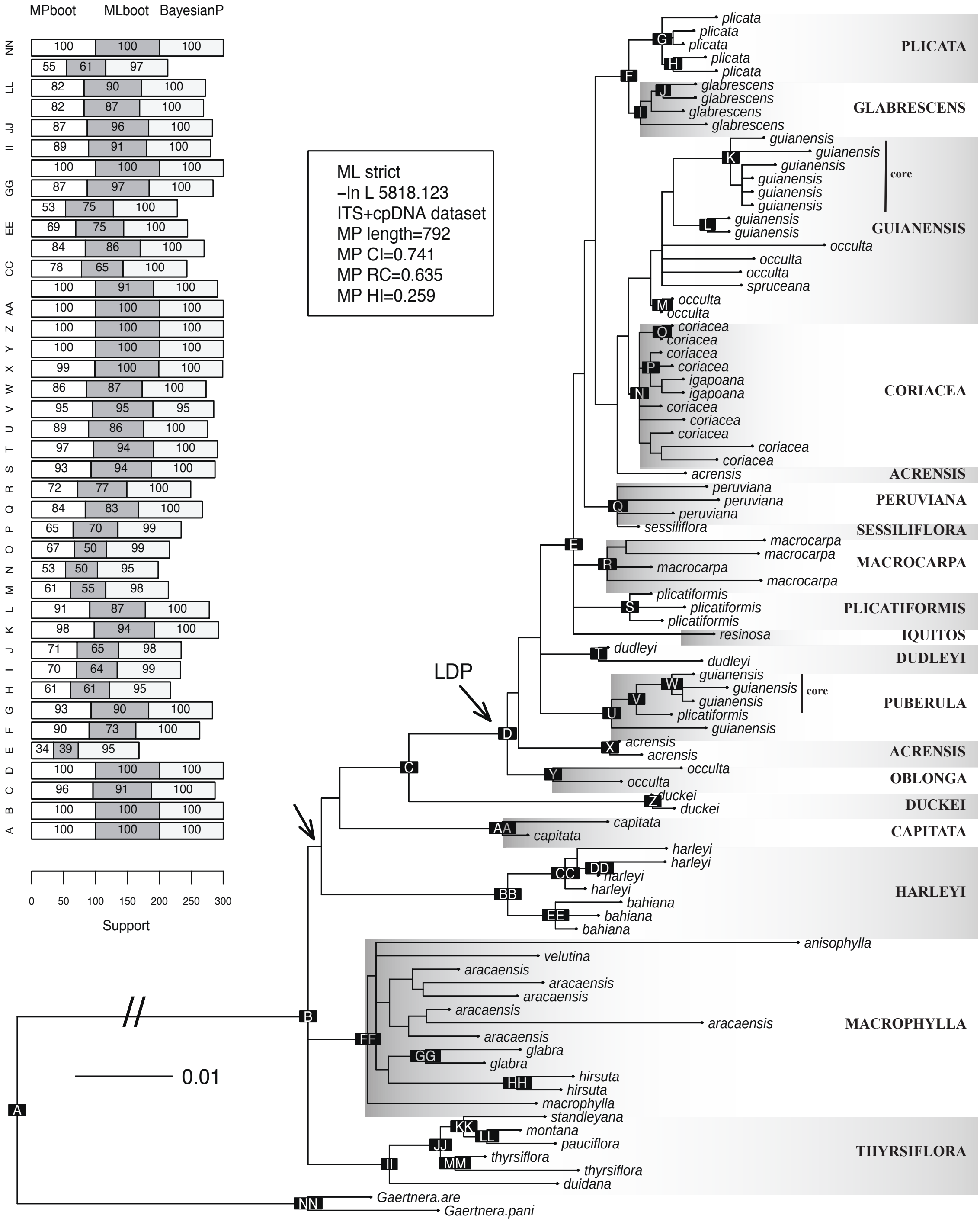


Fig. 3. Strict consensus of four ML trees for the combined ITS+cpDNA datasets, indels excluded. Nodes "C" and "D" are the only well-supported internal nodes. Node "D" defines the Late Diverging Pagamea (LDP) clade (arrow). Unlabelled arrow indicates node at which there is a ~ 60 bp insert in the *rps16* intron1. Note that Guianensis is the only clade with no support and Acrensis, Iquitos and Sessiliflora are represented by single accessions. Support shown only for nodes with at least 70% bootstrap (for either MP or ML analyses) or with 95% Bayesian posterior probability.

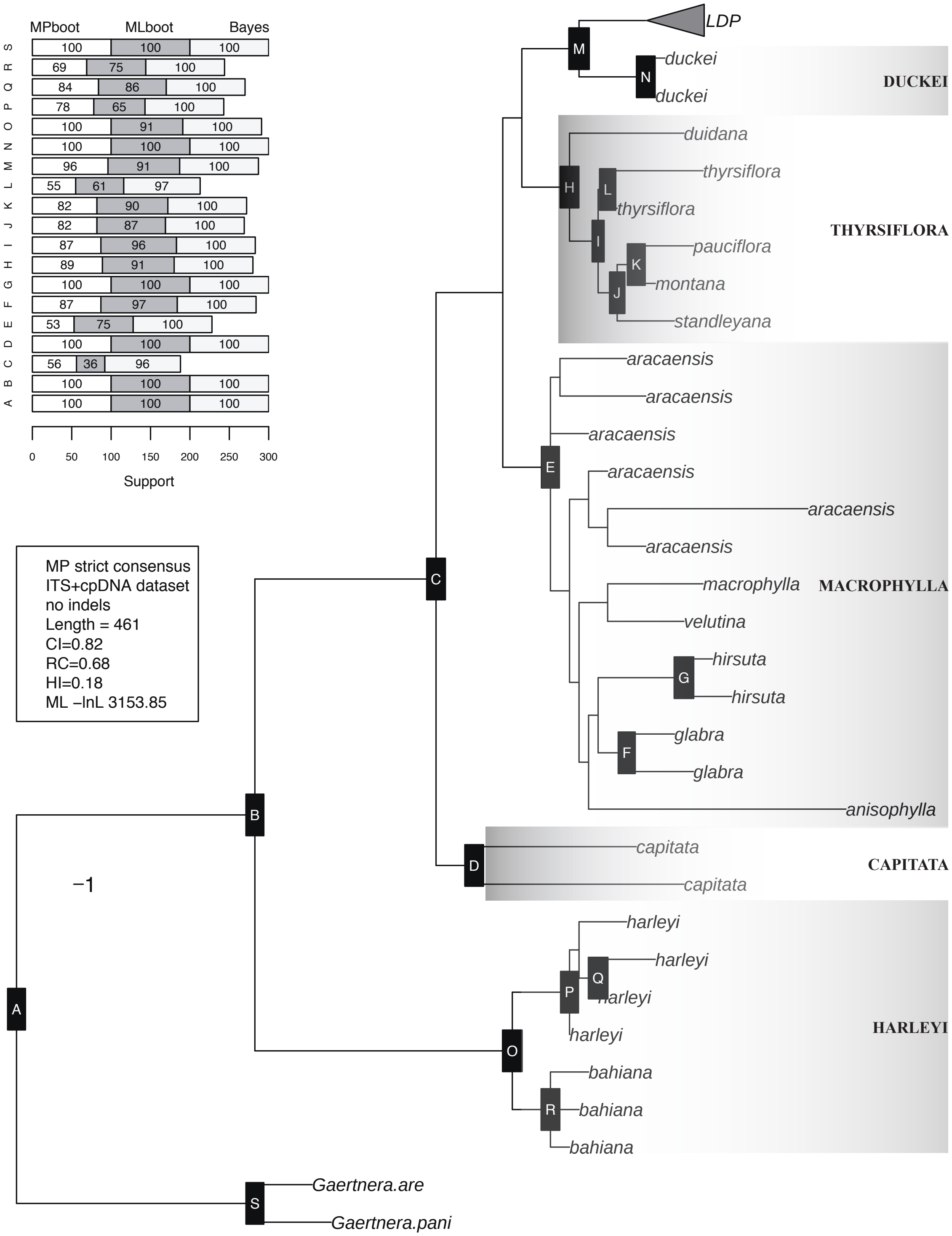


Fig. 4. MP strict consensus for the combined ITS+cpDNA dataset for a subset of samples to explore relationships at the root within Pagamea (i.e. LDP represented by only one accession; indels excluded). Note that in this tree the Harleyi clade is sister to rest of the genus. Support shown only for nodes with at least 70% bootstrap (for either MP or ML analyses) or with 95% Bayesian posterior probability.

LDP clade (Table 3), and both combined and chloroplast datasets also rejected the ITS ML tree (SH test $P=0.023$ and $P<0.001$, respectively). However, most of the 13 major clades of the combined tree are also monophyletic in the ITS tree, with the exceptions of Plicatiformis and Puberula, and of Guianensis, because these and Oblonga are placed within it ("Guianensis complex", see Fig. 2). To test whether these differences were significant, I enforced the monophyly of each of these 13 clades separately, using the ITS dataset and Maximum Likelihood, and then compared the resulting best trees with the unconstrained ITS topology (Table 3). Only the monophyly of Guianensis was rejected according to the SH test, while the monophyly of Puberula (node "U" in Fig. 3) was rejected by the AU test only (Table 3; Shimoidara [2002] recommends using the AU test for typical cases of tree selection, the SH test tending to be more conservative). The monophyly of Plicatiformis and that of the core Puberula clade (nodes "O" in Fig.1 and "V" in Fig. 3) were not rejected. The accessions of Puberula that cause incongruence are from Suriname and French Guiana, and in the chloroplast tree they form a well-supported clade (node "N" in Fig. 1) sister to the core Puberula. In the ITS dataset, one of these accessions forms a well-supported clade with an accession of Guianensis from French Guiana (long branch Guianensis; node "G" in Fig. 2). This clade is also nested within a well-supported monophyletic group with other samples of Guianensis from the Altantic Coast of Brazil, both from the state of Amapá, the northern most of Brazil and Belém, on the margin of the Amazon fan, and from the state of Bahia (core Guianensis clade; nodes "F" in Fig. 2 and "K" in Fig. 3). Therefore, well-supported clades in the combined tree are not rejected as monophyletic by the ITS data.

Table 3. Results of topological comparisons between the unconstrained ITS ML tree and the ITS ML trees resulting from enforcing as constraints the monophyly of clades present in the combined ITS+cpDNA tree (Fig. 3). Comparisons are for the LDP clade only; dataset is ITS.

rank	topology	-ln L	Obs diff.	Au test	Sh test
1	ITS ML tree unconstrained	1254.45	-5.1	0.890	0.963
2	ITS core Puberula monophyly enforced (node “V” in Fig. 3 and node “O” in Fig.1)	1259.5	5.1	0.209	0.709
3	ITS Plicatiformis monophyly enforced	1259.62	5.1	0.057	0.752
4	ITS Puberula monophyly enforced (node “U” in Fig. 3 and node “M” in Fig.1)	1273.75	19.3	0.009	0.286
5	ITS Guianensis monophyly enforced	1288.95	34.5	4e-07	0.068
6	Combined ITS+cpDNA ML tree	1373.93	119.5	7e-14	3e-04

The position of some LDP clades in the combined and ITS trees differ. Puberula, Oblonga, Dudleyi, and Parviflora are the earliest diverging branches within the LDP clade according to the cpDNA and combined trees. In the ITS, in addition to the clades that cause Guianensis to be paraphyletic (Puberula, Oblonga and Plicatiformis), Dudleyi is placed as sister to Macrocarpa and Parviflora as sister to Acrensis. Both the ITS and the combined datasets suggest that Sessiliflora is sister to Peruviana (nodes “L” and “Q” in Fig. 2 and 3, respectively), rather than to Plicatiformis as suggested by the chloroplast (node “K” in Fig. 1). Some of these conflicts are strongly supported (nodes “I”, “F” and “M”, Fig. 2), and there is only one internal node within the LDP clade (node “E” in Fig. 3) with support (only Bayesian, 95% posterior probability) in the combined tree, possibly caused by the incongruence between chloroplast and ITS. The chloroplast dataset also rejected the relationship between Sessiliflora and Peruviana according to the AU test but not according to the SH test (-ln L 1347.23 and 1352.84, AU test P=0.02, SH test P=0.16), while the ITS dataset strongly rejected the relationship between Sessiliflora and Plicatiformis according to both tests (P<0.001).

Morphology and phylogeny

There is a strong relationship between morphology and the combined ITS+cpDNA tree. The four statistics proposed by Ollier et al. (2006) to test the association between quantitative variation and phylogeny strongly rejected the null hypothesis of phylogenetic independence for three variables representing morphological space (the three axes of a NMDS ordination; Table 4, Fig. 5). Although the concept of explained variation as used in Principal Component Analyses (PCA) does not make sense for NMDS techniques, there is a strong correlation between the morphological distance calculated from the scores of these three axes and the observed morphological distance ($r = 0.94$, obtained with function “stressplot” from package Vegan in R, Oksanen et al. 2006), indicating that the three axes explain most of the variation (94%) in the data. The “stress” of this NMDS analysis is 11.35%; a stress of zero would indicate a perfect fit between the distance in reduced space and the actual morphological distance. The characters most strongly correlated with the three morphological axes are given in Table 5.

The decomposition of variance of each morphological axis onto the orthonormal vectors representing the topology of the combined ITS+cpDNA tree (Fig. 3, 5A-C) indicates that the well-supported clades in this tree are also morphologically distinct. The topological variables that account for most of the variation in each morphological axis correspond to the nodes separating these clades (nodes indicated in Fig. 5D; note that

T**able 4**. Results for the four statistics testing the association between phylogeny and morphology. R2Max is the maximum variance explained by a single orthonormal vector (node), and is expected to peak (100%) when one node on the tree accounts for most of the morphological variance in the trait; Dmax is derived from the cumulative orthogram (cumulative variance decomposition from root to tips), and tests for "diffuse phylogenetic dependence", i.e. when variance in morphology is partitioned among several nodes; the SCE tests the "average local variation of the orthogram values"; the SkR2k statistics indicates whether the variance distribution is skewed towards the root (negative values) or the tip (positive values) of the phylogenetic tree (see Ollier et al. 2006 for details on statistics; tests performed on 999 permutations). See also Figures 5-7.

Tree	**Variable**	**R2Max**	**SkR2k**	**Dmax**	**SCE**
ITS+cpDNA	NMDS1	0.39 (P=0.001)	-15.37 (P=0.001)	0.651 (P=0.001)	13.13 (P=0.001)
ITS+cpDNA	NMDS2	0.162 (P=0.009)	-23.373 (P=0.001)	0.431 (P=0.001)	6.406 (P=0.001)
ITS+cpDNA	NMDS3	0.362 (P=0.001)	-22.192 (P=0.001)	0.425 (P=0.001)	6.64 (P=0.001)
ITS	NMDS1	0.41 (P=0.001)	-12.631 (P=0.001)	0.685 (P=0.001)	15.228 (P=0.001)
ITS	NMDS2	0.125 (P=0.038)	-23.521 (P=0.001)	0.415 (P=0.001)	6.279 (P=0.001)
ITS	NMDS3	0.3 (P=0.001)	-24.61 (P=0.001)	0.426 (P=0.001)	5.917 (P=0.001)

numbers on nodes correspond to orthonormal vectors as in Fig. 5A-C). Furthermore, several additional topological vectors account for morphological variation, in particular in NMDS2 values, although the intensity of phylogenetic dependence for morphology at these nodes is below the confidence limit of 5% (Fig. 5B; see bars above mean). Overall, the four statistics proposed by Ollier et al. 2005 to diagnose the intensity and nature of phylogenetic dependence are all highly significant (Table 4). Two of these statistics (R2Max and SkR2l) indicate that the effect is observed at the level of the well-supported clades, i.e. few nodes account for most of the variation in morphology (R2MAX), and that the variance distribution is skewed towards the root of the tree (SkR21, negative values). The other two statistics (Dmax and SCE) indicate that there is also localized morphological variation, i.e. closely related terminals are also closer in morphological

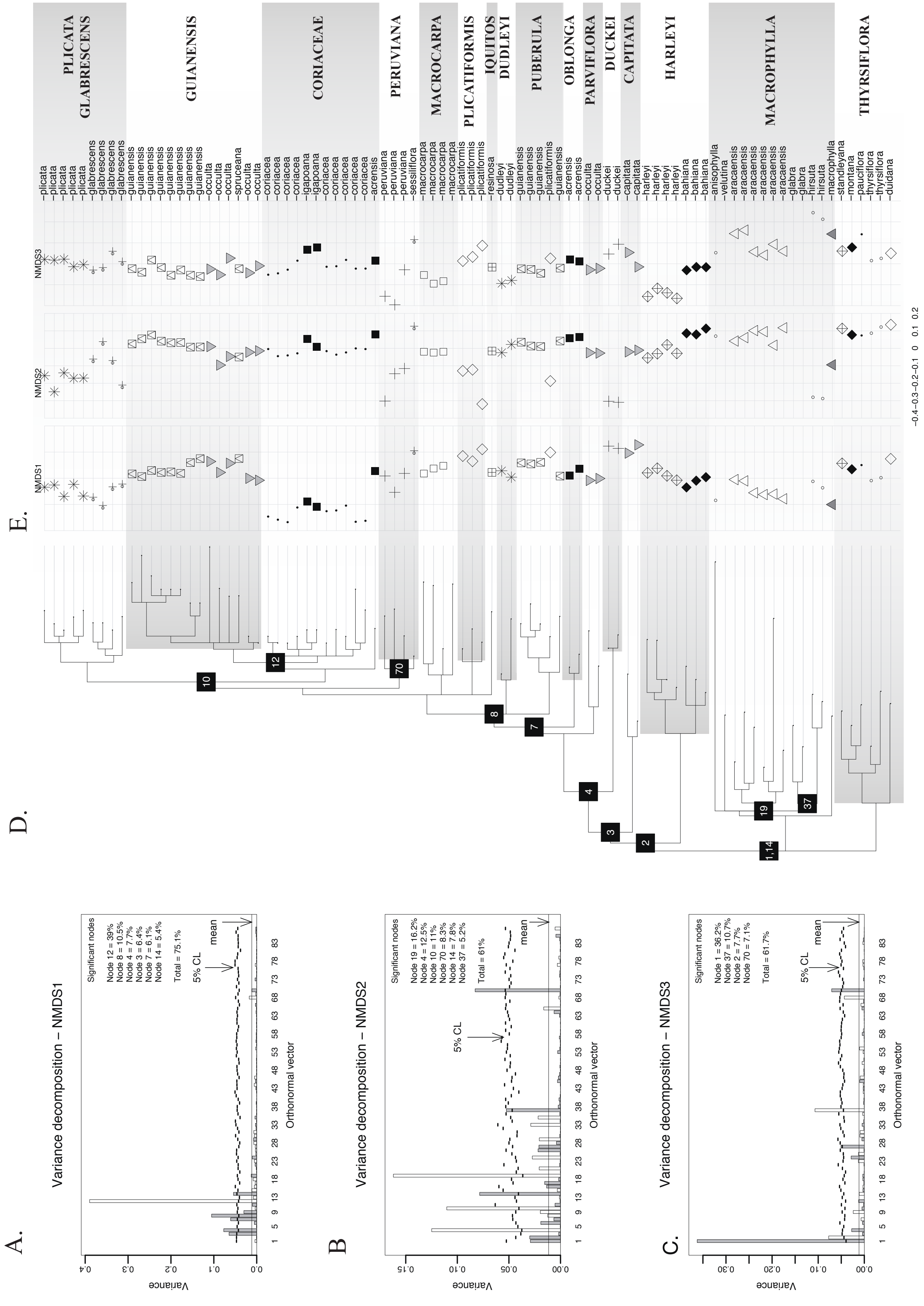

A.
Variance decomposition – NMDS1
Significant nodes
Node 12 = 39%
Node 8 = 10.5%
Node 4 = 7.7%
Node 3 = 6.4%
Node 7 = 6.1%
Node 14 = 5.4%
Total = 75.1%
5% CL
mean
Variance
Orthonormal vector
B.
Variance decomposition – NMDS2
Significant nodes
Node 19 = 16.2%
Node 4 = 12.5%
Node 10 = 11%
Node 70 = 8.3%
Node 14 = 7.8%
Node 37 = 5.2%
Total = 61%
5% CL
mean
Variance
Orthonormal vector
C.
Variance decomposition – NMDS3
Significant nodes
Node 1 = 36.2%
Node 37 = 10.7%
Node 2 = 7.7%
Node 70 = 7.1%
Total = 61.7%
5% CL
mean
Variance
Orthonormal vector
D.
E.
NMDS1
NMDS2
NMDS3
PLICATA GLABRESCENS
GUIANENSIS
CORIACEAE
PERUVIANA
MACROCARPA
PLICATIFORMIS
IQUITOS
DUDLEYI
PUBERULA
OBLONGA
PARVIFLORA
DUCKEI
CAPITATA
HARLEYI
MACROPHYLLA
THYRSIFLORA
10
12
70
8
7
4
3
2
1,14
19
37

Table 5. Morphological characters significantly correlated with the three ordination axes of the morphological space for all samples of *Pagamea* (N=901; only significant correlations at P<=0.01 are shown; values = Spearman correlation). For character descriptions see Table 1.

Character	NMDS1	NMDS2	NMDS3
INFLNO1 - count	-0.82		
INFLLEN - mm	-0.79	-0.38	-0.19
PETIPUB - score	-0.78		-0.11
INFLBRAN - mm	-0.76		-0.09
INFLSH4	0.76		
INFLNO2 - count	-0.74		-0.09
PETIOLEN - mm	-0.68	-0.59	-0.18
INFLPEDU - mm	-0.68	-0.45	-0.23
NFLOWERS - count	-0.66	-0.27	-0.2
LEAFWID - mm	-0.59	-0.67	-0.15
LEAFLEN - mm	-0.58	-0.69	-0.18
PUBADAX - score	-0.57	0.21	-0.16
INFLSH1 - ratio	0.55	-0.09	
INFLSH2 - ratio	-0.54		-0.13
VENADENS - ratio	0.53	0.42	0.2
CALYXRAT - ratio	0.53	-0.33	-0.41
LFSHAPE3 - ratio	-0.51	-0.09	
CALYXLOB - mm	0.5	-0.32	-0.31
REVPROP - ratio	0.45		0.15
LFSHAPE1 - ratio	-0.45	-0.18	0.22
OVARYPUB - score	-0.4	0.54	0.5
PUBABAX - score	-0.4	0.58	
LFSHAPE2 - ratio	-0.36	-0.15	0.1
INFLPUB - score	0.35	-0.62	-0.13
CALXYPUB - score	-0.32	-0.33	0.11
DOMADENS - ratio	0.24	0.18	-0.77
CALYXTUB - mm	-0.22		0.34

← **Fig. 5**. Relationship between morphology and the combined ITS+cpDNA tree (Fig. 3). **A-C**. Bar plots: variance decomposition for three axes representing morphological space (Fig. 6) onto the vectors representing the phylogenetic tree. CL = 5% confidence limit obtained with 999 permutations of values among tips. All three axes have a significant effect (see Table 4). **D**. Combined tree (see Fig. 3). Nodes are labeled by the orthonormal vector they represent (same numbers as in A-C; only those explaining variance above the 5% limit are shown). The root node accounts for vector 14 and 1, which represent the contrasts between Macrophylla and Thyrsiflora and that between (Macrophylla+Thyrsiflora) and rest, respectively. Vector 70 represents the distinction between Sessiliflora and Peruviana. The remaining vectors represent the contrasts between the two daughter clades at each node. **E**. Distribution of actual morphological values across the phylogeny. Value = mean of morphological scores for all tips that could be unambiguously assigned to tip. Empty rows are terminals for which no fertile material is available. Symbols represent names of species recognized in this study.

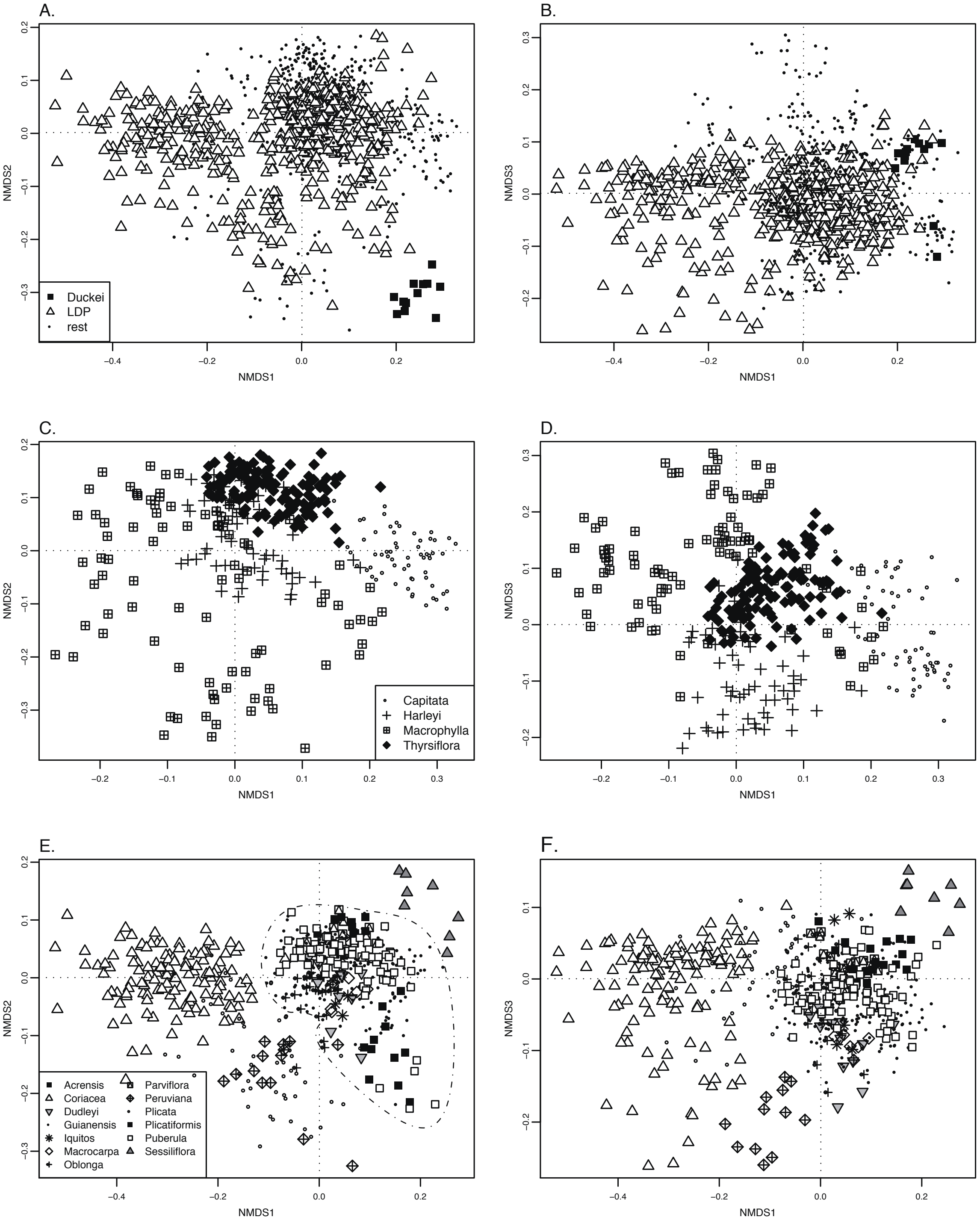
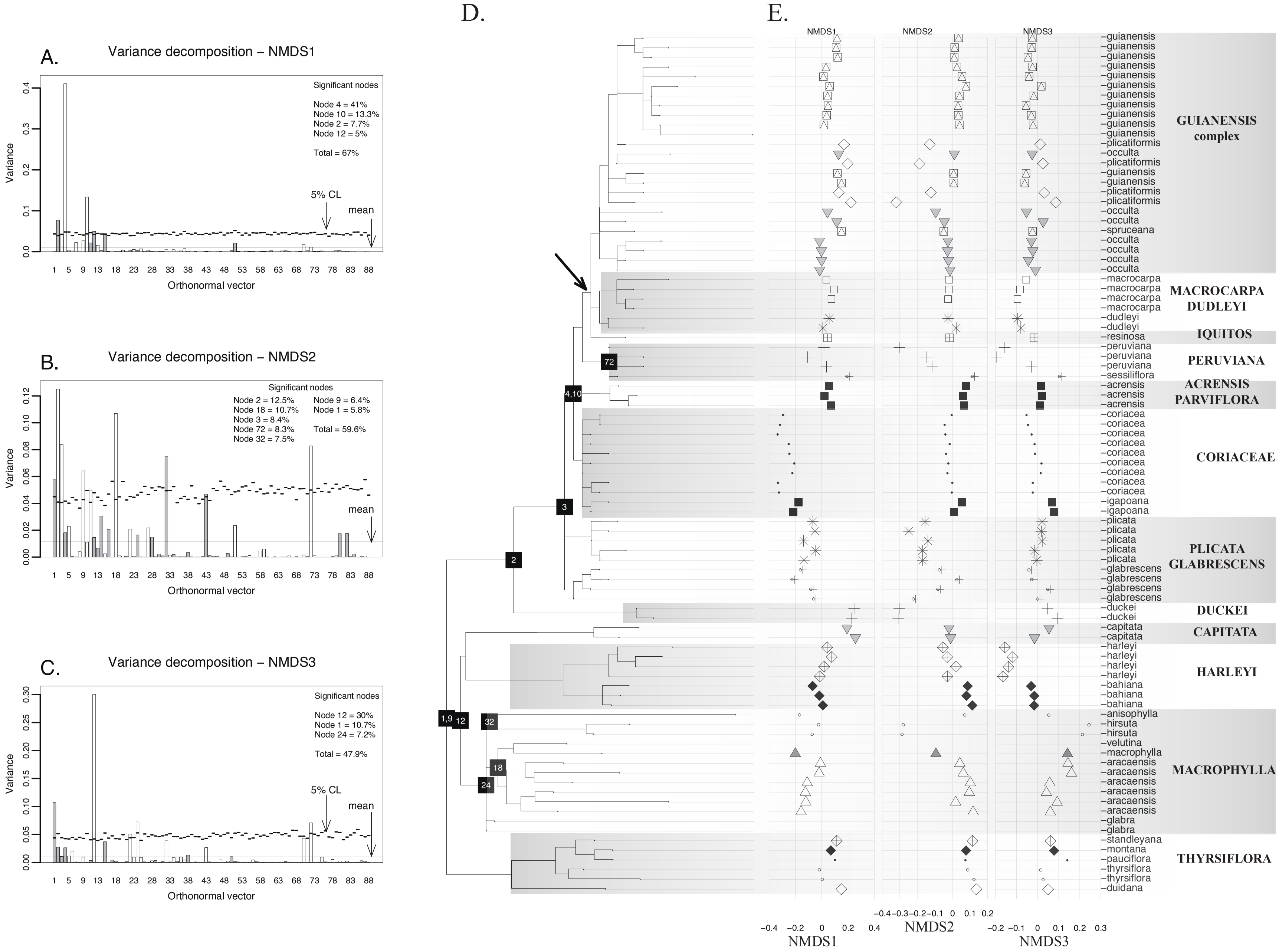


Fig. 6. Morphological space for *Pagamea* (N=901). A-B: all samples and three labels: the Duckei and LDP clades and the rest (Macrophylla, Thyrsiflora, Capitata and Harleyi). Note that Duckei is distinct from both groups. C-D: only samples for Macrophylla, Thyrsiflora, Capitata and Harleyi. Note that morphological overlap between clades is caused in part by the Harleyi clade, which is allopatric to rest. E-F: only samples for the LDP shown. Dotted line indicates clades that strongly overlap in morphological space. For characters correlated with axes refer to Table 5.

values. This is more obvious from the distribution of morphological values across the phylogenetic tree — compare trait values in Fig. 5E between the daughter clades of nodes indicated. The phylogenetic signal of morphological variation can also be seen by plotting clades in a tri-dimensional morphological space defined with non-metric multidimensional scaling (NMDS; Fig. 6). The Duckei clade is morphologically distinct from all other samples, having notably high values on axis 1 along with low values on axis 2. The LDP clade largely overlaps in morphological space with samples from the Macrophylla, Thyrsiflora, Harleyi and Capitata clades (Fig. 6A-B), an effect that is detected by the first two ordination axes (see node 4 in Fig. 5A-B).There is also a strong phylogenetic effect for the morphological variation among the Macrophylla, Thyrsiflora, Harleyi and Capitata clades (vectors # 1, 2, 3 and 14 in Fig. 5A-C), which are clearly seen in the distributions of samples of these clades in morphological space (Fig. 6C-D). Among the LDP clades, the analysis indicates that the contrast between Coriacea and Guianensis accounts for most of the variance in NMDS1 values (~40%, vector 12, Fig. 5A). Two other nodes among the LDP that indicate differences in NMDS1 scores between daughther clades (vectors 7 and 8) account for less than ~10% of the variance, and the effect is driven by the values of the Coriacea, Plicata and Peruviana clades. These clades, in particular Coriacea, are the clades that are best discriminated in morphological space among the LDP clades (Fig. 6E-F). The effect within the Peruviana clade (vector 70 in Fig. 5B, D) reflects the great distinction between Sessiliflora and Peruviana in morphological space (Fig. 6E-F). The remaining LDP clades strongly overlap in morphological space (circumscribed by a dash-dot line in Fig. 6E), a


A.
Variance decomposition – NMDS1
Significant nodes
Node 4 = 41%
Node 10 = 13.3%
Node 2 = 7.7%
Node 12 = 5%
Total = 67%
5% CL
mean
Variance
Orthonormal vector
B.
Variance decomposition – NMDS2
Significant nodes
Node 2 = 12.5%
Node 18 = 10.7%
Node 3 = 8.4%
Node 72 = 8.3%
Node 32 = 7.5%
Node 9 = 6.4%
Node 1 = 5.8%
Total = 59.6%
mean
Variance
Orthonormal vector
C.
Variance decomposition – NMDS3
Significant nodes
Node 12 = 30%
Node 1 = 10.7%
Node 24 = 7.2%
Total = 47.9%
5% CL
mean
Variance
Orthonormal vector
D.
72
4,10
3
2
32
18
24
12
1,9
E.
NMDS1
NMDS2
NMDS3
GUIANENSIS complex
MACROCARPA DUDLEYI
IQUITOS
PERUVIANA
ACRENSIS PARVIFLORA
CORIACEAE
PLICATA GLABRESCENS
DUCKEI
CAPITATA
HARLEYI
MACROPHYLLA
THYRSIFLORA
guianensis
plicatiformis
occulta
spruceana
macrocarpa
dudleyi
resinosa
peruviana
sessiliflora
acrensis
coriacea
igapoana
plicata
glabrescens
duckei
capitata
harleyi
bahiana
anisophylla
hirsuta
velutina
macrophylla
aracaensis
glabra
standleyana
montana
pauciflora
thyrsiflora
duidana

similarity that is in agreement with the ITS topology.

In contrast to the combined ML topology, the ITS topology places morphologically similar clades together and, in consequence, fewer nodes in the ITS tree have a significant effect of morphological differences between daughter clades (or parts of polytomies) than nodes in the combined tree. For example, the differences in morphology between the daugther clades of nodes (vectors) 7 and 8 in Figure 5, is not detected when the ITS tree is used instead of the combined tree (Fig. 7). These nodes correspond to the comparisons between Parviflora and the rest of the LDP clade, and that between Dudleyi+Puberula *vs.* rest of the LDP clade, respectively. In the ITS tree the clades between nodes 7 and 10 in Figure 5 form a monophyletic group with the Guianensis clade (arrow in Fig. 7, see also Fig. 2). There is little morphological differentiation within this monophyletic group, except for Sessiliflora+Peruviana *vs.* the rest. There is also a localized effect within this monophyletic group: clades placed in Guianensis (i.e. Puberula, Oblonga and Plicatiformis) are placed closer to terminals that

← **Fig. 7**. Relationship between morphology and the ITS ML tree (Fig. 2). **A-C**. Bar plots: variance decomposition for three axes representing morphological space (Fig. 6) onto the vectors representing the phylogenetic tree. CL = 5% confidence limit obtained with 999 permutations of values among tips. All three axes have a significant effect (see Table 4). **D**. Combined tree (see Fig. 3). Nodes are labeled by the orthonormal vector they represent (same numbers as in A-C; only those explaining variance above the 5% limit are shown). The root node accounts for vector 1 and 9, which represent the contrasts between Macrophylla and Thyrsiflora and that between (Macrophylla+Thyrsiflora) and rest, respectively. Vectors 4 and 10 represent the constrast between (Coriacea+Acrensis+Parviflora) *vs.* rest, and that between Acrensis+Parviflora *vs.* Coriacea, respectively. Vector 72 represents the distinction between Sessiliflora and Peruviana. The remaining vectors represent the contrasts between the two daughter clades of each node. **E**. Distribution of actual morphological values across the phylogeny. Value = mean of morphological scores for all tips that could be unambiguously assigned to tip. Empty rows are terminals for which no fertile material is available.

are also morphologically similar (see distribution of values in Fig. 7D-E). In addition, the placement of Acrensis with Parviflora, a strongly supported relationship in the ITS tree (node “M” in Fig. 2), is also matched by morphological similarity in all three axes, and Macrocarpa plus Dudleyi show a similar pattern (Fig. 7D-E). Morphological differences between clades within *Pagamea* are mostly quantitative. However, most samples of the Macrophylla clade have features that are unique within *Pagamea,* and which may constitute the only qualitative synapomorphies within this lineage (note that these features are not included in the morphological dataset). With the exception of a clade (node “DD” in Fig. 1) for which only chloroplast data are available, all other Macrophylla have: (a) a conical stipule that opens laterally; (b) calices covered inside by adpressed hairs; and, (c), calices with short lobes and a long tube, which when fruiting tend to enclose the drupe by half of its length. All other samples of *Pagamea* have cylindrical stipules that open apically, calices that are glabrous inside or with erect minute hairs, and the calices with either very long lobes, or when short the tube is also very short, so that when fruiting the drupe sits in a shallow cupule.

There is also a phylogenetic correlation with variation in breeding systems (Fig. 8). Macrophylla, Thyrsiflora, Capitata and Harleyi largely have homostylous perfect flowers, although a few are apparently dioecious, while the LDP and Duckei are dioecious. The morphologically distinct Coriacea clade is an exception, showing great variation in breeding system including distylous flowers.

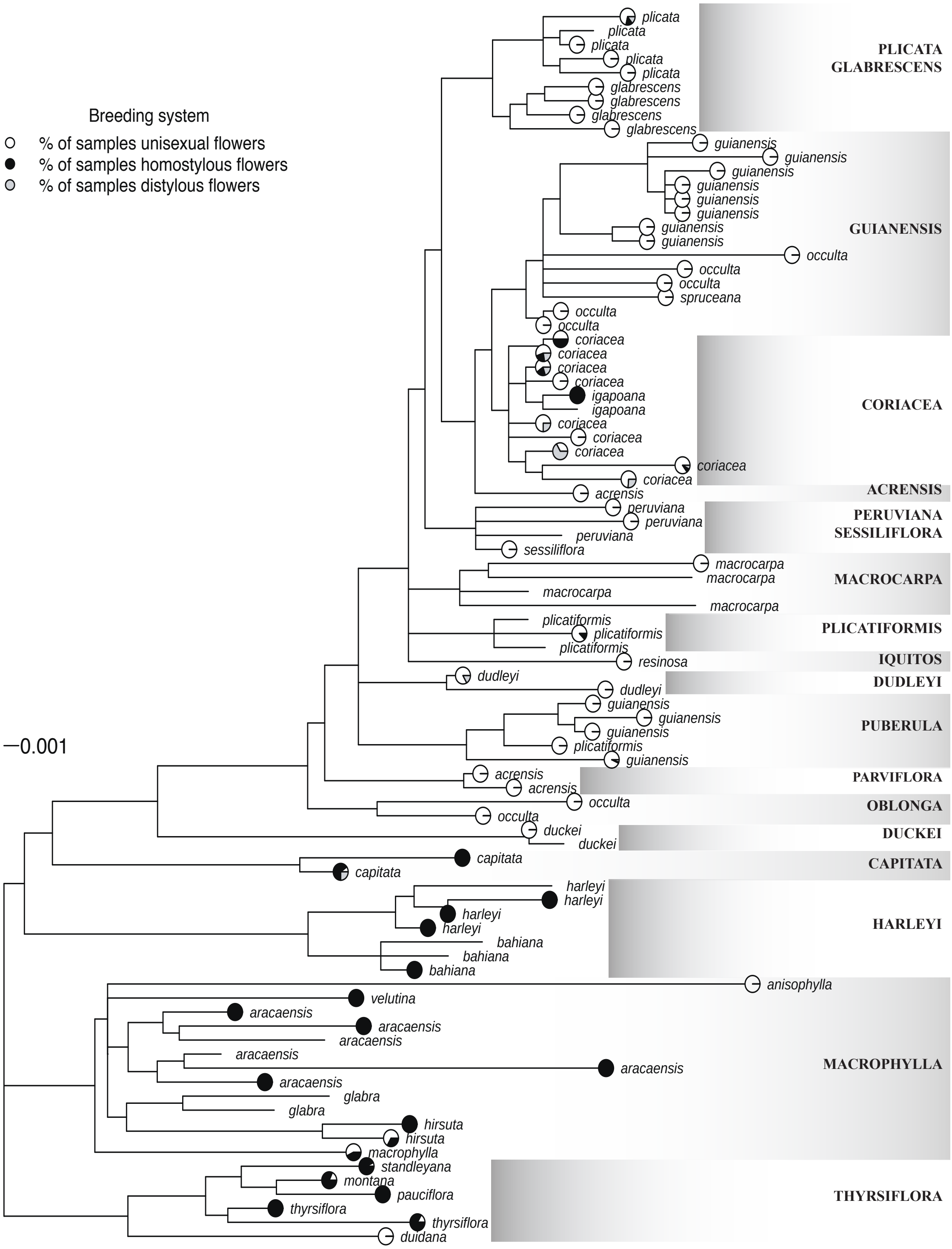


Fig. 8. Distribution of breeding system variation on the phylogeny. Pies on tips summarize the breeding system for all samples that could be assigned to each tip. Specimens were coded as having homostylous, pistillate, staminate, brevistylous, longistylous flowers or fruits. Breeding system is represented as the proportion of samples coded as a particular state over all samples containing flowers.

Geographical variation within and between clades

Most of the named clades in Figure 3 are morphologically coherent and appear in both chloroplast, ITS and combined analyses, the major exception being the Guianensis complex within which ITS and cpDNA clades differ. To determine the limits of provisional species, it is necessary to examine the spatial distribution of clades and examine patterns of morphological variation in sympatry. Accordingly, distribution maps are presented along with information on geographical proximity (proxy for sympatry) between groups, geographically localized analyses of morphological variation, and the correlation of altitude with phylogeny.

The Harleyi clade overlaps in morphological space with the other three closely related clades, Thyrsiflora, Macrophylla and Capitata (Fig. 6C-D). However, the Harleyi clade is allopatric and endemic to the Atlantic Coast of Brazil, and is thus geographically quite distinct from the other three. However, Harleyi is sympatric with the unrelated Guianensis clade (Fig. 9A-B, 10). Within the Harleyi clade are two reciprocally monophyletic and well-supported groups in both the ITS and combined trees (nodes “EE” and “CC” in Fig. 3; here called *harleyi* and *bahiana*). A map showing the relative locations of the two Harleyi subgroups plus the sympatric Guianensis is shown in Fig. 11A, along with a local morphometric analysis. Although the two Harleyi clades are somewhat more similar in the region of sympatry (Fig. 11B), samples included in the molecular analyses were collected from individuals found side by side at the same sites, and they are morphologically distinct (see Table 6 for characters correlated with ordination axes). One of the Harleyi clades (*bahiana*) is morphologically more similar to the unrelated but sympatric Guianensis samples than to the other Harleyi clade (*harleyi* in Fig. 11B), although Guianensis is dioecious and both Harleyi clades have perfect homostylous flowers (Fig. 8). The two Harleyi clades also have fruits with orange calices when mature, while those of Guianensis are bright red.

Thyrsiflora, Macrophylla and Capitata have Amazonian distributions and are largely sympatric, but are clearly morphologically distinct from each other (Fig. 6C-D, 9). Molecular data do not identify any clear subgoups within Macrophylla or Capitata. However, the Macrophylla clade has great morphological variation when compared to other clades (Fig. 6C-D), and within this clade samples form morphological groups that are sympatric (Fig. 10**,** 12). The only two well-supported nodes within the Macrophylla clade ("GG" and "HH", Fig. 3), correspond to samples from sympatric morphological groups. Node "HH" represents samples that form a separate group (*hirsuta* in Fig. 12) in morphological space (see Table 7 for character correlations). Note that samples of *velutina* in Figure 12 are distinct from *hirsuta* in the 3rd dimension (not shown). The other well-supported relationship within Macrophylla refers to node "GG", which is represented only by sterile samples from a single population (*glabra*). These samples are predicted by a Discriminant Analyses (DA; not shown) of vegetative characters to belong to a different Macrophylla morphological group (*aracaensis* in Fig. 12).

A combination of morphology, geographical distribution and breeding system identifies

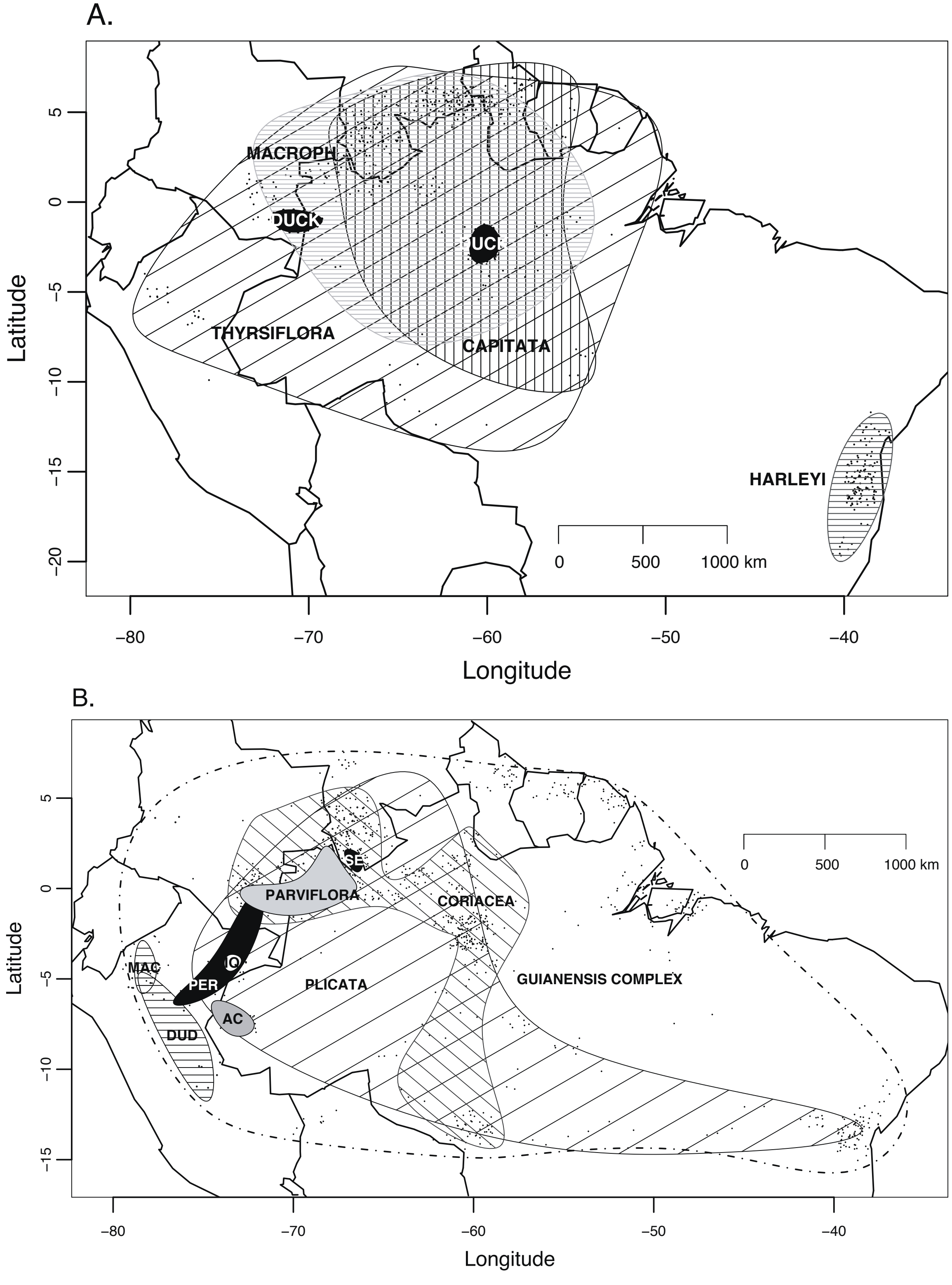


Fig. 9. Geographical distribution of clades. A. Macrophylla, Thyrsiflora, Duckei, Harleyi (includes Bahiana) and Capitata. B. LDP clades and Guianensis complex. Plicata refers to both Plicata and Glabrescens (see Fig. 15); MAC = Macrocarpa; DUD = Dudleyi; SE = Sessiliflora; PER = Peruviana; IQ = Iquitos; AC = Acrensis.

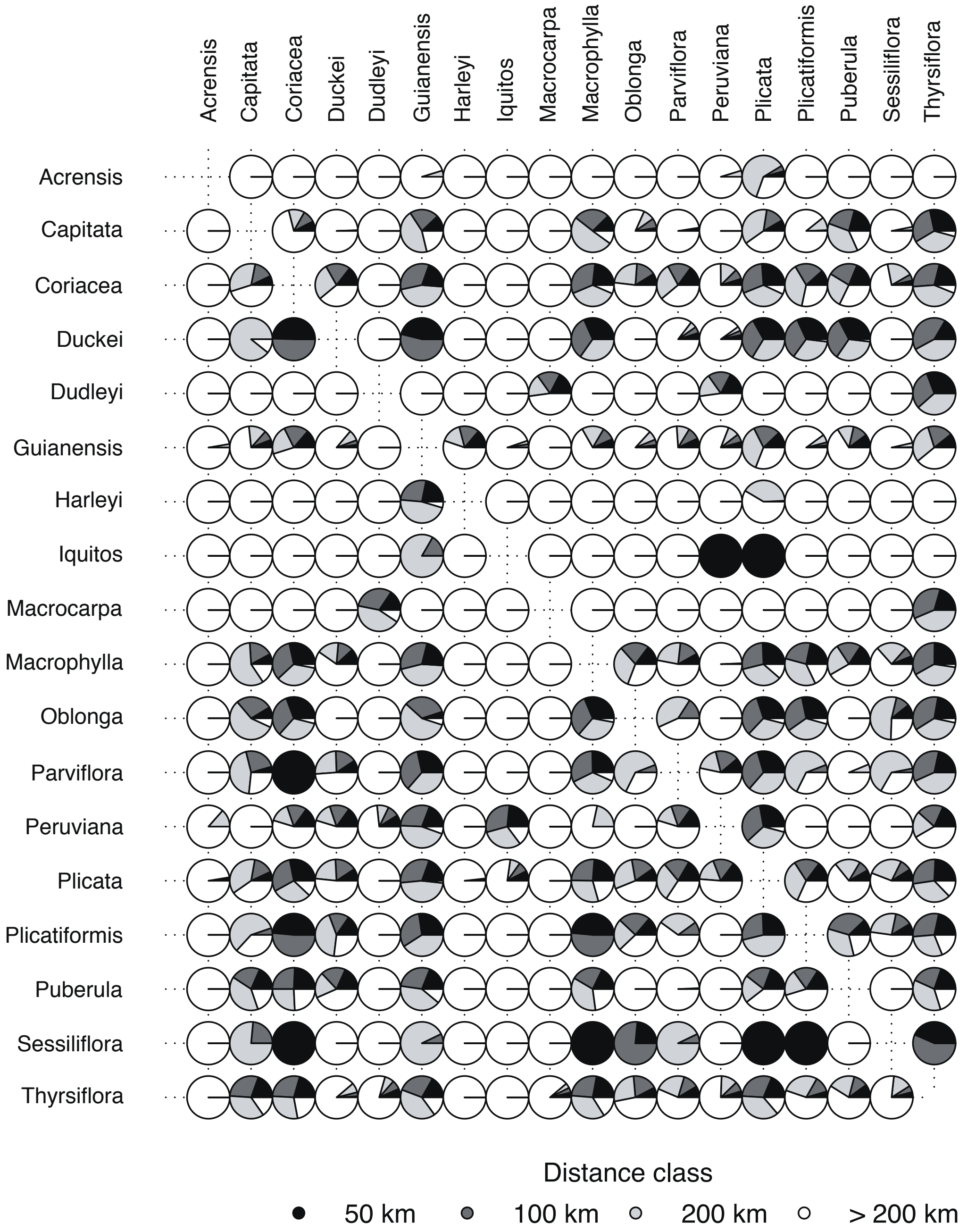


Fig. 10. Geographical relationships between major clades in the combined tree (Fig. 3). Pies represent the proportion of samples of one clade (row) that are found within a distance class from at least one sample of another clade (column). The maximum distance shown in these pies is 200 km. The "matrix" is not symmetrical. For example, the Harleyi clade (row) occurs (at a 200 km level) only with the Guianensis and Plicata clades (columns), but very few Harleyi and Plicata are in close proximity and these are found at more than 100 km of distance (they appear only at the 200 km class); while most samples of Harleyi are found within a 200 km of the Guianensis clade, few samples of the Guianensis clade (row) are found in close proximity with samples of the Harleyi clade (column). A white pie indicates allopatry. [Note that Plicata and Glabrescens are combined here].

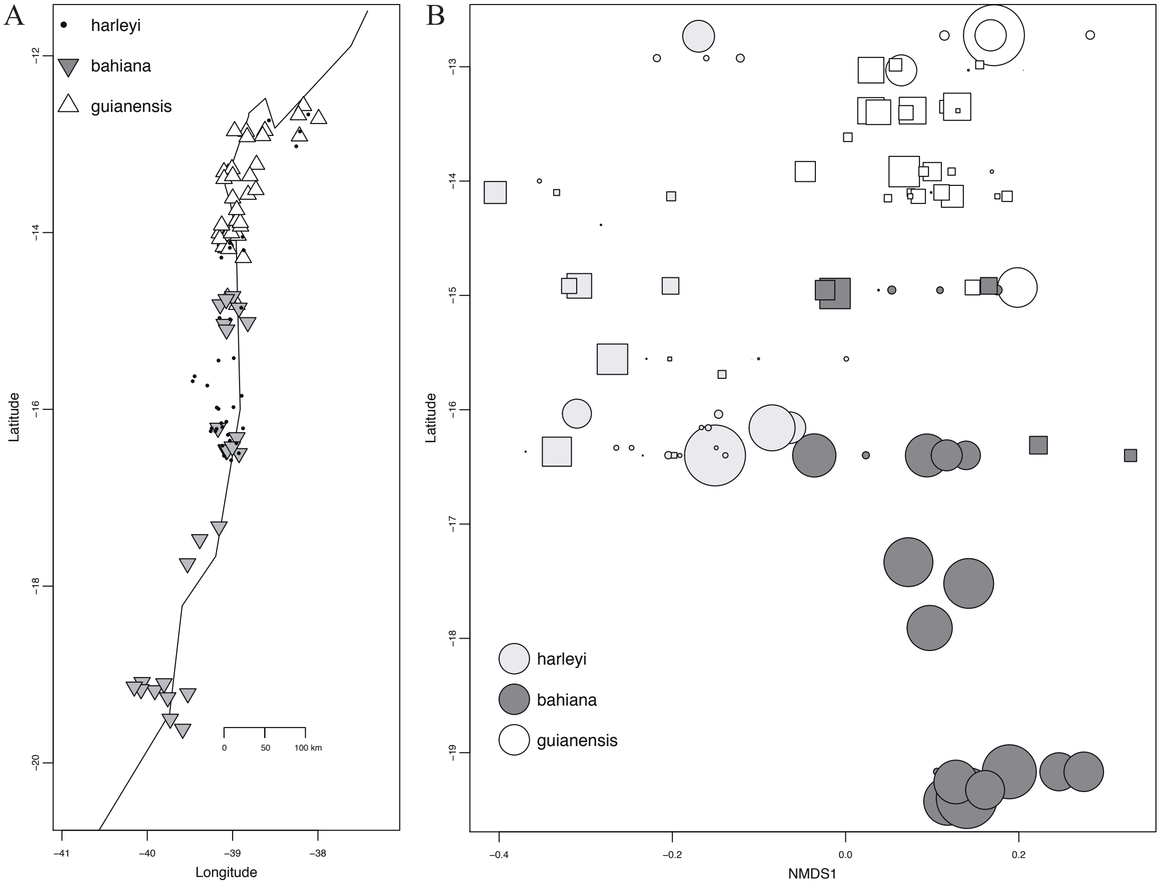


Fig. 11. Harleyi clade and sympatric Guianensis samples. **A**. Geographical distribution of samples of the Harleyi and Guianensis clades along the Atlantic Coast of Bahia, Brazil. **B**. Pattern of morphological variation in NMDS1 and NMDS2 scores over geographical space (here only Latitude). NMDS2 values are represented by symbols, positive values as circles and negative values as squares -- the largest the symbol the greatest the distance from 0. Note that the Guianensis and the Bahiana clade are more similar to each other on NMDS1 scores than they are to Harleyi. Note also that the close approach in NMDS1 scores between the two Harleyi clades occurs in the region of sympatry.

several groups (Fig. 12). For example, *aracaensis* and *anisophylla* largely overlap in this two-dimensional morphological space (Fig. 12A), but have different breeding systems (homostyly and dioecy, respectively) and allopatric distributions, the former being restricted to the Central Amazon region and the latter to the Ventuari River basin in Venezuela. There is also interesting variation within each of these groups that is not further explored due to the lack of phylogenetic resolution. For example, *aracaensis* forms two morphologically rather different subgroups (Fig. 12A) that are also allopatric and differ in habitat type. One is from the white-sand savannas near the Aracá tepui in Brazil, the other from the understory of tall campinarana forests south of this region; these morphotypes are also separated by the Negro river. Despite these allopatric morphological groups within the Macrophylla clade, some are sympatric (Fig. 12B), suggesting they may represent different species.

The association of altitude and phylogeny (ITS tree) is highly significant, according to the same method used to test for phylogenetic dependence of morphology. Although high-altitude specimens are known from at least seven clades, only two nodes account for most of the variance in altitude (Fig. 13). One node refers to the Thyrsiflora clade (vector 9 in Fig. 13A and node in 13B), which includes most high-altitude collections of *Pagamea,* particularly from the tepuis of the Guayana Shield, but also from the Andes.

T**able 6**. Harleyi clade and sympatric Guianensis. Morphological characters significantly correlated (at P<=0.01) with the two axes of a 2 dimensional space (Fig. 11). Values = Spearman correlation. See Table 1 for character descriptions.

Characters	**NMDS1**	**NMDS2**	**Characters**	**NMDS1**	**NMDS2**
LEAFLEN - mm	-0.83		PUBABAX - score	-0.55	
LEAFWID- mm	-0.82		INFLLEN - mm	-0.51	-0.69
CALYXLOB - mm	-0.76		INFLNO2 - count	-0.49	
INFLSH2 - ratio	-0.72		CALYXTUB - mm	-0.49	0.41
CALYXRAT - ratio	-0.71		NFLOWERS - count	-0.44	-0.6
INFLPEDU - mm	-0.69	-0.49	OVARYPUB - score	-0.41	-0.27
INFLPUB - score	-0.68		VENADENS - ratio	0.26	
CALXYPUB - score	-0.66	0.46	LFSHAPE1 - ratio		0.53
PETIOLEN - mm	-0.63	-0.39	LFSHAPE3 - ratio		-0.46
INFLSH1 - ratio	-0.63	0.32	INFLNO1 - count		-0.63
DOMADENS - ratio	-0.61	0.26	INFLSH4 - ratio		0.48
INFLBRAN - mm	-0.6				

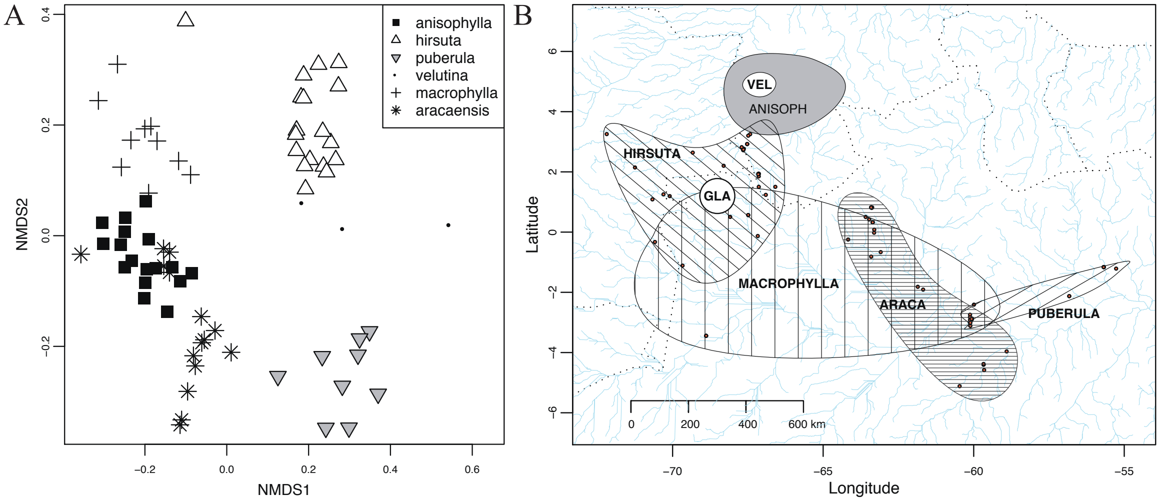


Fig. 12. Macrophylla clade. **A**. Morphological variation reduced to two dimensions with non-metric multidimensional scaling (NMDS). Labels refer to species recognized in this study (see text). Note that *aracaensis* largely overlaps with *anisophylla*, but they have different breeding systems (homostyly and dioecy, respectively), and apparently are not immediately related (Fig. 1, 3). **B**. Geographical distribution of species in the Macrophylla clade. GLA = the *glabra* species, for which fertile material is unknown; VEL = *velutina*. Note that *puberula* is placed in the Macrophylla clade according to chloroplast data only (Fig. 1), and the two accessions collected from the opposite ends of its range had very long branches in the cpDNA tree. *Puberula* lacks apomorphies shared by all other members of this clade, and its placement in this clade may be wrong. Two “species” in the Macrophylla clade have not been sampled for molecular data and are included in this figure (see Chapter 3).

Table 7. Macrophylla clade. Morphological characters significantly correlated (at P<=0.01) with the two axes of a 3 dimensional space (Fig. 12). Values = Spearman correlation. See Table 1 for character descriptions.

Character	NMDS1	NMDS2	NMDS3	Character	NMDS1	NMDS2	NMDS3
PETIPUB - score	0.772	0.252		NFLOWERS - count	-0.366	0.437	0.25
PUBADAX - score	0.767	0.44		CALYXRAT - ratio	0.35	-0.372	0.465
PUBABAX - score	0.758	0.422		INFLSH3 - ratio	0.342		-0.5
INFLPUB - score	0.723	0.406		INFLSH1 - ratio	0.305		-0.71
LFSHAPE2 - ratio	-0.675			INFLLEN - mm	-0.239	0.763	
INFLSH4 - ratio	0.652	-0.495	-0.416	PETIOLEN - mm		0.665	0.317
INFLSH2 - ratio	-0.621	0.528	0.221	LEAFLEN - mm		0.753	
INFLNO2 - count	-0.621	0.591	0.282	LEAFWID - mm		0.77	
INFLBRAN - mm	-0.593	0.643	0.282	LFSHAPE1 - ratio		0.6	-0.35
INFLNO1 - count	-0.549	0.498	0.256	DOMADENS - ratio		-0.41	0.399
LFSHAPE3 - ratio	-0.433	-0.236	0.379	VENADENS - ratio		-0.59	-0.339
OVARYPUB - score	0.41	-0.255	0.632	INFLPEDU - mm		0.69	-0.392
CALXYPUB - score	-0.399	0.668	-0.323	CALYXTUB - mm		0.548	-0.362
CALYXLOB - mm	0.381	-0.295	0.435				

The other node refers to the combined Dudleyi and Macrocarpa clades, which are restricted to the Andes. A few high-altitude (> 1500 m) collections are also found in the the Capitata (not sampled) and Macrophylla (accessions *velutina vs. macrophylla* in Fig. 13) clades, although most samples in these clades are from mid (500-1000 m) or low (< 300) altitudes, respectively. High-altitude samples of the Glabrescens clade are from the Brazilian Shield (Chapada Diamantina and Veadeiros; Fig. 13B). The LDP clade has not been found at mid- or high-altitudes in the Guayana Shield.

Relationships within the Thyrsiflora clade are strongly supported both by the ITS and combined analyses (Fig. 2, 3). These trees strongly support *duidana* as sister to the rest. *Duidana* represents a group of specimens from Duida tepui in Venezuela that are dioecious, while the remaining Thyrsiflora samples have perfect homostylous flowers (a few populations of the lower altitude *thyrsiflora* appear to be dioecious). *Duidana* is sister to a clade comprising two reciprocally monophyletic groups (nodes “MM” and “KK” in Fig. 3; here called *thyrsiflora* and *tepui*, respectively). *Tepui* includes high-altitude (> 1000 m) samples from different tepuis in the Guayana Shield, while *thyrsiflora* (node “MM”) includes samples from lower elevations in the Guayana Shield (< 500 m.a.s.l.) and from mid- to high altitudes in the Andes (~ 1000 m.a.s.l.; Fig. 9, 14D). *Duidana* and the *tepui* form a separate morphological group from *thyrsiflora* (Fig. 14A-B; Table 8 for character correlations), and both are also sympatric with *thyrsiflora*, although they usually differ in altitudinal distribution (Fig. 14C-D). Besides *duidana* and *thyrsiflora*, a third group of high-altitude specimens (*montana*) also occurs on Duida

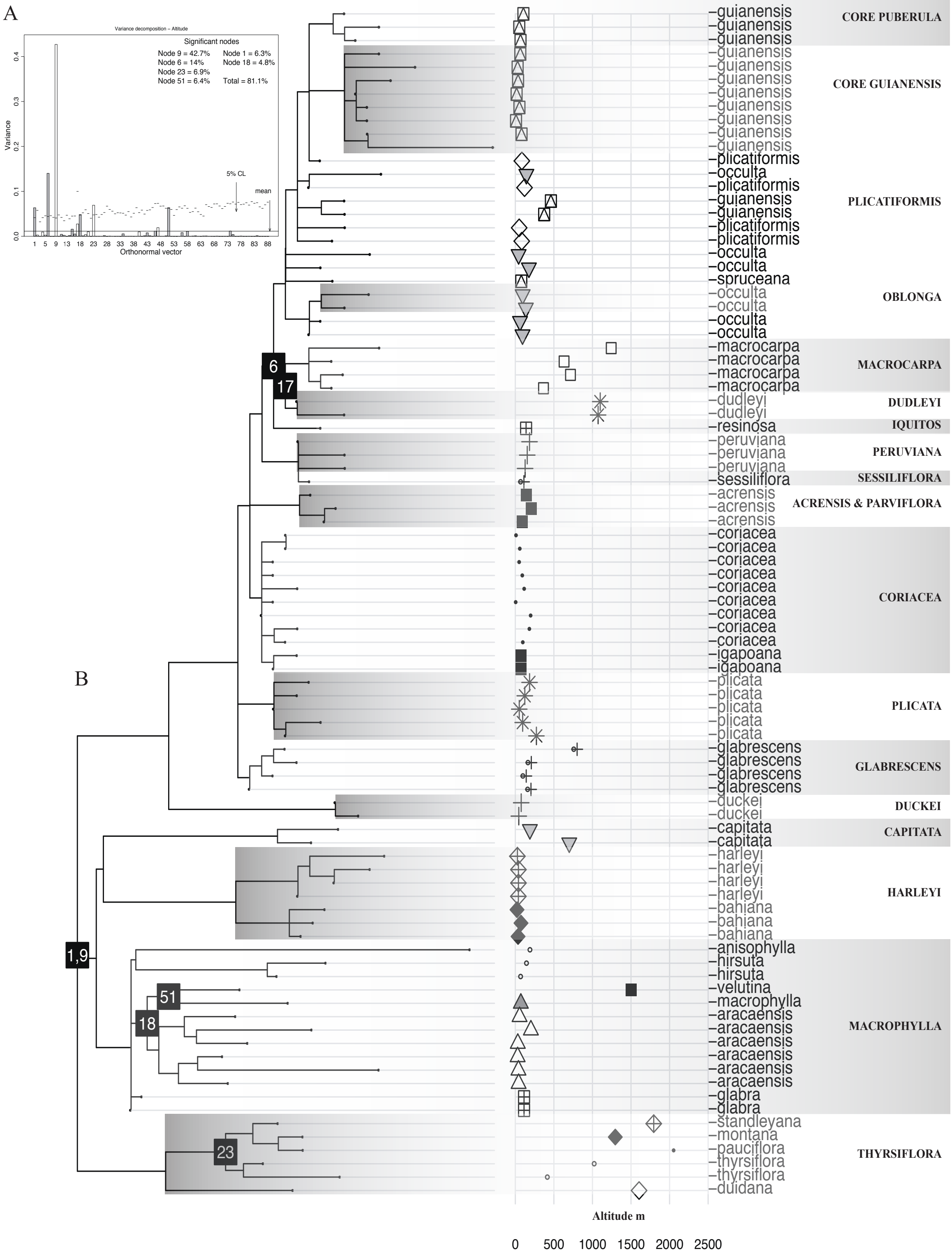


Fig. 13. Relationship between phylogeny and altitude. Nodes indicated show a significant relation with altitude (P<0.0001). High altitude samples from Macrocarpa and Dudleyi are from the Andes, where Thyrsiflora also is found at high-altitudes (Fig. 14). Those of Plicata are from the Atlantic Shield of Brazil. The remaining high-altitude samples are from the Guayana Shield.

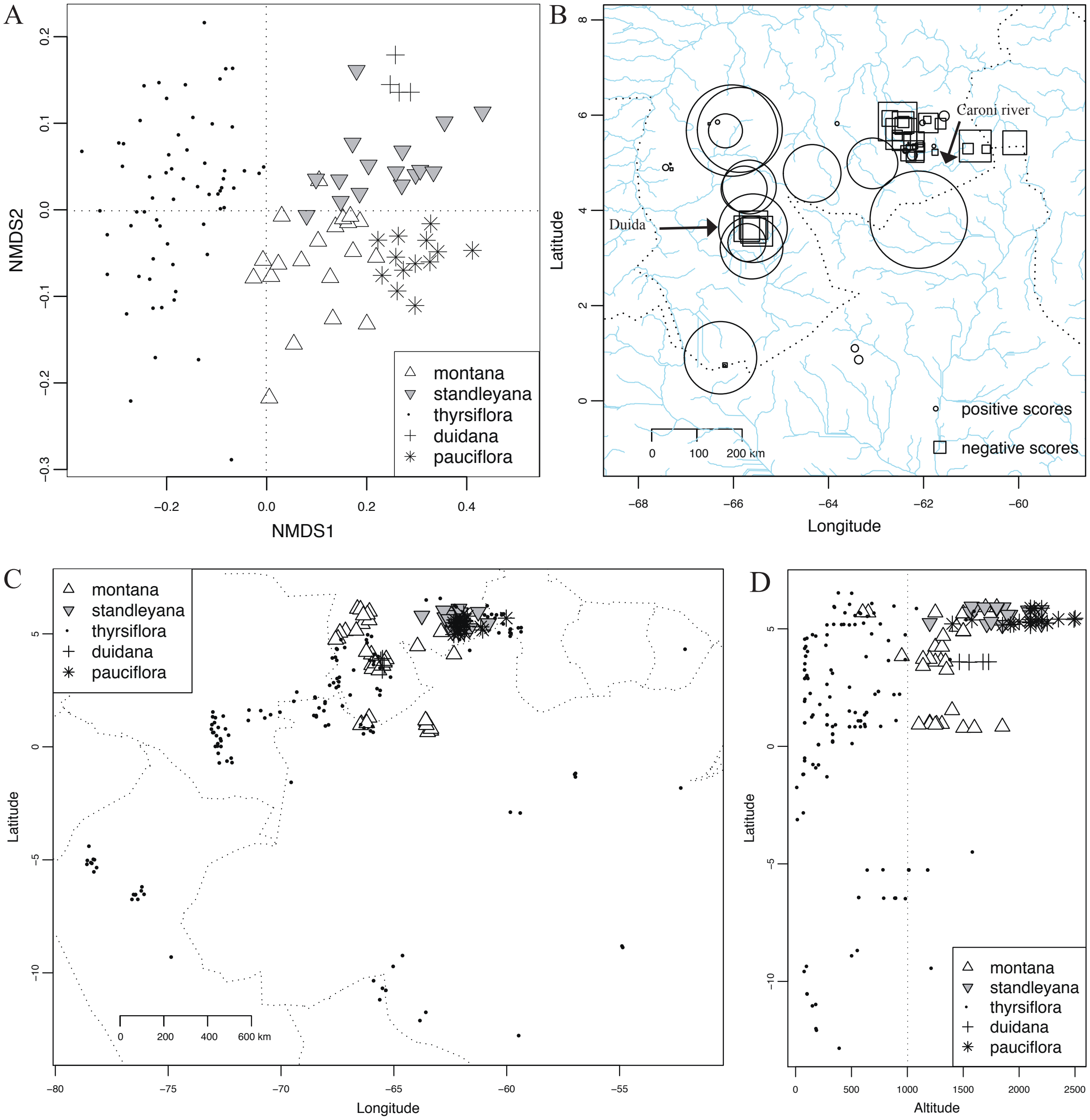


Fig. 14. Thyrsiflora clade. **A**. Morphological space. **B**. Morphological variation in space for the high-altitude species of the Guayana Shield (*duidana*, *pauciflora*, *montana*, *standleyana*). Circles and squares represent positive and negative scores on a single axis obtained with Non-Metric Multidimensional Scaling; size of symbols indicate distance from 0. Note the different symbols and/or symbols of different sizes at several localities, indicating that morphologically distant samples are sympatric. The extremes of such variation in the whole group occurs at Duida (horizontal arrow), where large circles (*montana*) and large squares (*duidana*) are found. Note also a tendency for morphological values to decrease (correlates with an overall decrease in the size of parts) between the Western and Eastern Guayana Shield, as divided by the Caroni river. **C-D**. Spatial and altitudinal distribution for all species in the Thyrsiflora clade. Note that *thyrsiflora* is predominantely at mid elevations and is widespread, while all the other species are restricted to higher altitudes in the Guayana Shield.

Table 8. Thyrsiflora clade. Morphological characters significantly correlated (at P<=0.01) with the two axes of a 3 dimensional space (Fig. 14). Values = Spearman correlation. See Table 1 for character descriptions.

Characters	NMDS1	NMDS2	NMDS3	Characters	NMDS1	NMDS2	NMDS3
INFLBRAN - mm	-0.98			REVPROP - ratio	0.57		
INFLNO2 - count	-0.92			LFSHAPE1 - ratio	0.54		
NFLOWERS - count	-0.9			LFSHAPE2 - ratio	0.52		0.39
INFLSH2 - ratio	-0.89			PETIOLEN - mm	-0.44		
INFLNO1 - count	-0.88			CALYXRAT - ratio	0.4		
LEAFLEN - mm	-0.87			DOMADENS - ratio	-0.39		0.8
INFLLEN - mm	-0.85	-0.26		VEDENS - ratio		0.37	
INFLSH4 - ratio	0.82	-0.27		INFLPEDU - mm		-0.54	-0.3
INFLSH1 - ratio	0.81	-0.33		PETIPUB - score		0.7	
CALYXLOB - mm	0.67			PUBABAX - score		0.52	
LEAFWID - mm	-0.66	-0.28		PUBADAX - score		0.65	
LFSHAPE3 - ratio	0.64			INFLPUB - score		0.52	
CALYXTUB - mm	0.61	-0.29					

tepui. These specimens also belong to the Thyrsiflora clade according to the chloroplast datasets (herbarium material; I could not amplify the ITS), and they also belong to the morphological group that includes the *duidana* and the *tepui* clades. *Duidana* and these specimens are morphologically very different, representing the extremes of the variation within the high-altitude samples (squares and circles on Duida tepui in Fig. 14B). This indicates that at Duida tepui the three main lineages of the Thyrsiflora clade as represented by *duidana*, *montana* and *thyrsiflora*, are sympatric. Furthermore, within the *tepui*+*duidana* morphological group, which corresponds to high-altitude plants of the Guayana Shield, there is an overall decrease in the size of parts between plants from western to eastern Guayana Shield, coinciding with the position of the Caroni river (circles and squares in Fig. 14B); this is a major geographical barrier (Funk and Brooks 1990).

Among the LDP, the ranges of Plicata+Glabrescens and Coriacea completely overlap, and both are widespread. Macrocarpa, Dudleyi, Iquitos, Peruviana, Acrensis, Parviflora and Sessiliflora have restricted distributions in Western Amazonia; those of Iquitos and Sessiliflora are less than 100 km across (Fig. 9). Most of these clades are sympatric with Plicata, Glabrescens and/or Coriacea, and with members of the Guianensis complex (Fig. 9). Duckei is known from two allopatric populations (only one sampled for molecular and moprhological data; see Chapter 3), which are sympatric with several other clades (Fig. 9, 10).

Although there is morphological overlap between some LDP clades, this is reduced when geography is taken into consideration. The morphological overlap between [Plicata+Glabrescens] and Coriacea (Fig. 6E, F), for example, is caused by samples that are allopatric to each other. This is indicated by the observation that average morphological distance is much greater between clades than within clades at each site where these two clades are sympatric (Fig. 15A). Likewise, samples of the Plicata and Glabrescens clades, reciprocally monophyletic, form two major morphological groups. However, these do not correspond precisely to the two clades (Fig. 15B; Table 9 for character correlations) as suggested by phylogenetic dependence at the node separating these clades (Fig. 5). My sampling does not allow a clear understanding of the morphological distinction and geographical distribution between these two clades. However, although accessions of Plicata are from North of the Amazon river, these clades were sampled in close proximity (~ 100 km) in Central Amazon, where

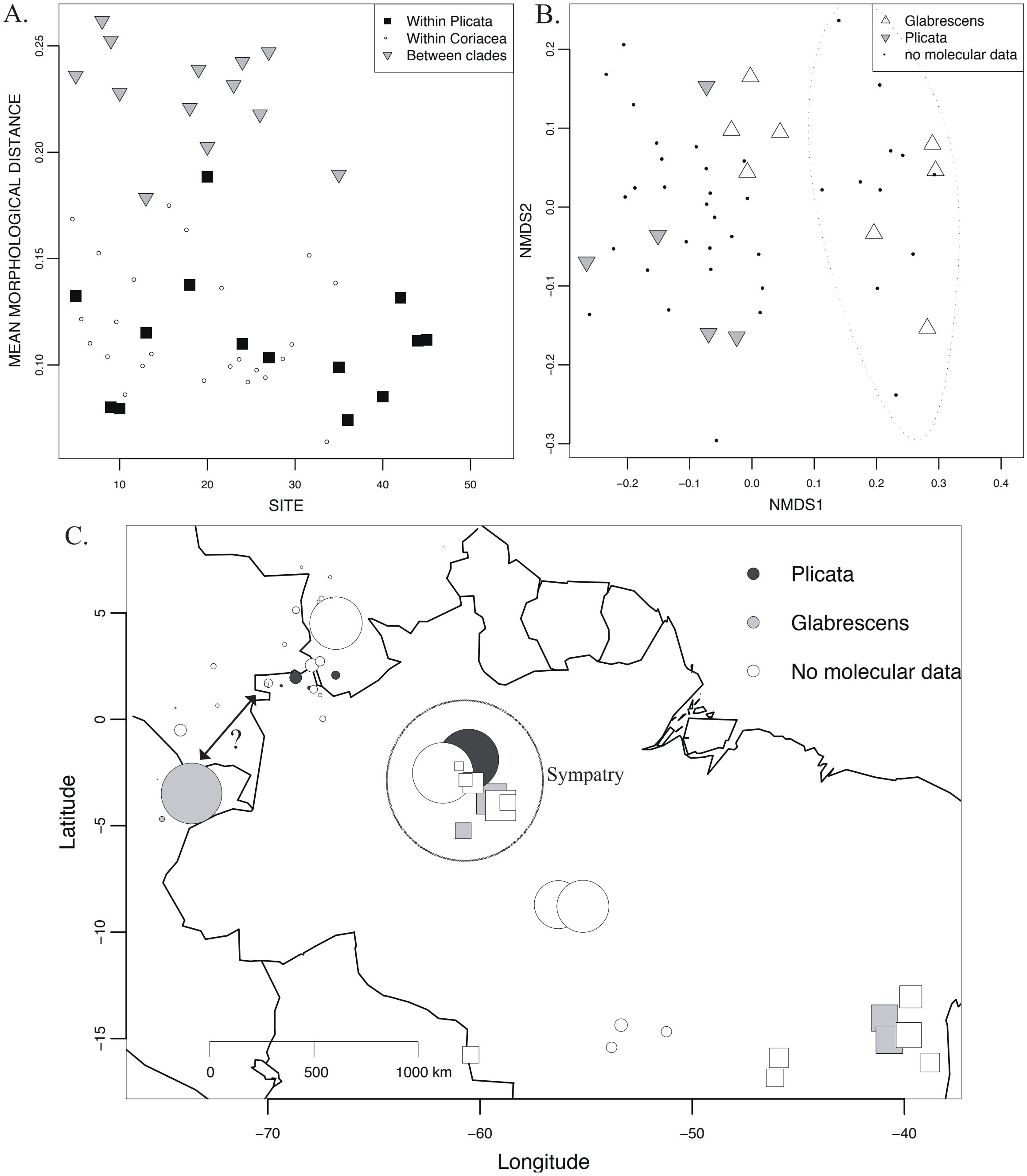


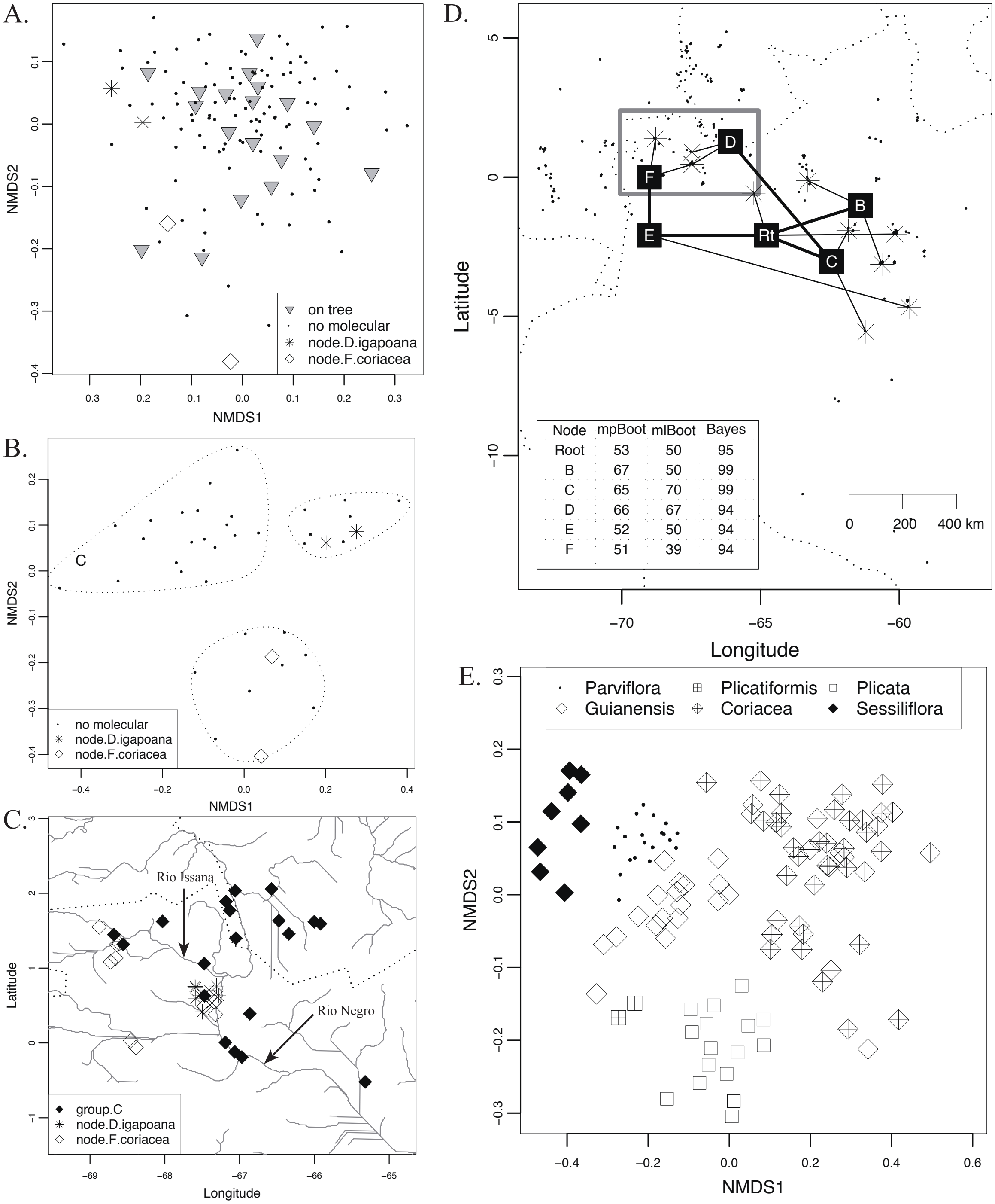
Fig. 15. Variation within the LDP clade. **A**. Comparison between [Plicata+Glabrescens] and the Coriacea clade. Average pairwise morphological distance within and between these two clades at different sites. . Sites defined by cluster analysis of geographical distances (average method, cut off value of 100 km). **B-C**. Plicata+Glabrescens clade: **B**. morphological space with position of samples included in the phylogenetic trees indicated; **C**. spatial distribution of morphological variation within this clade (NMDS single-axis: squares = negative values, circles = positive values, symbol size proportional to absolute value). Note that in the region of sympatry the two clades are morphologically different. There may also be overlap towards the South (squares and circles), while samples of Glabrescens from Western Amazon are morphologically more similar to Plicata. Arrow indicates region where the two clades may also overlap in distribution, but sympatry is unknown. Noise was added to spread points.

specimens form two morphological groups (squares and circles in the sympatry area in Fig. 15C). The samples of Glabrescens that overlap in morphology with samples of Plicata are from Western Amazon (Peru; Fig. 15C), where only Glabrescens is found. Hence, Glabrescens and Plicata are morphologically distinct where sympatric, and the morphological overlap is caused by allopatric samples.

There are no obvious morphological groups within the Coriacea clade when specimens from the whole range are considered (Fig. 16A). However, in the Upper Rio Negro region there are two Coriacea clades that are morphologically distinct and sympatric (Fig. 16B-D; Table 10 for character correlations). These clades are indicated by both the chloroplast and ITS data and there is one well-supported node separating them (node "P" in Fig. 3, and "C" in Fig. 16D). In the Upper Rio Negro region, these clades also occur in different habitats: samples of node "D" (*igapoana*) in Figure 16D are from a single locality in flooded forests (igapó), while one sample of node "F" (*coriacea*) was collected on non-flooded white-sand forests at the same locality. Morphological analyses

Table 9. Plicata+Glabrescens clade. Morphological characters significantly correlated (at P<=0.01) with the two axes of a 2 dimensional space (Fig. 15B). Values = Spearman correlation. See Table 1 for character descriptions.

Characters	**NMDS1**	**NMDS2**	**Characters**	**NMDS1**	**NMDS2**
INFLBRAN - mm	-0.82	-0.44	PETIPUB - score	-0.5	
INFLSH2 - ratio	-0.79	-0.46	LEAFWID - mm	-0.45	
INFLNO2 - count	-0.76	-0.37	OVARYPUB - score	-0.42	
INFLNO1 - count	-0.7	-0.44	LFSHAPE2 - ratio	-0.42	
NFLOWERS - count	-0.62	-0.47	DOMADENS - ratio		0.51
INFLSH1 - ratio	0.6	0.66	INFLPEDU - mm		0.5
INFLLEN - mm	-0.59		PUBABAX - score		0.56
PETIOLEN - mm	-0.53		PUBADAX - score		0.44
INFLSH4 - ratio	0.5		INFLPUB - score		0.58



Node	mpBoot	mlBoot	Bayes
Root	53	50	95
B	67	50	99
C	65	70	99
D	66	67	94
E	52	50	94
F	51	39	94

Fig. 16. Coriacea clade. **A**. Morphological space. **B-C**. Morphological space and geographical distribution for samples from the Upper Rio Negro region (square in D). **D**. Phylogeny in space: ITS-cpDNA topology for these collections (Fig. 3), but support for all nodes is indicated. Positions of ancestral nodes are arbitrary. Thick lines indicate internal branches, thin lines tip branches, root node is indicated (Rt; corresponds to node "N" in Fig. 3). Asteriks indicate tips. Node "C" corresponds to node "P" in Figure 3. Black dots represent all collections of the Coriacea clade. **E**. Morphological space for all samples from within the range of the Parviflora clade (also Upper Rio Negro).

Table 10. Coriacea clade: Upper Rio Negro. Morphological characters significantly correlated (at P<=0.01) with the two axes of a 2 dimensional space (Fig. 16B). Values = Spearman correlation. See Table 1 for character descriptions.

Characters	NMDS1	NMDS2	Characters	NMDS1	NMDS2
NFLOWERS - count	-0.85		CALYXTUB - mm	0.62	
INFLBRAN - mm	-0.8		VENADENS - ratio	0.58	0.72
INFLNO2 - count	-0.79		INFLLEN - mm	-0.53	-0.45
LFSHAPE2 - ratio	-0.77		INFLPUB - score	0.49	
INFLNO1 - count	-0.77		CALYXLOB - mm	0.48	-0.57
PETIOLEN - mm	-0.72		LEAFLEN - mm		-0.83
INFLSH1 - ratio	0.7		DOMADENS - ratio		-0.78
LFSHAPE1 - ratio	-0.67		INFLPEDU - mm		-0.55
LEAFWID - mm	-0.65		INFLSH4 - ratio		0.43
INFLSH2 - ratio	-0.65		CALYXRAT - ratio		-0.58
INFLSH3 - ratio	0.63		OVARYPUB - score		-0.68
LFSHAPE3 - ratio	-0.63	0.43			

also suggest a third morphological group occurring in this region (*group.c*; not sampled for molecular data). There is a significant association between habitat type and the three morphological groups (Chisq = 31.413, df = 4, P<0.0001). *Group C* occurs mostly in non-flooded but open habitats (scrublands and open caatinga). Both *group C* and *coriacea* are dioecious, whereas a single collection with flowers of *igapoana* suggests that this group may have perfect flowers. The areas inhabited by the two dioecious groups in this region are separated by the Rio Issana and the Rio Negro (Fig. 16C). These patterns indicate that, at least in the Upper Rio Negro, the Coriacea clade includes sympatric morphologically distinct groups, two of which have also a phylogenetic basis, the third being unsampled as yet. Furthermore, *coriacea* and *group C* are consistently found in sympatry throughout the range of the clade (see also Chapter 3).

The pattern of morphological distinction in sympatry also appears among the remaining LDP clades that strongly overlap in morphological space (“dash-dot” area in Fig. 6E).

The only "exception" is Dudleyi and Macrocarpa, which are allopatric to the rest (Fig. 9B, 10). Although these two clades are sympatric in northern Peru, there are too few fertile specimens from the region of sympatry to understand patterns of morphological variation there.

Acrensis and Parviflora, which are sister clades according to the ITS dataset (node "M", Fig. 2), are morphologically very similar (see values on Fig. 7E) and strongly allopatric (Fig. 9B, 10). Acrensis is also allopatric with all clades that are morphologically similar and closely related to it (Fig. 10). Parviflora, on the other hand, is sympatric with several of these clades, and in the region of sympatry, samples of Parviflora form a coherent morphological group (note that it discriminates from Guianensis in a third dimension, cf. Fig. 16E).

The clades that according to the ITS tree form the Guianensis complex (Fig. 2), are also morphologically very similar when specimens from the entire range are compared. This analysis also fails to discriminate the four clades (Puberula, Oblonga, Guianensis and Plicatiformis) when considering only the position of accessions included in the phylogenetic trees (Fig. 17A). However, these clades are found sympatric in the both the Orinoco and Negro rivers basins (areas a and b in Fig. 17B). In the Central Amazon, the Guianensis, Puberula and Plicatiformis clades are all sympatric (area b in Fig. 17B). There is no incongruence between the ITS and chloroplast datasets in the samples from this region (see above). If the morphological analysis is confined only to samples from the Central Amazon, morphological clusters can be identified that correlate with the phylogenetic differences (Fig. 17C-F). Samples of Guianensis are distinct from samples of Puberula+Plicatiformis (Fig. 17C and Table 11 for character correlations), although the latter two intergrade. This difference is also correlated with habitat difference. Samples of Guianensis in this region are from flooded habitats (*igapó*), while samples of Puberula+Plicatiformis are both from unflooded white-sand forests (*Campinarana*).

The relationship between Puberula and Plicatiformis is more complex. First, two accessions of the Puberula clade are morphologically more similar to samples of Plicatiformis than they are to other samples of Puberula (Fig. 17C). The morphological group including only Puberula samples (group A in Fig. 17C) forms a well-supported monophyletic group in both the ITS and combined analyses (Core Puberula in Fig. 2, 3). In the chloroplast tree, this Core Puberula clade is sister to a clade containing the samples that overlap morphologically with the Plicatiformis clade (accessions in group B, Fig. 17C). These two chloroplast clades are sympatric in the Central Amazon (Fig. 17D; Table 12). In the chloroplast data, although the reciprocal monophyly of these lineages is indicated in strict-consensuses and ML trees, there is no support (node “O” in Fig. 1). ITS data do not indicate the monophyly of group B, i.e. Plicatiformis and the Puberula accessions morphologically similar to it. However, branches are very short and their monophyly is not rejected (SH test, P=0.56). Therefore, the Core Puberula clade, monophyletic according to both ITS and chloroplast data, is morphologically and phylogenetically distinct from Plicatiformis (i.e. group B) in the region of sympatry (Fig. 17C-D).

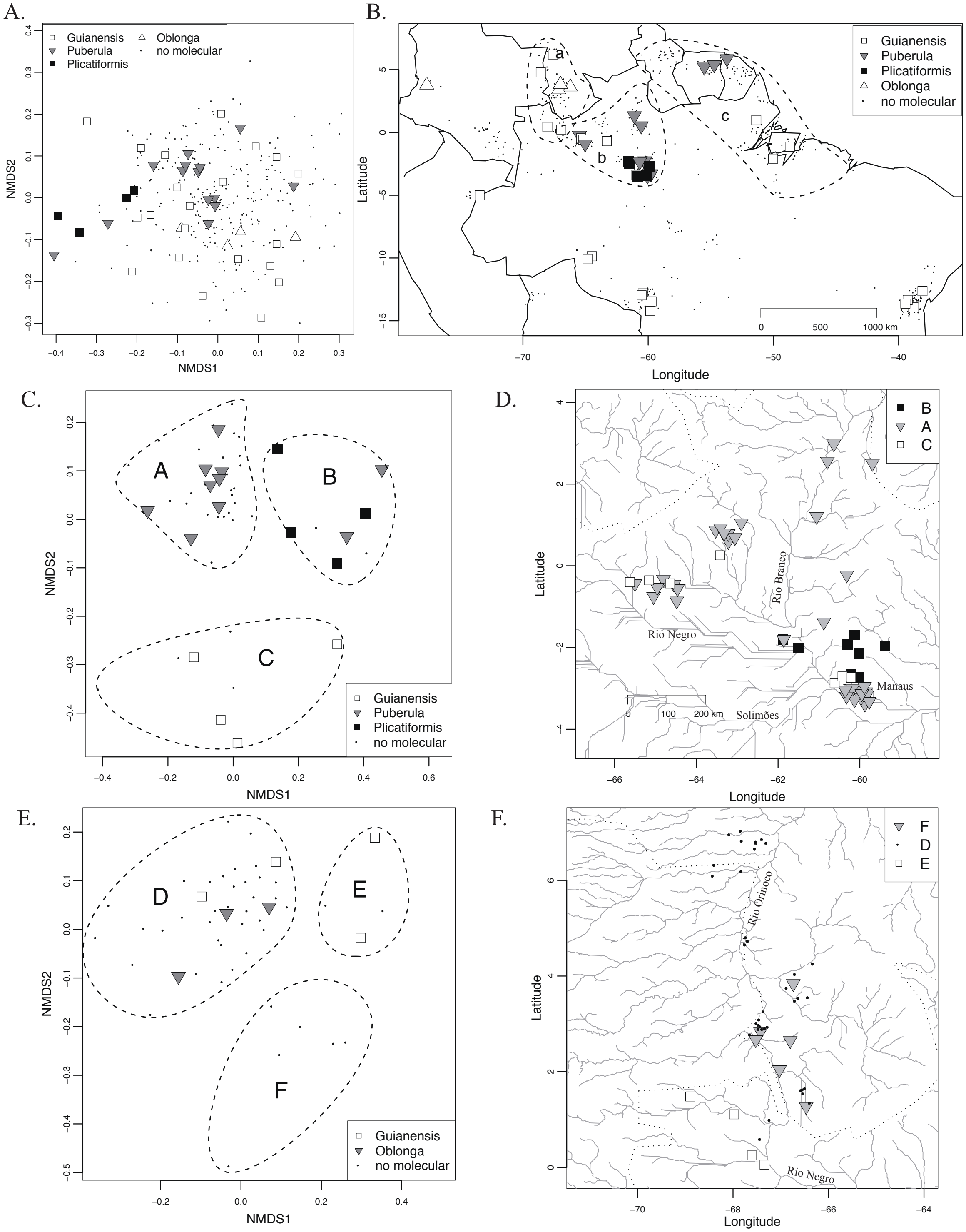


Fig. 17. Guianensis complex. **A**. Morphological space with position of samples from the different clades in the combined tree (see Fig. 3). **B**. Geographical distribution of these samples. The dotted areas indicate local analyses: (a) Venezuelan samples; (b) Central Amazon; (c) North Atlantic Coast. **C-F**. Local analyses: **C-D**. Morphological space and geographical distribution of samples from Central Amazon. **E-F**. Same for samples from Venezuela and the Upper Rio Negro region.

Clades from the Guianensis complex are also sympatric in the Orinoco basin in Venezuela. In this region, the Oblonga clade is found sympatric with accessions of Guianensis (Fig. 17F). Morphological analyses of samples from this region indicate three morphological groups, one of which was not sampled for the phylogenetic analyses (Fig. 17E). One of these groups includes the samples of Oblonga and two samples of the Guianensis clade. In the ITS tree these Oblonga samples form a monophyletic group (node I in Fig. 2) with samples of Guianensis from Central

Table 11. Guianensis complex: Central Amazon. Morphological characters significantly correlated (at P<=0.01) with the two axes of a 2 dimensional space (Fig. 18A). Values = Spearman correlation. See Table 1 for character descriptions

Characters	**NMDS1**	**NMDS2**	**Characters**	**NMDS1**	**NMDS2**
CALYXLOB - mm	0.72	-0.42	PETIOLEN - mm	0.38	-0.73
PUBABAX - score	0.64		LFSHAPE1 - ratio		-0.39
CALYXRAT - ratio	0.62		LFSHAPE3 - ratio		-0.57
CALYXTUB - mm	0.6	-0.42	VENADENS - ratio		0.61
INFLSH4 - ratio	0.57		INFLPEDU - mm		-0.46
INFLNO1 - count	-0.54	-0.48	INFLLEN - mm		-0.65
INFLPUB - score	0.54		INFLBRAN - mm		-0.46
PUBADAX - score	0.52		INFLNO2 - count		-0.38
PETIPUB - score	0.5		INFLSH2 - ratio		-0.38
LEAFLEN - mm	0.42	-0.68	OVARYPUB - score		0.45
LEAFWID - mm	0.42	-0.64			

Table 12. Guianensis complex: Venezuela. Morphological characters significantly correlated (at P<=0.01) with the two axes of a 2 dimensional space (Fig. 18B). Values = Spearman correlation. See Table 1 for character descriptions.

Characters	**NMDS1**	**NMDS2**	**Characters**	**NMDS1**	**NMDS2**
INFLBRAN	-0.82	-0.44	Characters	NMDS1	NMDS2
INFLSH2	-0.79	-0.46	LEAFWID	-0.45	
INFLNO2	-0.76	-0.37	OVARYPUB	-0.42	
INFLNO1	-0.7	-0.44	LFSHAPE2	-0.42	
NFLOWERS	-0.62	-0.47	DOMADENS		0.51
INFLSH1	0.6	0.66	INFLPEDU		0.5
INFLLEN	-0.59		PUBABAX		0.56
PETIOLEN	-0.53		PUBADAX		0.44
INFLSH4	0.5		INFLPUB		0.58

Amazon (group C in Fig. 17C). A second morphological group comprises two additional samples of Guianensis (group E in Fig. 17E) and this group is restricted to the Rio Issana and Rio Negro area (*spruceana*). This group is sympatric to the Guianensis+Oblonga group (Fig. 17F), yet is morphologically distinct from it, having capitate inflorescences (inflorescence shape characters in Table 12), a character that is found in no other samples among the Guianensis complex. Both groups D and E are found, like Guianensis in Central Amazon, in flooded habitats. Finally, the third group of specimens in the Orinoco basin (group F in Fig. 17E) comprises a few samples that are morphologically similar to the Plicatiformis group from the Central Amazon, and which is not found in flooded environments. This group was not sampled for molecular data, but is sympatric with group D at several localities (Fig. 17F).

The samples of the Puberula clade from Suriname and French Guyana are morphologically indistinguishable from the other samples of the core Guianensis clade (node “F” in Fig. 4). There is also no evidence of morphological differences for area “c” in Figure 17B (not shown), indicating that the two chloroplast clades are morphologically indistinguishable in this region.

DISCUSSION

In this study, I combined phylogenetic evidence from both chloroplast (*rps16* intron and *rpl20-rps12* intergenic spacer) and nuclear (ITS) genomes with phenetic analyses of morphological data, and in an explicit geographical context, to recognize putatively reproductively isolated lineages in the genus *Pagamea.* Although the levels of genetic variation in the sampled markers were low, perhaps expected giving the lack of variation in its sister taxon *Gaertnera* (Malcomber 2002), there was sufficient variation to suggest the monophyly of several clades. Phenetic analysis of morphological characters and its distribution across the phylogenetic tree indicated that these clades are morphologically distinct, and when looking at their geographical distribution, they are clearly largely sympatric, suggesting these clades are reproductively isolated. In addition, geographically localized phenetic analyses indicated that some of these clades may themselves include more than one species. Incongruence between the chloroplast and nuclear phylogenetic trees also indicate scenarios of hybridization and lineage sorting.

The level of resolution in the phylogenetic data and the method here applied for species delimitation allowed the recognition of 29 species, most of which are also monophyletic. However, two species, *coriacea* and *occulta*, are paraphyletic, and the cpDNA/combined trees make four species polyphyletic, although these are monophyletic according to the ITS tree (Table 13). The ITS tree better correlates with morphology and ecological (altitude) variation and appears to better indicate species relationships. In a few cases, the inference that phylogenetically closely related and phenetically distinct groups are reproductively isolated remains uncertain. In these cases, I recognize a single species, despite the possibility, as suggested by previous taxonomy and great morphological variation, that two or more reproductively isolated lineages may be involved (e.g. *coriacea*). In addition to the 29 species, there are two additional morphologies endemic

Table 13. Species recognized by this study, boundaries, monophyly and comments

Species	**Clades from combined tree/phenetic clusters**	**Monophyly**
P. acrensis	Parviflora and Acrensis	Monophyletic – ITS only; cpDNA polyphyletic
P. anisophylla	Anisophylla	Monophyletic – cpDNA only;
P. aracaensis	Aracaensis	Monophyletic, but no support
P. bahiana	Bahiana	Monophyletic – ITS+combined
P. coriacea	Two dioecious phenetic clusters from the Upper Rio Negro (node "D" and "group c", Fig. 16) and other sites	Paraphyletic – both markers
P. duckei	Duckei	Monophyletic – both markers
P. dudleyi	Dudleyi	Monophyletic – both markers
P. duidana	Duidana	single accession only
P. glabra	Glabra accessions of Macrophylla clade	Monophyletic – both marker
P. glabrescens	Glabrescens	Monophyletic – both markers
P. guianensis	Most of Guianensis clade (but accessions labeled occulta) and Puberula clade (but Plicatiformis subclade)	ITS monophyly not rejected ITS; cpDNA polyphyletic
P. harleyi	Harleyi	Monophyletic – ITS+combined
P. hirsuta	Hirsuta	Monophyletic – both markers
P. igapoana	Clade node "F" in Fig. 16 corresponding to bisexual phenetic cluster from the Upper Rio Negro	Monophyletic – both markers; nested in P. coriacea
P. macrocarpa	Macrocarpa	Monophyletic – both markers
P. macrophylla	Macrophylla	Monophyletic – cpDNA only;
P. montana	Sister and morphologically distinct from pauciflora; sympatry uncertain, species status uncertain	One population sampled, two accessions, monophyletic
P. occulta	Oblonga clade and part of Guianensis clade	ITS paraphyletic in relation to spruceana; cpDNA polyphyletic
P. pauciflora	Phenetic cluster sympatric to standleyana in the Thyrsiflora clade (Fig. 11)	Monophyletic cpDNA; ITS single accession
P. peruviana	Peruviana	Monophyletic – both markers
P. plicata	Plicata	Monophyletic – both markers
P. plicatiformis	Plicatiformis and Puberula clade sister to core Puberula clade	Monophyletic – ITS only; cpDNA polyphyletic
P. puberula	Pilosa	Monophyletic, cpDNA only
P. resinosa	Iquitos	Monophyletic cpDNA only; ITS single accession
P. sessiliflora	Sessiliflora	single accession only
P. spruceana	Phenetic cluster of the Guianensis complex in the Upper Rio Negro region (Fig. 17E)	Monophyletic cpDNA only, but no support; ITS single accession
P. standleyana	Phenetic cluster sympatric to pauciflora in the Thyrsiflora clade (Fig. 11)	Single accession
P. thyrsiflora	Widespread phenetic cluster of the Thyrsiflora clade (Fig. 11)	Monophyletic – combined
P. velutina	Phenetic cluster in the Macrophylla clade; high-altitude, poorly known	Single accession

to tepuis in the Guayana Shield that were not sampled for molecular data and may comprise two additional species (see Chapter 3). Therefore, *Pagamea* includes 31 species. In two cases, I recognize morphologically distinct but allopatric sister-taxa as separate species: *P. velutina vs. P. macrophylla*, *P. peruviana vs. P. sessiliflora.* These patterns could suggest they comprise a single species with two subspecies, but in the first case there is uncertainty in the relationship. In the second case, *P. peruviana* and *P. sessiliflora* (100% ML bootstrap, see Fig. 3), these species are morphologically very distinct, comprising the extremes of the variation within the LDP as a whole (Fig. 6E), they have different chloroplast lineages (see Fig. 1), and sampling in both cases is too small and scattered to rule out the possibility of sympatry. For all other species of *Pagamea,* reproductive isolation can be inferred indirectly because their closely related species was sympatric.

Clades and species

Clades that are indicated by both the chloroplast and the ITS datasets, and are morphologically distinct and sympatric, are probably independent, reproductively isolated lineages. These are candidates for recognition as species. This does not mean, however, that clades include only a single species, nor that monophyly should be the sole criterion for species recognition. This will depend also on levels of genetic variation and sampling, which are not trivial to assess when studying species-level patterns in widespread and poorly collected plant groups. Furthermore, recently diverged species may well appear not to be phylogenetically distinct in a study such as this. Here, I have focused only on well-supported phylogenetic patterns to recognize reproductively isolated entities; inference of reproductive isolation must be indirect in a study such as this. However, the identification of clades, independent lineages, also allowed focus on patterns of morphological variation within each clade, and on the geographical distribution of this variation. If there are morphological groups within clades that are sympatric, then they may be considered species. Strongly reproductively isolated taxa tend to be phenotypically distinct (Rieseberg et al. 2006), and morphological distinctiveness in sympatry suggests reproductive isolation. Only in sympatry is there potential for gene flow, and reproductive barriers must be present for the maintenance of morphologically discrete groups (Coyne and Orr 2004). Although this last approach does not depend on phylogeny, but rather on exploring patterns of morphological variation at different geographical scales (e.g. Coronado 2003), constraining the analysis to well-supported clades reduces the possibility of comparing unrelated samples that are morphologically convergent. Furthermore, it permits focus on comparisons that matter most, i.e. those between closely related morphological groups. Finally, discrete morphological groups in a single geographical location, but which are associated with altitude or other environmental gradients, may only reflect phenotypic plasticity associated with habitat differences, but phylogenetic data may help reject this hypothesis when these groups are not immediately related (e.g. McGowen *et al*. 2001).

The Harleyi clade constitutes a case in which morphological convergence could have misled if phylogenetic relationships for *Pagamea* were unknown. This clade is endemic to the Atlantic Coast of Bahia, Brazil, where it is sympatric with members of the unrelated Guianensis clade (Fig. 3). The results of this study indicate that the Harleyi clade comprises two reciprocally monophyletic groups that are morphologically distinct and sympatric. Therefore, the clade contains two species. However, one of these species (*P. bahiana*) is morphologically similar to samples of the Guianensis clade (Fig. 11), sharing a very similar inflorescence structure, and these have usually been identified as the same species. The other Harleyi species (*P. harleyi*) has a different inflorescence structure. Because *P. guianensis* is sympatric with *P. harleyi* and parapatric with *P. bahiana* (Fig. 11B), the phylogenetic data was fundamental for recognition of *P. bahiana* as a different species. The results of this study indicate that most of the well-supported clades in the combined ITS+cpDNA tree are different species, because they are phylogenetically independent according to both chloroplast and nuclear markers and they are morphologically distinct when sympatric. However, some of these clades cannot be considered species by all these criteria. These are Acrensis and Parviflora, Macrocarpa and Dudleyi and the Oblonga clade. In addition, although the use of these species criteria indicate that the Guianensis complex is made up of reproductively isolated lineages, these can be clearly circumscribed only at local geographical scales.

Acrensis and Parviflora are sister clades according to the ITS dataset, a well-supported relationship (node “M” in Fig. 4; reciprocal monophyly is unclear), and are morphologically indistinguishable and allopatric (Fig. 6, 9,10). The chloroplast relationships (Fig. 1) suggest that the two are not immediately related. The chloroplast differences correlate with geography and the ITS relationship with morphology. Because Acrensis and Parviflora are allopatric, reproductive isolation between them cannot be inferred. Acrensis is also mostly allopatric in relation to the other closely related clades (LDP), while Parviflora is sympatric to all other LDP clades (Fig. 10). Because Parviflora is also morphologically distinct from the populations of LDP clades that are sympatric to it (Fig. 16E), reproductive isolation between them can be inferred. Here, Parviflora and Acrensis are recognized as a single species (*P. acrensis*) despite their chloroplast differences, because these clades are allopatric, morphologically very similar (but see Chapter 3) and form a well-supported monophyletic group in the ITS data. This species appears to be reproductively isolated from other LDP species, because Parviflora is sympatric, morphologically distinct and not immediately related to most LDP species.

The sister-relationship between Macrocarpa and Dudleyi as suggested by the ITS results correlates with geography and morphology. Both clades are restricted to the Andes and are found at high altitudes (~ 1000 m). Ordination of samples in morphological space failed to yield morphological groups, but the sampling is very poor. Nonetheless, the geographical distribution of samples included in the molecular analyses suggests that these clades are reproductively isolated. The molecular samples for Dudleyi are from northern and central Peru, while those of Macrocarpa are from the same site in northern Peru and southern Ecuador. Thus, the two clades are sympatric in northern Peru (Fig. 9, 10). At this site, Dudleyi was found in dwarf scrub vegetation while

Table 14. Results of topological comparisons for the Andean accessions according to the ITS dataset.

rank	item	Obs diff.	au	sh
1	Unconstrained ITS ML tree	-0.0	0.719	0.881
2	Enforced monophyly of Macrocarpa+Dudleyi+Iquitos	0.0	0.674	0.870
3	Enforced monophyly of Macrocarpa+Dudleyi+Iquitos+Sessiliflora+ Peruviana	2.5	0.084	0.576
4	Enforced monophyly of Macrocarpa+Dudleyi+Iquitos+Peruviana	16.4	4e-04	0.025

Macrocarpa was inside the forest. Unfortunately, there are too few fertile specimens of both clades from this site to provide a clear understanding of morphological variation. Although my sampling is small, since the sympatric accessions of both clades are genetically more closely related to samples from other sites, according to both ITS and chloroplast data, reproductive isolation is suggested. Therefore, I recognize these clades as different species (*P. macrocarpa* and *P. dudleyi*). However, whether these species are reproductively isolated from other LDP clades that are also morphologically very similar to them (*P. resinosa*) is unclear, because these are allopatric. The only LDP clade that is sympatric with either of these species is Peruviana (Fig. 10), which is also morphologically distinct and, consequently, represents a different species. *Pagamea peruviana*, *P. iquitos*, *P. macrocarpa* and *P. dudleyi* are all endemic to Western Amazon. Although they form a paraphyletic complex in the ITS (Fig. 2), the monophyly of these species is not rejected (when including also *P. sessiliflora*; see Table 14), suggesting they may represent a single colonization event to Western Amazon.

Clades forming the Guianensis complex comprise different species when the analyses are constrained to local areas like the Central Amazon and the Upper Rio Negro. In these regions, clades indicated by both chloroplast and ITS markers are morphologically distinct and sympatric (Fig. 17). Hence, they are distinct species by the criteria adopted here. However, the delimitation of these species becomes problematic because these morphological distinctions disappear when all specimens are taken into consideration. Species comprising the Guianensis complex can only be delimited in a local scale. In Central Amazon three species can be recognized: *Pagamea guianensis*, *P. occulta* and *P. plicatiformis* (Table 13). In the Upper Rio Negro, the species criteria suggest that Oblonga and Guianensis are the same species (*P. occulta*) despite the chloroplast differences. Morphology and sympatry further suggest that in this region there are two additional species that belong to the Guianensis complex. One conforms to the morphology of *P. plicatiformis* from Central Amazon and is here provisionally recognized as such. The other has capitate inflorescences unlike all other samples of the Guianensis complex, and is also recognized as a separate species (*P. spruceana*). The Core Guianensis clade, as delimited by the ITS data (Fig. 2), which corresponds to plants from the Atlantic Coast from French Guyana to Bahia in Brazil is recognized as *P. guianensis*. Therefore, *P. guianensis* includes two major chloroplast lineages (cpDNA Core Guianensis clade, and two of the Puberula clades -- a third is also in *P. plicatiformis*), and is distributed from the coast inland up to a line defined by the Madeira and Negro rivers. On the other hand, *P. occulta* includes, in addition to the Orinoco and Central Amazonian accessions, samples from West of the Madeira river and Peru. This *P. occulta* is paraphyletic according to ITS because of *P. spruceana*, but there is not support for the clade comprising these two species. The morphological boundaries between *P. guianensis* and *P. occulta* along the Mamoré-Madeira river remains unclear, but phylogenetic position (no support) and morphology (weak) of samples from this region suggest two species (see Chapter 3 for adopted boundaries). Therefore, the Guianensis complex includes four species, *Pagamea guianensis, P. occulta, P. plicatiformis* and *P. spruceana*. These species are monophyletic according to the ITS data, with the exception of *P. occulta* (Table 13), although support is low. The chloroplast data indicate that *P. guianensis*, *P. occulta* and *P. plicatiformis* each contains two chloroplast lineages (Guianensis, Puberula and Plicatiformis in Fig. 1). Furthermore, although the chloroplast lineage Puberula is present in all three species, each species has a different Puberula sub-clade (but no support, Fig. 1; Table 13). Furthermore, within each species, the different chloroplast lineages are allopatric.

Variation within some clades indicates they comprise more than one species. In the case of the Thyrsiflora clade, the criteria of phylogenetic independence and morphological distinction in sympatry indicate three species (*P. thyrsiflora*, *P. pauciflora* and *P. standleyana*), and a third species (*P. montana*) that is also morphologically distinct but has a parapatric distribution with its sister-species, *P. pauciflora*. Most of the sampled tepui endemics form a single monophyletic group in my analysis (node “KK” in Fig. 3) and their morphological differences are not clear (see Fig. 14). However, *P. pauciflora* is sister to the allopatric *P. montana*, and is sympatric with the more distantly related *P. standleyana*. Hence there are clearly two species among these samples. I also recognize *P. montana* as separate species from *P. pauciflora,* because these are morphologically distinct (see Chapter 3) and because there are additional morphotypes from the tepuis of the Guayana highland that could not be sampled for molecular data, as indicated by the great morphological variation within *P. montana* (circles in Fig. 14B; see also Vicentini and Steyermark 2004). Additional sampling, both for morphological and molecular analyses, is needed to clarify species diversity among the high-altitude endemics of the Guayana highlands.

Multivariate analyses of morphology revealed sympatric phenetic clusters also in the Coriacea and Macrophylla clades. In the Coriacea clade there are clearly two species in the Upper Rio Negro region (*P. igapoana* and *P. coriacea*), where there are three sympatric phenetic clusters. Two species can be inferred because two of these phenetic clusters are also not phylogenetically immediately related according to both nuclear and chloroplast markers. The third phenetic cluster was not sampled for molecular data. However, this cluster is found on the east side of the Issana-Negro rivers that separates it from the more similar (*P. coriacea*) of the other two species, and these two coriacea morphologies co-occur at other locations (see also Chapter 3). Thus, it is possible that there is a third Coriacea species in this region, but additional molecular evidence is needed to clarify the hypothesis that there is a third species in this clade. The Macrophylla clade also clearly has two species, *P. glabra* and *P. hirsuta*, according to the three criteria, but great morphological variation in sympatry indicates this clade could include up to 7 species (Fig. 12). Such within-clade morphological patterns are striking. However, an exhaustive exploration of the patterns of local variation in order to identify sympatric phenetic clusters within clades is beyond the scope of this study.

Here, I have focused only on sites for which there was also some phylogenetic data. Nevertheless, these patterns indicate that some of the species recognized by this study may include more than one reproductively isolated lineage.

Chloroplast and ITS incongruence

Incongruence between nuclear and chloroplast phylogenies, in particular at or near the species level, is usually attributed to introgression of the organellar genome from one species into the nuclear background of another (i.e. chloroplast capture; Soltis and Kuzoff, 1995 ; Kellogg *et al.* 1996; Soltis *et al.* 1996, 2000; Hardig et al. 2000, Yoo et al. 2002). Another major process that may cause such incongruence is the sorting of ancestral polymorphisms (e.g. Jakob and Blattner 2006). Because the usually maternally inherited chloroplast is haploid while the nucleus is diploid, the effective population size of the chloroplast genome will be 1/4 that of the nucleus in a monoecious (diploid) species, and still less in a dioecious one. Thus, the effects of genetic drift will be intensified in the chloroplast genome because of the smaller effective population size (Schaal et al. 1998). In *Pagamea*, because of the island-like distribution of its habitats, gene flow among "islands" is more likely to be predominantly through seeds, while pollen dispersal is less likely. This patchy habitat type also suggests that genetic drift may play an important role in the diversification of *Pagamea*. It may be difficult to distinguish chloroplast capture (introgression) from lineage sorting, but some lines of evidence suggest that in *Pagamea*, both processes may be occuring.

In this study, incongruence between the chloroplast and ITS trees was localized in a few clades within the LDP clade. The ITS tree for these clades correlates better with morphology, geography and ecology (altitude), and appears to be a better indicator of species relationships. *Pagamea guianensis*, *P. occulta*, *P. plicatiformis* and *P. acrensis* are polyphyletic for the chloroplast (Table 13). Other clades have different positions in chloroplast and ITS tree (significantly different according to SH tests), but chloroplast clades are still monophyletic in the ITS tree. Furthermore, the chloroplast clades that show incongruence with the ITS tree may form a single monophyletic group in the chloroplast tree (hypothesis not rejected according to a SH test). Even in the case of *Pagamea plicatiformis*, which shares a chloroplast lineage with *P. guianensis* from the Central Amazon, where both are sympatric, the shared chloroplast lineage forms two reciprocally monophyletic groups that correpond to species. Because clades are still monophyletic according to both genomes, and the two chloroplast lineages within species are always allopatric to each other, a scenario of ongoing hybridization seems unlikely. These patterns are more consistent with a scenario of lineage sorting, although ancient chloroplast capture cannot be ruled out.

Additional studies are needed to fully understand the patterns of incongruence between ITS and chloroplast phylogenies. However, none of the cases seems to indicate ongoing hybridization (chloroplast lineages are fixed in each species, even in the sympatric *P. plicatiformis* and *P. guianensis*). This is also true for *P. acrensis*, which has two chloroplast lineages (Acrensis and Parviflora) that are allopatric to each other. In *P.*

guianensis and *P. occulta,* the chloroplast lineage that indicates the same phylogenetic position as the ITS tree (Guianensis clade) is widespread, whereas the other chloroplast lineage (Puberula) has a more restricted, peripherical distribution; in *P. guianensis* it is found only in populations from Central Amazon and the coast of the Guianas, while in *P. occulta*, it is restricted to the Ventuari river basin. These patterns seem to point to a scenario of differential sorting of ancestral polymorphism. This hypothesis is in agreement with a putative role for genetic drift associated with the small populations and island distributions of species of *Pagamea*, because chloroplast lineages may become fixed for particular isolates and have their persistence time increased. Information on ploidy level will also be crucial to understand these patterns, but unfortunately there are no chromosome counts for *Pagamea.*

Pagamea and Gaertnera

The phylogenies presented here complement the phylogeny of *Gaertnera*, and together provide a detailed evolutionary account of a lineage of Rubiaceae that arose in the Middle Miocene (Chapter 2), diversified into circa 100 species and colonized all major tropical regions of the world (see also Malcomber 2002). This study is the first to provide molecular evidence for the monophyly of *Pagamea* and for relationships among its species. Previously, the monophyly of the genus had been largely inferred because of its geographical isolation rather than any possession of morphological synapomorphies. *Pagamea* is endemic to South America and *Gaertnera* to the Old World tropics.

Although their sister relationship has long been established by morphological characters rarely seen in other Rubiaceae (Jansen *et al.* 1996, Igersheim *et al.* 1994), and more recently by molecular data (Andersson and Rova 1999, Bremer and Manen 2000, Malcomber 2002), there are no obvious morphological synapomorphies for either of these reciprocally monophyletic groups. Malcomber (2002) suggested glabrous and partially fused corolla lobes as apomorphies for *Gaertnera*. However, glabrous corolla lobes are also found in *Pagamea* among high-altitude samples of the Thyrsiflora clade, and in a few samples of the Capitata clade. Partially fused corolla lobes may be a synapomorphy for *Gaertnera*. This character is found only in one specimen of *Pagamea,* which has a very distinct ratio between calyx lobes and tube (not shown) from all other specimens of *Pagamea,* and the flowers appear to be diseased. The level of genetic variation in the ITS marker for *Pagamea* is far greater than that in *Gaertnera*, despite the fact that *Gaertnera* includes 68 species and is found in Africa, Madagascar, the Mascarenes, Sri Lanka and Southeast Asia (Malcomber 2002). A detailed comparison of morphological and ecological variation in these two genera will be made elsewhere. However, the greater genetic variation in *Pagamea* despite its lower species-level diversity and smaller geographical range, strengthen the hypothesis of Malcomber (2002) that *Gaertnera* underwent a more rapid radiation.

Breeding system variation

Pagamea has been reported to be a distylous group (Steyermark 1974; but cf. Bentham

1857), while *Gaertnera* includes distylous, homostylous and dioecious species (Malcomber 2002). However, *Pagamea* too has both dioecious and homostylous species. A pollination study of a population of the Capitata species from Venezuela reports the presence of two flower morphs that differ in pollen production and size, but not in the relative position of stamens and style, i.e. flowers are homostylous (O. Hokche pers. comm. 2006). Such pollen dimorphism is typical of distylous species (Barrett 1992). Whether homostylous flowers in other clades also have dimorphic pollen remains to be seen, but the phylogenetic pattern of breeding system variation indicates a certain conservatism in the transitions between breeding systems. The Capitata clade includes specimens that have all three types of flowers observed in *Pagamea* (Fig. 8), suggesting that breeding system may vary continuously between distyly and homostyly (e.g. Faivre and MacDade 2001). In addition, some samples of the Capitata clade appear to be dioecious. There is one major transition from homostyly/distyly to dioecy at the branch joining the Duckei and the LDP clades, although there are a few independent reversals within the LDP clade and independent transitions to dioecy within the Thyrsiflora and Macrophylla clades (Fig. 8). Although the Duckei+LDP clade is the most diverse and most widespread clade within *Pagamea,* Duckei itself includes only one species and has a very limited distribution, suggesting that there is no causal link between evolution of dioecy and increased diversification (see Vamosi and Vamosi 2004).

Flowers of *Pagamea* fit the syndrome of generalized pollination by insects: small flowers with the tube mouth closed by long white hairs and usually covering also the inner part of the frequently spreading corolla lobes. The flowers also produce little nectar, and are visited by bees, flies and moths (pers. obs). There is little variation in flower morphology among species, although high-altitude species of the Thyrsiflora clade (node "KK" in Fig. 3) have larger flowers and glabrous corolla lobes. Therefore, breeding system variation and pollination shifts seem to have played no obvious role in the diversification of this genus. In a few cases, however, sympatric species of the same clade have different breeding system (e.g. within the Coriaceae, Thyrsiflora and Macrophylla clades), but it remains unclear whether such variation causes reproductive isolation.

CONCLUSIONS

In this study, I applied a method for species delimitation that makes explicit the reasoning behind the decision process for recognizing species, which I consider to be putatively reproductively independent lineages. This is despite the fact that *Pagamea* grows throughout most of tropical South America in regions that are poorly sampled (Nelson et al. 1990; Prance et al. 2001), and where auxiliary information such as ploidy levels, pollination and reproductive biology are mostly unknown. Here I used only morphological data from herbarium material combined with phylogenetic data that was sampled in a way to maximize its coverage of morphological variation (i.e. maximize the coverage of *a priori* defined morphotypes) and the geographical distribution of such variation. Monographs of tropical plant groups rarely make explicit the patterns of variation that underly decisions of species delimitation. This seems true for plant species in general (MacDade et al. 1995; Rieseberg et al. 2006). Indeed, phenetic analyses have rarely been used to and in species delimitation in a genus-wide fashion. Monographs that use phenetic techniques to define species as discrete morphological groups also fail to take into consideration the geographical context of morphological variation, which may result in an under-estimation of diversity (Coronado 2003; Henderson 2005). Furthermore, phylogenetic studies of tropical plants attempt to reconstruct relationships only among *a priori* defined species. This study is clearly not an exhaustive account of the diversity in *Pagamea,* but the entities recognized here either represent biological species or evolutionary lineages in the early stages of divergence. In addition, it also indicates several interesting evolutionary scenarios, such as cases of localized divergences, in the Andes (*P. macrocarpa* and *P. dudleyi*), and the Altantic Coast of Bahia (*P. harleyi* and *P. bahiana*), the hypothesis of sorting of ancient chloroplast lineages among species within the Guianensis complex, and examples of closely related species that show complete range overlap (*P. hirsuta* and *P. resinosa*, and *P. igapoana* and *P. coriacea*). This study has allowed the recognition of 10 previously unrecognized species in *Pagamea,* but it also indicated a great deal of overdifferentiation in previous species delimitation, in particular, in the high-altitude habitats of the Guayana Shield (Steyermark 1965, 1974). At the same time, substantial genetic and morphological variation within some of the species recognized here suggest, that when better understood, may warrant the recognition of additional species.

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CHAPTER 2

Tempo and mode of speciation in tropical South America – the case of *Pagamea* Aubl. (Rubiaceae), a white-sand specialist

INTRODUCTION

Several hypotheses have been postulated to explain speciation in tropical South America, including vicariance caused by historical changes in the landscape associated with climatic cycles (Haffer 1969; Colinvaux 1993, 1998), tectonic movements (Salo et al. 1986; Räsãnen et al. 1995; Silva and Patton 1998), sea-level fluctuations (Frailey et al. 1988; Marroig and Cerqueira 1997; Nores 1999), the development or presence of major rivers, or a combination of these factors (see Haffer 1997 for a review). Some of these hypotheses have been criticized on the grounds of lack of geological or paleoecological evidence (e.g. Bush 1994; Colinvaux et al. 2001; Tuomisto 1992). Recent studies applying phylogenetic dating techniques suggest that the search for a single model of vicariance, which is in part reason for controversy, may be misleading. All the processes mentioned above may have caused diversification in tropical South America, with different lineages responding in different ways to these processes. Thus, changes in forest cover caused by climatic fluctuations (the refuge hypothesis of Haffer 1969) may have promoted divergence in some lineages (e.g. Monteiro et al. 2003; Ribas and Miyaki 2004), while other studies of within-species genetic variation found no support for population subdivision and expansion in the Amazon during the Pleistocene, as predicted by the refuge hypothesis (e.g. Silva and Patton 1998; Dick et al. 2003; Lessa et al. 2003). Molecular studies also suggest that in some groups divergence took place during the Tertiary (e.g. Zamudio and Greene 1997; Clough and Summers 2000; Boubli and Ditchfield 2000; Glor et al. 2001), contrary to the traditional view that speciation has occurred during the Quaternary (Haffer 1969; Prance 1973; Brown 1979). Of course, the hypotheses mentioned above are largely based on a model of allopatric speciation, and little attention has been given to other models of divergence (but see Fine et al. 2005).

Species-level phylogenies based on molecular data provide two sources of information that are crucial if we are to understand the importance of historical factors, if any, in generating diversity in tropical South America: hypotheses of relationships and estimates of divergence times. Species-level phylogenies may also help distinguish among alternative modes of geographical speciation (Barraclough and Vogler 2000; Fitzpatric and Turelli 2006; but see Losos and Glor 2003). The more such phylogenies are produced, the more generalities about speciation we will be able to make. Here, I apply a Bayesian dating approach to the phylogeny of *Pagamea* Aubl. (Rubiaceae) to gain insights into the processes leading to the diversification of this genus.

Pagamea comprises about 29 species of shrubs and trees and is widespread in tropical South America. *Pagamea* is also an edaphic specialist, occurring only on white-sand soils and sandstone formations from sea level to 2800 m (Vicentini and Steyermark

2004). White-sand habitats where *Pagamea* is found show gradients of forest structure: (a) very open savanna-like habitats or montane scrublands; (b) dense scrublands; (c) low-height (< 10 m) dense forests; and (d), in the lowlands, tall (25-30 m) forests. These gradients are also associated with a flooding gradient. The more open and low structured vegetation is usually flooded or at least associated with a water-table very close to the surface (Ferreira 1997; Vicentini 2004); some species of *Pagamea* even occur in highly flooded habitats (*igapó*, *chavascal*) of black-water river systems in the Amazon. These systems are biologically linked, at least in the Guayana shield region, sharing many taxa adapted to conditions of both nutrient and water stress (Kubitzki 1989, 1990).

In a previous study (Chapter 1), I have combined phylogenetic and morphological data in an explicit geographical context to recognize and delimit species in this genus under a lineage-based, evolutionary species concept (de Queiroz 1998; cf. Coyne and Orr 2004). This is a necessary first step if we want to understand speciation.

There are few phylogenetic studies of taxa from white-sand systems in tropical South America (Albert and Struwe 1997; Givnish *et al.* 1997, 2000; Gould and Struwe 2004). Although these studies imply a much more recent and dynamic history than previously thought (e.g. Funk and Brooks 1990, Steyermark 1986), they focused on taxa mainly restricted to the Guayana Shield region. *Pagamea* is also found in the Atlantic Coast of Brazil, in the Eastern slopes of the Andes, the Amazon, and in the Choco region of Colombia. Recent studies found several lineages of plants (David Neill, pers. comm. 2006) and birds (Whitney and Alonso 1998) in the Andes have that were thought to be endemic to the Guayana Shield region. The biogeographical connections between these regions are still poorly understood and, to date, no studies have estimated the divergence time between taxa from these regions.

Within the white-sand habitats, the extent to which species of *Pagamea* have more specific habitat preferences is unknown. Habitat specificity can evolve in such resource-limited environments to avoid competitive exclusion (e.g. Coomes and Grubb 1998), allowing closely related species to coexist. Thus, if species of *Pagamea* show habitat specialization, the phylogenetic patterns of such specialization may reveal the importance of ecological variation in promoting divergence. Few shifts would indicate phylogenetic niche conservatism (Wiens 2004), whereas multiple independent shifts would suggest a primary role for habitat heterogeneity in the diversification of the genus (e.g. Fine et al. 2005).

Pagamea is sister to the paleotropical genus *Gaertnera* L., a relationship that is supported by morphological and molecular evidence (Jansen *et al.* 1996; Igersheim *et al.* 1994; Andersson and Rova 1999; Bremer and Manen 2000; Malcomber 2002). However, the timing of divergence between these genera remains unclear due to the lack of good fossil records for Rubiaceae. Using the oldest fossil of Rubiaceae (54 million years; Roth and Dilcher 1979**)** as a calibration for the divergence between *Pagamea* and *Gaertnera*, Malcomber (2002) obtained very recent divergence times (< 5.6 million years) for the diversification of *Gaertnera,* which includes 68 species and is found throughout the paleotropics, from Africa to South East Asia. However, this calibration may likely cause an overestimation of divergence times because of the derived position of Gaertnereae in Rubiaceae phylogeny (see Andersson & Rova 1999; Bremer and Manen 2000; Robbrecht and Manen 2006). Therefore, more realistic estimates of the divergence time between *Pagamea* and *Gaertnera* are needed to time speciation events in *Pagamea* and to be able to relate them to historical factors promoting diversification in tropical South America.

In this study, I first estimate the divergence time between *Pagamea* and *Gaertnera* using six different calibration schemes and a phylogenetic tree including the representatives of major clades of Rubiaceae (Manen and Bremer 2000) and several Asterid outgroups, which allowed the use of two pollen fossils of Rubiaceae (as in Nie et al. 2005), and some of the age estimates from Bremer *et al*. (2004). I then use the best estimate to obtain divergence times for speciation events in *Pagamea,* and attempt to understand the processes causing diversification in light of the divergence time estimates and the geographical distributions of species. I apply the method of Barraclough and Vogler (2000) to understand the predominant mode of geographical speciation in *Pagamea*. Finally, I characterize the relationship between species and both habitat and altitudinal variation, and the phylogenetic basis of this variation, to gain insights into the role of habitat shifts in the diversification of *Pagamea.*

METHODS

Phylogenetic trees

For dating the split between *Pagamea* and *Gaertnera,* a dataset of two chloroplast markers was obtained from Genebank (NCBI): the *rbcL* large subunit and the first intron of the *rps16* gene. These markers were downloaded for representatives of the major clades of Rubiaceae and Rubioideae, including all available Psychotrieae, Morindeae and Schradereae (see Robbrecht and Manen 2006). I used the phylogenetic trees of Anderson and Rova (1999), Bremer and Manen (2000) for taxon selection, and selected representatives of the major nodes in the asterid tree of Bremer *et al*. (2004) for which a date was estimated to serve as outgroups, including representatives of Solanaceae, Gentianaceae, Gelsemiaceae, Loganiaceae, Garryaceae and Asteraceae.

The two markers were aligned with BlastAlign (Belshaw and Katzourakis 2005) to detect regions of homology among all sequences and to identify insertion and deletion events, in particular for the *rps16* intron which is quite variable in length. BlastAlign usually removes parts of sequences that are unalignable or autapomorphic as it compares all sequences in the dataset against each other and retrieves the areas that are conserved among all sequences. The original dataset was then aligned manually for the regions excluded by BlastAlign. Insertions were considered homologous if they were in the same position and differing by no more than 2 bp in composition or length. Two inserts were treated as non-homologous if they were in the same position and each was a repetition of an adjacent motif but differed in length by 4 or more base pairs. Motifs in the same position but of completely different base composition were considered non-homologous. Homopolymeric regions of A's or T's, which are extremely variable in length, were excluded from the analyses.

To select a topology for tree dating, I first performed a Bayesian analysis and then selected the best topology by ranking the resulting trees. The two datasets were initially tested for congruence using the ILD test (Farris 1994), which indicated they were congruent (P>0.1). The same model of evolution (TVM+G) was also the best-fit model for both markers according to MrModeltest v2 (Nylander 2004). Therefore, markers were treated as a single partition in the analyses. Bayesian analyses were performed with MrBayes 3.01 (Ronquist and Huelsenbeck 2003), with following options: 10,000,000 generations with a sample frequency of 1000 trees. *Burnin* was set to 0 and defined *post hoc* by saturation of all output parameters of MrBayes. All unique topologies found among the trees produced by the Bayesian approach were then ranked using the program CONSEL (Shimodaira and Hasegawa 2001), and the best tree was used for dating.

Three different trees were used to date divergences within *Pagamea,* representing phylogenetic hypotheses according to three datasets: the ITS, a chloroplast (*rps16* intron and *rpl20-rps12* intergenic spacer), and a combined ITS+chloroplast tree (see Chapter 1 for phylogenetic analyses). For the chloroplast and combined trees I used the best tree obtained from maximum likelihood analyses; both trees included polytomies (Chapter

1). The combined tree reflects the cpDNA topology with better-resolved relationships towards the tips caused by signal in the ITS data. Because the interpretation of patterns and dating focused on the ITS tree, which seems the best indication species relationship (Chapter 1), I selected a fully dichotomous ITS tree for dating. To obtain this tree, I first compared the likelihood scores for several trees, including the best ML topology and all trees obtained from a Bayesian analyses. This was done by first ranking trees using the program CONSEL (Shimodaira and Hasegawa 2001). Among the sets of trees that were found to be equally valid hypotheses according to the AU test (Shimodaira 2002), I selected a topology in which *Pagamea plicatiformis* and *P. aracaensis* were monophyletic. Although there is no support for the monophyly of these species, their monophyly is not rejected by the ITS data (Chapter 1).

Bayesian dating

All dating analyses were performed using the Bayesian method as implemented in the Multidivtime software (Thorne et al., 1998; Kishino et al., 2001; Thorne and Kishino, 2002). Model parameters were estimated separately for each gene partition. Priors for the parameters *rtrate* and *rtratesd* were selected by taking the median amount of evolution from tips to ingroup root and dividing this amount of evolution by the prior age for the ingroup node (*rttm*, parameter), as suggested in the Multidivtime manual (Rutschman 2005)

To estimate the divergence time between *Pagamea* and *Gaertnera* the following date constraints were used: (1) crown node of Lamiids (split *Aucuba vs.* rest) at 119 mya (see Fig. 1); (2) crown node of Core Lamiids (split Gentianales *vs. Solanum*) at 108 myBP; (3), crown node of Gentianales (split Rubiaceae *vs.* rest) at 78 myBP; (4) crown node of Rubiaceae (split Ixoreae+*Luculia vs.* rest) at 54 my BP; and (5) crown node of the Coussareae (split between *Coussarea* and *Faramea*) at 40 my BP. The first three dates are mean estimates from Bremer *et al*. (2004), the fourth is the age of the oldest Rubiaceae fossil (pollen; Roth and Dilcher 1979), and the last is the oldest *Faramea* fossil (pollen, Graham 1985; see also Nie *et al*. 2005). These constraints were used in different combinations and by constraining node dates either as minimum or both minimum and maximum ages. The following schemes were used (see Fig. 1): (1) nodes A, B and C were fixed with the date estimates from Bremer et al. 2004, i.e. dates were constrained as both upper (U) and lower (L) values for these nodes; (2) the same as (1), but nodes constrained to be at least (L) the age estimes; (3) only node D, the oldest fossil of Rubiaceae, constrained to be at least (L) 54 my old; (4) only node F, the *Faramea* fossil, constrained to be at least (L) 40 my old; (5) schemes 1 and 3 combined; and (6), schemes 1, 3 and 4 combined.

To estimate divergence times within *Pagamea,* I calibrated the split between *Pagamea* and *Gaertnera* as 12.64 million year for all three datasets, an age corresponding to the mean estimate obtained when using as calibration both the oldest Rubiaceae fossil (pollen), and the three ages for Asterids nodes from Bremer et al. 2004 (constraint scheme 5).

Speciation models

The fits of different models of speciation to the timing of speciation events were tested following Rabosky (2006), as implemented in the package Laser in R. To test for significance in departures from rate constancy, I first simulated 1000 sets of speciation times under the best model of rate constancy, and then compared the delta AICrc statistics of observed times, to a null distribution of delta AICrc generated from the simulated data (Rabosky 2006). The delta AICrc is difference in AIC score between the model of interest and the best model under rate constancy.

Geography

The geographical range of a species or clade was assumed to be the minimum convex polygon (MCP) enclosing all samples belonging to the species or clade. This was done using function *mcp* in the package adehabitat in R (available at http://cran.r-project.org). To obtain the degree of overlap between ranges I used package gcplib in R to calculate the area of intersection between the respective MCPs. The indices of Barraclough and Vogler (2000) were calculated using a script in R as described below.

Allopatry vs. sympatry

For each node in the ITS tree I calculated the degree of sympatry between sister-clades and plotted this degree of sympatry against node age, degree of sympatry being the percentage of the range of the clade with smaller range overlapped by its sister-clade. If speciation is mostly allopatric, then recent nodes are expected to display little or no overlap, whereas if speciation is mostly sympatric, the opposite pattern is expected. The intercept of the plot between range overlap and node age summarizes the predominant geographical mode of speciation in the lineage under consideration (Barraclough and Vogler 2000). Whether older nodes display high or low overlap will depend on the extent of range movement after speciation, and the slope of the plot between degree of sympatry and node age summarizes the extent of such movement. If speciation is mostly allopatric, one might expect that the degree of sympatry increases with time (a positive slope), while if speciation is largely sympatric then the degree of sympatry may decrease for relatively older nodes (Barraclough and Vogler 2000). These predictions have several limitations, for example, they assume no extinction, and if the extent of range movement is very high, present-day ranges may retain little information on the geographic mode of speciation. The degree of sympatry was arcsine transformed prior to the regression because it ranged from 0 to 1.

Range size symmetry

To assess whether the geographical patterns of sister-clades conform to a scenario of peripatric speciation, I first calculated the degree of range size symmetry for each node in the ITS phylogeny and plotted it against node age. The degree of range size symmetry is defined as the area of the clade with smaller range divided by the sum of the areas of both daughter clades at each node, which is assumed to be the range of the ancestral species (Barraclough and Vogler 2000). The measure range from 0 to 0.5, the latter indicating that sister clades have equal-sized ranges. If speciation is predominantly peripatric, then recent divergences should display asymmetry in range size, otherwise there should be no particular pattern of range size symmetry with age. Furthermore, in a finite continental area, older clades should occupy a greater proportion of the available area and range symmetry may increase with node age (ibid.). The intercept of the plot between the degree of range size symmetry and node age summarizes the predominant mode of speciation, with a lower intercept indicating an important role of small ranges in speciation. To test for significance, I also performed a simulation of 1000 intercept values under a null model in which the range of the ancestral species, i.e. the sum of the range of daughter clades, is split in two randomly sized ranges ("phylogenetic broken-stick" model of Barraclough and Vogler 2000). Again, this simplistic approach assumes no extinction and complete sampling, and as the level of range movements or expansion increases the ability to detect a general geographical mode at speciation decreases. The degree of range size symmetry index was first doubled and then arcsine transformed prior to regression because it varied from 0 to 0.5.

Plant fecundity and range size

To estimate plant fecundity, I calculated the average number of flowers per inflorescence per species. For dioecious species, I included only information on pistillate or fruiting specimens. Flower number per inflorescence was obtained by counting the number of calices in the inflorescence axes, which are also present when the specimen is fruiting. This obviously does not take into consideration the overall number of inflorescences per plant or seed viability, but this information is not available from herbarium specimens. Fruits of *Pagamea* usually contain two seeds (Vicentini and Steyermark 2004).

Ecology of species

Information from labels referring to habitat structure were classified according to three main variables: type (shrubland or forest); tree density (open or dense); canopy height (low or tall; for forest only). A single rank value was then assigned to each specimen according to the information available to it. Ranks corresponded to: (1) open savanna/shrubland; (2) dense shrubland; (3) open low forest; (4) dense low forest; or (5) tall forest. When only partial information was available, the specimen was ranked with intermediate values. For example, if the label stated only ‘forest’, then the mean value between the ranks of ‘low forest’ and ‘tall forest’ was given to it. Information on flooding and altitude were treated separately. Flooding regime was also ranked: (1) non-flooded (including the word ‘dune’); (2) marsh/moist (including the word ‘riverine’); or (3) flooded.

To calculate the ecological distance between species and/or populations, i.e. the tips in the phylogenetic tree, I used Gower's coefficient (Gower 1971). The variables used to calculate this distance were habitat structure rank, shade index, flooding rank, and altitude. I first calculated the pairwise distance among all specimens for which this information was available. The ecological distance between species and/or populations was then obtained as the mean distance among all specimens assigned to each category.

RESULTS

*When did **Pagamea** diverge from **Gaertnera**?*

Estimates of divergence date between *Pagamea* and *Gaertnera* were very similar for both the analysis constraining the nodes with the dates estimated by Bremer et al. (2004), and the analysis constraining the crown-node of Rubiaceae by the first appearance of Rubiaceae pollen (Fig. 1). These analyses estimated the split between *Pagamea* and *Gaertnera* to be around 12 my BP, both when constraining ages as the minimum, or as both minimum and maximum ages. However, constraining nodes using *Faramea* fossil pollen (as in Nie *et al*. 2005) produced older age estimates for most nodes, with the split between *Pagamea* and *Gaertnera* estimated to be around 21 my BP (Fig. 1B). The inclusion of this fossil also increased the error of the estimate for this split (Fig. 1B). For obtaining divergence times within *Pagamea,* I used the estimates obtained without the *Faramea* calibration because they were largely congruent.

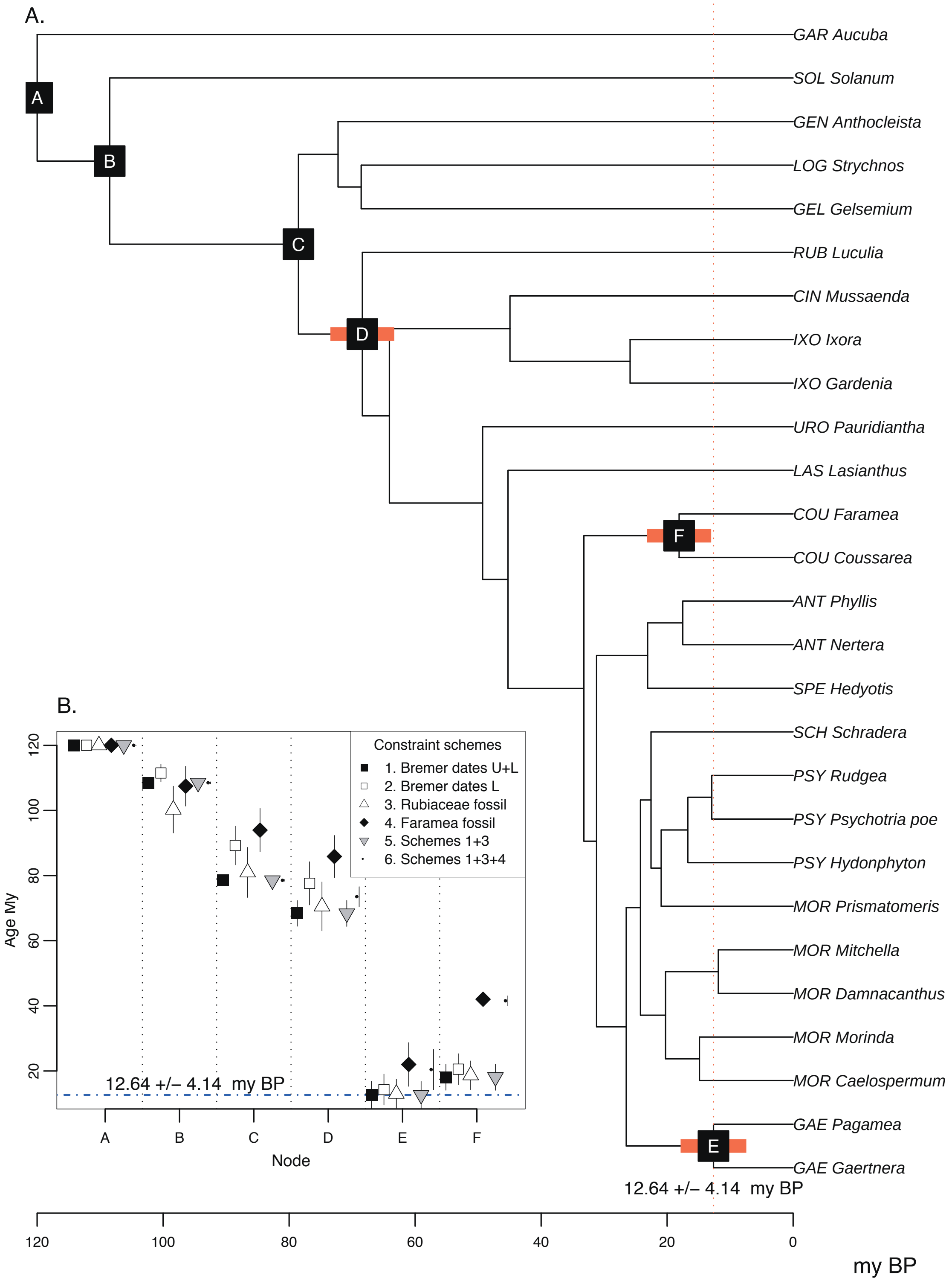
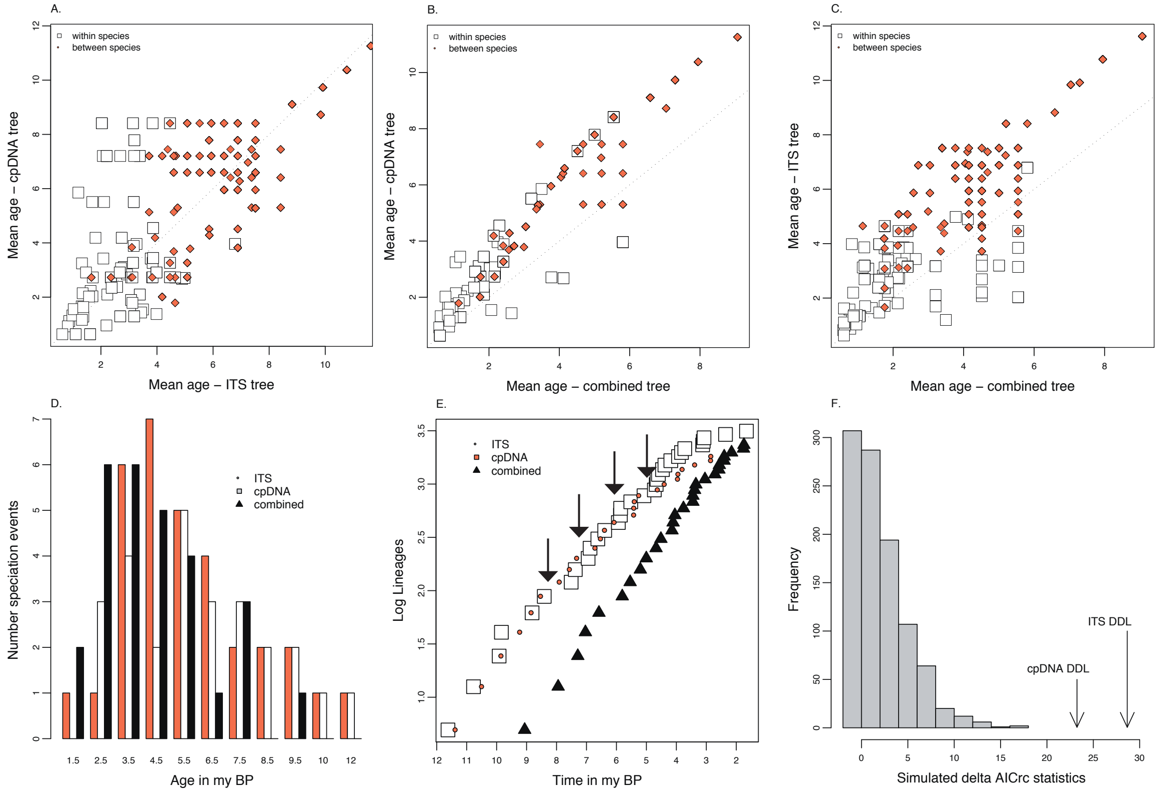


Figure 1. Dating the split between *Pagamea* and *Gaertnera*. **A**. Chronogram resulting from the calibration scheme 5, i.e. using only the oldest Rubiaceae pollen fossil and the age estimates of Bremer et al. 2004. Nodes for which a calibration age was available are indicated; gray bar is the 95 % confidence limit of the age estimate. **B**. Age estimates for nodes in A according to the different calibration schemes.

Timing of speciation

The ages estimated for the most recent common ancestor (MRCA) of all pairs of tips included in the phylogenetic trees differ when using the chloroplast and ITS data. A group of MRCAs are estimated by the chloroplast data to be older than the estimates of the ITS data by ca. 2-4 my (Fig. 2A). Within this group, the MRCAs, both between and within species, are estimated to be 6-8 my old by the chloroplast data, while the ITS dataset estimates these divergences to be 4-6 my old and 2-4 my old, for inter- and intra-specific comparisons, respectively (grey diamonds and white squares in Fig. 2A, respectively). These differences reflect the difference in topology between trees, and the fact that some species are not monophyletic in the chloroplast analyses (Chapter 1). On the other hand, the remaining MRCAs have either similar mean age estimates in the two datasets, or the ITS estimate is older, both for inter- and intraspecific comparisons (Fig. 2A). Younger nodes, from both within and between species comparisons, are largely congruent between the different analyses. The combined tree is more similar to the chloroplast tree (see Chapter 1), and age estimates are shifted towards the present, although younger splits have age estimates similar to those of the individual analyses (Fig. 2B-C, E). The within-species comparisons, which according to the chloroplast analyses fail to form a monophyletic group, correspond to populations of the same species that are in different geographical areas (see Chapter 1), and these populations represent older divergences than their ITS counterparts.

Both the chloroplast and the ITS chronograms show a peak of speciation events between



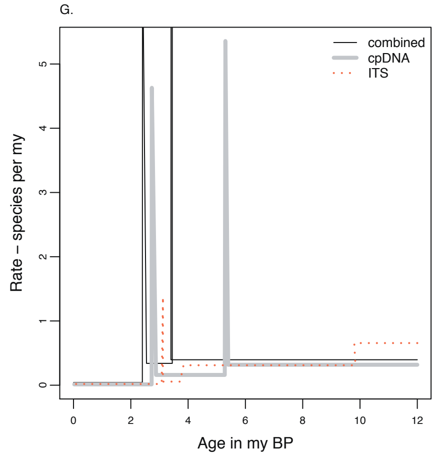


Figure 2. The timing of speciation events in *Pagamea*. **A-C** Comparisons between the age estimates for the most recent common ancestor of each pairwise comparison included in the phylogenetic trees according to the three datasets: chloroplast, ITS and combined. Between and within species comparisons are indicated. **D**. Number of speciation events through time. **E**. Lineage-through time plots for the datasets. Note that the combined data shift most speciation events towards the present, although the estimates of the most recent events are similar to those in the individual analyses. **F**. The null distribution of delta AICrc for 1000 dataset of speciation times, simulated under a pure birth model (Yule). The delat AICrc is difference in AIC score between the best rate variable and the best rate constancy model of speciation. The delta AIC score for the best fit model to the observed age estimates is indicated, and fall outside the distribution of simulated values. Only two rate variable models are indicated, but all are highly significant (see Table 1). **G**. Variation of rates of speciation time for the three datasets according to the best multiple rate variable model.

Table 1. Fits of models of speciation to ITS, chloroplast and combined data. **DDL** = logistic density dependent model; **Yule-n-rate** = Yule pure birth **n** rate variable models; **rvbd** = rate variable birth-death model; **DDX** = exponential density dependent model; **bd** = birth-death model. **Np** = number of parameters; **LH** = log likelihood; **AIC** = AIC score; **dAICrc** = difference in AIC score between model and best rate constancy model; **P** = p value for rejecting rate constancy; **dAIC.b** = difference in AIC score from best fit model; **a** = extinction parameter; **xp** = exponential rate; **K** = carrying capacity; **r1** to **r5** = the rates of speciation in species per million years; **st1 to st4** = time of shifts in rates. Models are ordered from best to worse fits.

Data	model	Np	LH	AIC	dAICrc	P	dAIC.b	a	xp	K	r1	st1	r2	st2	r3	st3	r4	st4	r5
ITS	DDL	2	9.85	-15.71	-28.66	0	0			35.1	0.66								
ITS	yule4rate	7	14.31	-14.62	-27.57	0	1.09				0.33	3.72	0.06	3.12	1.38	3.08	0.02		
ITS	yule2rate	3	10.03	-14.05	-27	0	1.66				0.3	3.08	0.02						
ITS	yule3rate	5	11.57	-13.13	-26.08	0	2.58				0.28	3.12	1.38	3.08	0.02				
ITS	rvbd	4	10.03	-12.05	-25	0	3.66	0			0.3	3.08	0.02						
ITS	yule5rate	7	14.93	-11.85	-24.8	0	3.86				0.66	9.84	0.31	3.72	0.06	3.12	1.38	3.08	0.02
ITS	DDX	2	1.86	0.28	-12.67		15.99		0.83		1.8								
ITS	pureBirth	1	-5.47	12.95	0		28.66				0.16								
ITS	bd	2	-5.47	14.95	2		30.66	0			0.16								
cpDNA	DDL	2	2.41	-0.82	-23.24	0	0			28.95	0.64								
cpDNA	yule5rate	9	8.9	0.21	-22.21	0	1.03				0.32	5.3	5.36	5.28	0.16	2.73	4.63	2.73	0.01
cpDNA	yule4rate	7	6.55	0.91	-21.51	0	1.73				0.32	5.3	5.36	5.28	0.18	2.73	0.01		
cpDNA	yule3rate	5	3.25	3.5	-18.92	0	4.32				0.25	2.73	4.63	2.73	0.01				
cpDNA	yule2rate	3	0.31	5.38	-17.04	0	6.2				0.3	3.68	0.04						
cpDNA	rvbd	4	0.31	7.38	-15.04	0	8.2	0			0.3	3.68	0.04						
cpDNA	DDX	2	-3.35	10.7	-11.72		11.52		0.94		2.05								
cpDNA	pureBirth	1	-10.21	22.42	0		23.24				0.15								
cpDNA	bd	2	-10.21	24.42	2		25.24	0			0.15								
Combined	DDL	2	12.29	-20.57	-21.31	0	0			31.29	0.82								
Combined	yule2rate	3	12.64	-19.28	-20.02	0	1.29				0.41	2.4	0.04						
Combined	yule3rate	5	14.56	-19.12	-19.86	0	1.45				0.39	2.41	6.99	2.4	0.04				
Combined	yule4rate	7	16.52	-19.05	-19.79	0	1.52				0.4	3.45	46.3	3.45	0.33	2.16	0.03		
Combined	yule5rate	9	18.43	-18.85	-19.59	0	1.72				0.4	3.45	46.3	3.45	0.34	2.41	6.99	2.4	0.04

4-6 million years ago (Fig. 2D). These peaks are followed by a decrease in the number of speciation events towards the present, and all analyses suggest that all inter-specific divergences are older than 1.5 million years. The decrease in speciation events towards the present suggests a decrease in the rate of speciation with time, although lineage-through-time plots suggest that the peaks of speciation events may correlate with an increase in the rate of speciation following short periods of stasis (arrows in Fig. 2E).

To test these hypotheses, I compared the fit of different models of speciation in which the rate of speciation varies through time (two density dependent speciation models, and five models that assume 1 to 4 shifts in the rate of speciation) to the fit of two rate constant models (a pure-birth and a birth-death model), and tested for significance using simulated datasets. This was done using all three datasets: chloroplast, ITS and combined.

All rate variable models clearly show a highly significant departure from rate constancy for all three datasets (only two shown in Fig. 2F; see Table 1). The best rate constancy model for all three datasets was a pure-birth model, which had the same likelihood scores as the birth-death model, but has one less parameter (Table 1). The two models that include an extinction parameter, both with rate constancy (bd) and rate variation (bvd), were the worse fits overall, and the estimated extinction fraction parameter (*a*) was zero in all cases (with the initial input values ranging from 0 to 0.99). The logistic density dependent speciation model (DDL), in which the rate of speciation decreases as the number of species increases, was the best fit rate variable model for all three datasets

(Table 1). However, the model having the highest log likelihood for all datasets was the pure birth (Yule) model with four shifts in speciation rates (*yule5rate* in Table 1). The delta AIC between most of the Yule rate variable models and the best model (DDL) was not significant for all datasets (less than 2 AIC units; see Burnham and Anderson 2002, pg. 131), indicating that the DDL and the Yule models are equally likely, but the DDL includes fewer parameters (Table 1). The Yule variable rate models indicate a general decrease in the rate of speciation that is in agreement with the DDL model, but they also suggest large increases in speciation rate during very short periods of time, two for the chloroplast and one for ITS dataset (Fig. 2G). That of the ITS is concordant in time with the most recent of the chloroplast peaks (between 2.7 and 3.1 my BP), while the combined data suggest two peaks of speciation rates like the chloroplast data but with a shorter time interval between the two (Fig. 2G). However, the older peaks in speciation rates indicated by both chloroplast and combined data are likely an artifact caused by the few species that are polyphyletic in these trees.

The geography of speciation

In order to gain insights into the geography of speciation, I first applied the method of Barraclough and Vogler (2000) to assess the general geographical mode of speciation in *Pagamea,* i.e. allopatric, sympatric or peripatric. I then looked for common patterns in age estimates and the current geographical distribution of sister-clades, which might indicate a common cause. In both cases I used the ITS phylogeny, because this tree has a better fit with both geographical distribution and with morphological variation in particular (see Chapter 1), and is likely better depicting species relationships (see discussion).

Allopatry vs. sympatry

The plot of the degree of sympatry with node age suggests that three of the most recent speciation events are completely sympatric, one is allopatric, but most older nodes are also largely sympatric (Fig. 3A). There are also a few nodes, within 4-6 million years old, for which sister-clades are completely allopatric. The intercept of this plot had an intermediate value (0.38) of the degree of sympatry, and the slope of the regression line was 0.07. These values and patterns suggest a great deal of range movement since speciation. Barraclough and Vogler (2000) found with simulations that the intercepts converge on an intermediate value for plots under these alternate modes of speciation

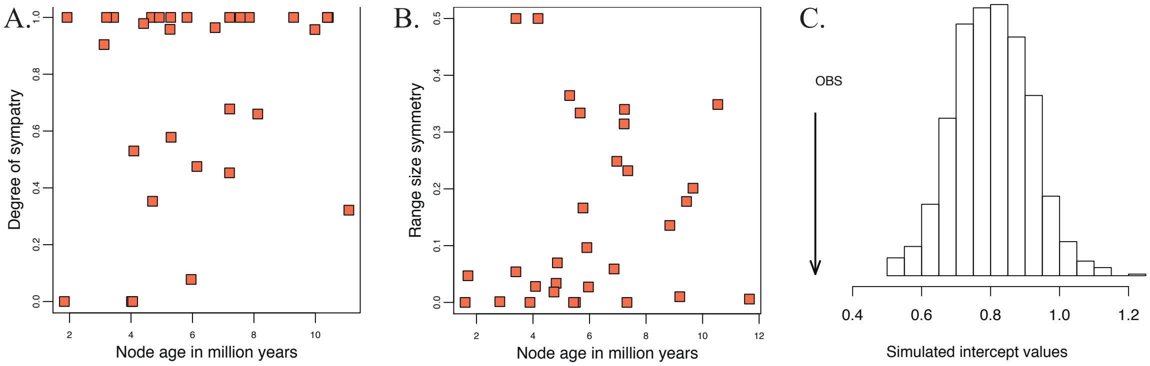


Figure 3. Geographical mode of speciation following the method of Barraclough and Vogler (2000). **A**. Degree of sympatry among all sister-clades in the ITS phylogeny by node age. **B**. Degree of range size symmetry by node age. **C**. Distribution of intercept values for the regression between degree of range size symmetry and node age for 1000 simulations. The observed intercept value from B is indicated.

when the level of range movements increases. A slope around 0 also indicates no general trend for the degree of sympatry with time, which would be expected if the level of range movements is high.

Although the highly-sympatric (~ 1) recent nodes suggest sympatric speciation, other lines of evidence indicate that even in these cases speciation might have been allopatric and that sympatry is a result of range movement after speciation. These highly-sympatric divergences are those of *Pagamea igapoana* and *P. coriacea* (Fig. 4C), *P. spruceana* and *P. occulta* (Fig. 4A), *P. pauciflora* and [*P. pauciflora* + *P. montana*] (Fig. 4G). In the first two cases, the species with larger ranges are paraphyletic with respect to the species with smaller ranges (tree in Fig. 4). Indeed, in both these cases, the sympatric accessions of the species pairs appear not to be their closest relatives, rather, *P. igapoana* is more closely related to accessions of *P. coriacea* from Central Amazon than to accessions of *P. coriacea* collected at the same site (see Chapter 1), and *P. spruceana* shows a similar pattern, being more closely related to an accession of *P. occulta* from Peru than to those collected in the same general area. In the latter case, however, there is no bootstrap nor Bayesian support for the relationship. The third case involves three species from the high-altitude mountains of the Guayana shield (Fig. 4G). According to the geographical location of samples (point data), *Pagamea standleyana* is sympatric only with *P. pauciflora.* These species are found together at Chimantá tepui in the eastern portion of the Guayana highland, but they also have somewhat distinct distributions, with *P. standleyana* found alone on Ayuán tepui, and *P. pauciflora* having a more southern distribution in this region (not shown). On the other hand, both species are allopatric to *P. montana*, which is found in the western portion of the

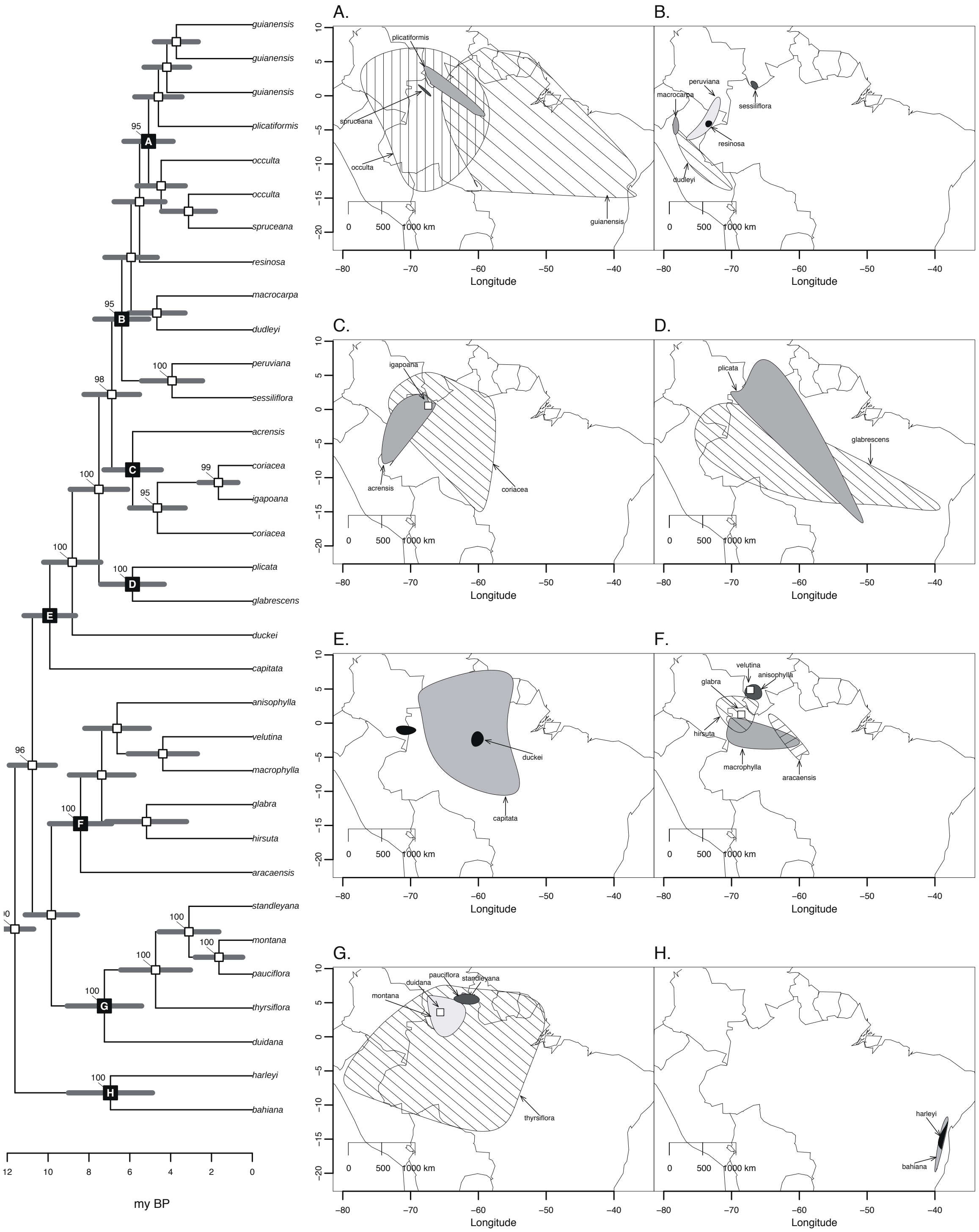


Figure 4. The ITS chronogram for speciation events in *Pagamea* and the geographical distribution of species. Multiple accession of some species were removed for clarity (see Fig. 7). Labeled nodes on chronogram indicate the maps on the right: **A**. Guianensis complex; **B**. Western Amazon species; **C**. Coriacea alliance; **D**. Plicata clade; **E**. *Pagamea duckei* and *Pagamea capitata*; **F**. Macrophylla clade; **G**. Thyrsiflora clade. **H**. Harleyi clade. Numbers at nodes are Bayesian posterior probabilities (shown only when >= 95%).

Guayana highland, and *P. montana* is sister to *P. pauciflora,* which corresponds to the second most recent allopatric divergence in *Pagamea* (Fig. 3A). These observations indicate that even in these cases speciation was allopatric.

Peripatry

The plot of range size symmetry against node age indicates that both the most recent divergences and several of the old divergences are highly asymmetrical (Fig. 3B). The intercept for this plot is 0.04 and the slope 0.034. The positive relationship between range size symmetry and node age increases (slope 0.05) if the oldest divergence, which is strongly asymmetric, is omitted. This oldest divergence is that between the Harleyi clade and the rest of the genus, and the Harleyi clade may have been strongly affected by extinction (see discussion). Therefore, there is a general trend of increasing range symmetry with node age. The observed intercept value is also significantly lower than the intercept values under the null model (Fig. 3C). These patterns suggest an important role for peripatric speciation in *Pagamea.*

However, range size asymmetry may have alternative explanations. For example, range contractions (extinction) or expansion are likely to occur after speciation events, and sister-clades may be affected in different ways. The geometry of the landscape, for example, may prevent a species from expanding its range because of a major barrier, while its sister-clade may have been free from such constraints (Barraclough and Vogler 2000).

In the oldest divergence in *Pagamea*, the split between the Harleyi clade and rest, a major barrier may have precluded range expansion. The Harleyi clade is endemic to the lowlands of the Atlantic Coast of Brazil (Fig. 4H), while all the other clades are found in the Amazon (Fig. 4). Two other species are found in the Atlantic coast, *P. guianensis* and *P. glabrescens,* but both represent much more recent colonization events (Fig. 4A, D). *Pagamea guianensis* is sympatric with the Harleyi clade, and its accessions in this region form a monophyletic group that is estimated to have diverged from Amazonian populations at 2.2 +/- 0.88 my ago (ITS) or 1.2 +/- 0.58 my ago (combined). *Pagamea plicata*, which in this region occurs in the mountains of the Atlantic Shield (Chapada Diamantina and Veadeiros), is estimated to have diverged from its Amazonian populations at a similar time, 2.6 +/- 1.3 my ago (ITS) or 1.85 +/- 0.82 my (combined). These mountains have a pluvial climate similar to that of both Amazonian and Atlantic forests. *Pagamea* is not found in the Cerrado biome of Central Brazil, except at scattered locations at high-altitudes, and the Cerrado represents a major climatic barrier between the Amazon and Atlantic regions (see Costa 2003).

The plot of range size symmetry and node age also indicates range asymmetry for several pairs of clades that represent old divergences within the Amazon region. These asymmetries are unlikely to have been produced by constraints of the landscape, because there are no major (current) barriers in the Amazon region. This suggests that the daughter-clades of these nodes have either not expanded their ranges at a similar rate, or that extinction has affected them differently, or that there were barriers in the past. Some of these asymmetries are quite striking, for example: the divergence between species restricted to the Western Amazon (Fig. 4B) and the Guianensis complex (Fig. 4A), that of *Pagamea plicata* and *P. glabrescens* (Fig. 4C), that between *P. coriacea* and *P. acrensis* (Fig. 4D), and that between *P. thyrsiflora* and its sister-clade (Fig. 4G). It is also remarkable that some species have very small distributions. All species in the Macrophylla clade, for example, have very small ranges (Fig. 4F). The pattern of range size in *Pagamea* follows the general left-skewed distribution observed in most lineages (Gaston 2003), with most species having very small ranges and a few species having relatively large ranges (Fig. 5A).

To see if differences in the rate of range expansion may have caused these patterns, I estimated the rate of range expansion by simply dividing the geographical area of a species by its age (Fig. 5A-C). Obviously, this assumes no extinction. I used two ages, both derived from the ITS tree: the first was the age separating a species from its closest relative (stem age), and the second was the oldest divergence within a species (crown age). Although the crown age was not available for all species, in all cases it represents the divergence time between accessions from the geographic extremes of a species range. Both estimates indicate that the species with larger geographical ranges have also expanded geographically at a faster rate (Fig. 5C).

Dispersal and plant fecundity

One of the processes that may lead to a higher rate of geographical expansion is greater dispersal ability (see Gaston 2003). Dispersal ability is perhaps the most likely

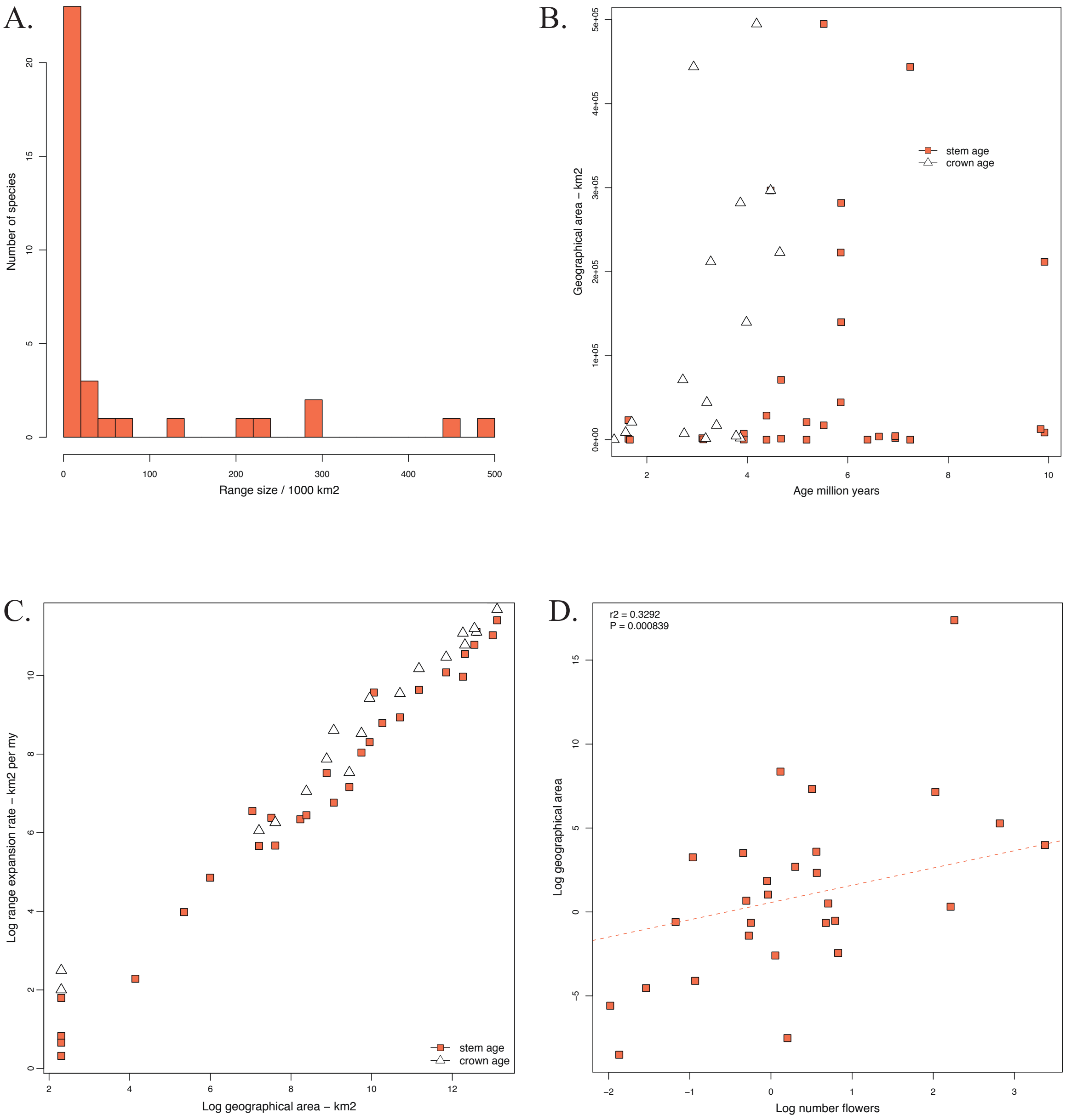


Figure 5. Relationship between species and geographical area. **A**. Distribution of range sizes for *Pagamea*. **B**. Relationship between range size and age of species according to the ITS estimates: the stem age is the age separating the species from its closest-relative, and the crown-age is the oldest age of divergence among accessions of a species. **C**. Relationship between range size and rate of range expansion. **D**. Relationship between range area and mean fruit productivity estimated by the number of flowers per inflorescence (for dioecious species only pistillate plants were counted), with phylogenetic dependence removed using phylogenetic independent contrasts.

explanation for a plant group, like *Pagamea*, which has a patchy distribution because of its habitat preference (see below). As a proxy for dispersal ability that could be obtained from herbarium specimens, I estimated the average number of flowers per inflorescences. I assume this to be a measure of plant fecundity, although it obviously does not take into account the number of inflorescences per plant, the rate of fruit productivity, the viability of fruits, generation time, etc. Despite these limitations, I found a strong relationship between species fecundity and its geographical area after accounting for phylogenetic dependence using phylogenetic independent contrasts ($r^2 = 0.35$, $P < 0.0005$; Fig. 5D).

Dispersal ability may also be related to population size. A species that is highly abundant will have greater likelihood of dispersal, and widespread species tend to be locally abundant (Gaston 2003). I have only anecdotal evidence in relation to species abundance. Field observations suggest that at least in some cases, endemic species, like those in the Macrophylla clade (Fig. 4F), are locally rare and mostly found within tall forests, while widespread species are usually abundant and/or found in more open habitats. However, among the very narrowly distributed species, this is clearly not the case for the two species endemic to the Atlantic Coast (Harleyi clade) or for *P. duckei* (Fig. 4E, H), which are all locally abundant. Dispersal ability may also be related to disperser vagility. Although, the dispersers of *Pagamea* remain unknown, all species have fruits that fit the general syndrome of bird dispersal, having a (usually) red cupule subtending a black drupe. In this context, differences in fruit size may indicate different bird dispersers, which might be associated with differences in dispersal ability. However, the relationship between the phylogenetic contrasts of fruit size and geographical area is not significant ($r^2 = -0.07$, $P = 0.15$), nor is that between fruit size and plant fecundity ($r^2 = 0.07$, $P=0.9$).

Biogeographical considerations

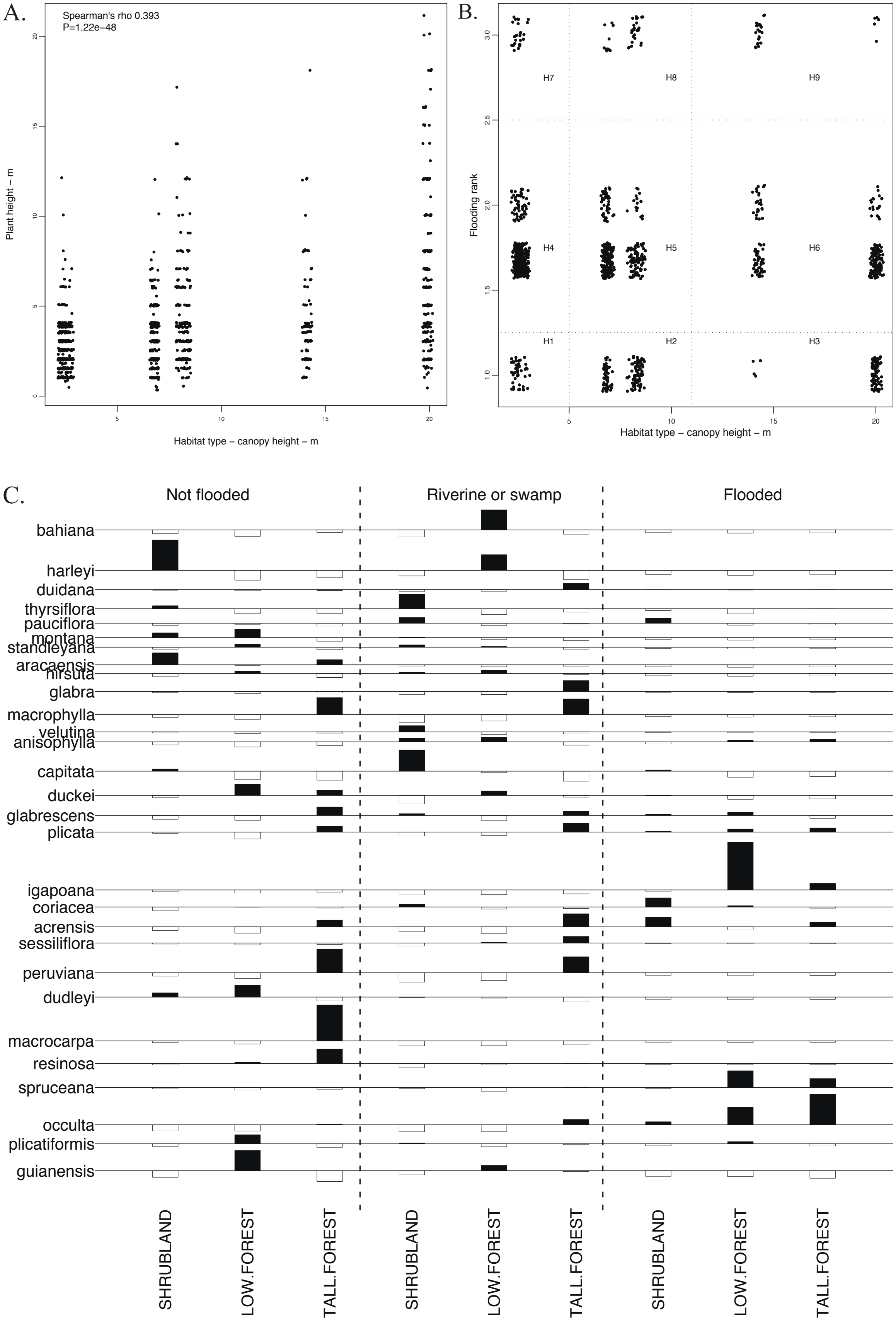
Pagamea is found in two disjunct areas, in the Atlantic Coast of Brazil and the Amazon region. Age estimates indicate three independent movements between these areas, two of which may have happened at a similar time (see above). With exception of the Harleyi clade, endemic to the Atlantic Coast, most other species are either endemic to, or at least present in, the Guayana Shield region, in particular in the rio Negro basin (Fig. 4A, C-G). This is the region of highest diversity of *Pagamea.* The only exceptions are the many species that are restricted to the Andes and the lowlands of Peru (Fig. 4B), and one poorly known species (both species status and phylogenetic placement) that is found in the Choco region of Colombia (not shown or discussed further). The species that are endemic to Peru form a grade in the ITS phylogeny (between nodes B and A in Fig. 4), but their monophyly is not rejected by the ITS data (Au test P = 0.084). According to the ITS topology, the colonization of the Andes and Western Amazon, as represented by the split between these species and the Coriacea clade (Fig. 4), happened around 6.8 +/- 1.36 my ago. In the combined tree, these species form a polytomy with Central Amazonian species, with a MRCA estimated to be 4.52 +/- 1.2 my old. The only other species occurring in Western Amazonia is the widespread *P. thyrsiflora,* which is closely related to three species endemic to the high altitudes of the Guayana Shield (Fig. 4G), a clade that includes most of the high-altitude species of *Pagamea* (see below). *Pagamea thyrsiflora* is estimated to have diverged from its closest relatives at 4.73 +/- 1.7 (ITS), or 3.45 +/- 1.25 (combined) million years ago. These age estimates suggest that the two lineages that colonized the Western Amazon and the Andes arrived there at different times. The sister-relationship between *P. peruviana* and *P. sessiliflora*, further indicate that one of these lineages returned to the Guayana Shield region at 3.9 +/- 1.5 (ITS), or 2.1 +/- 0.95 (combined) million years ago.

The ITS chronogram also indicates similar divergence times for three clades that have a a rather similar geographical pattern. These are the divergences between *Pagamea acrensis* and *P. coriacea* (Fig. 4C), between *P. plicata* and *P. glabrescens* (Fig. 4D), and between the Western Amazon species discussed above and the Guianensis complex (cf. Fig. 4A and 3B). The first two splits are estimated by the ITS dataset to be 5.86 +/- 1.4 my BP and 5.87 +/- 1.56 BP, respectively, a very close match. The Western Amazon species may have diverged from the Guianensis complex 5.52 +/- 1.23 my BP. However, given that range movements appear to be pervasive in *Pagamea* (see above), inferring a common vicariant event for these divergences may be misleading.

Ecology of speciation

Pagamea is clearly an edaphically restricted lineage – collectors refer to the words sand (79%) or sandstone (18%) in 97% of the specimens for which there is information about substrate (N=832). Information from labels about habitat type can be classified into ranks of vegetation structure and of flooding regime for 1286 specimens. In addition, there are 92 specimens for which there was information on canopy. The mean canopy for each habitat rank from these specimens was used as the canopy for each habitat type for the whole dataset, making it possible to calculate, tentatively, a shade index for each specimen, as the difference between canopy height and plant height. Plant height and canopy were positively correlated (Spearman's rho 0.39, P = 1.22e-48), but plant height in the forested habitats encompassed the whole range of variation in the genus (Fig. 6A). The combination of flooding rank and canopy (habitat rank) allowed the definition of nine habitat types, corresponding to three categories of flooding level, each with three kinds of vegetation structure (Fig. 6B).

There was a significant association between these nine habitat types and species (Chi-squared test, x^2 = 1312.57, P=5e-04), some species having much greater observed than expected preferences for one (seven species), or similar habitat types (eight species; Fig. 6C). For example, *P. occulta* includes plants that occur in tall forests either in riverine or flooded habitat types (Fig. 6C). There are also both similarities and differences between closely related species. Plants in highly flooded environments, for example, form two


A.
Spearman's rho 0.393
P=1.22e−48
Plant height – m
0
5
10
15
20
Habitat type – canopy height – m
B.
Flooding rank
1.0
1.5
2.0
2.5
3.0
H1
H2
H3
H4
H5
H6
H7
H8
H9
Habitat type – canopy height – m
C.
Not flooded
Riverine or swamp
Flooded
bahiana
harleyi
duidana
thyrsiflora
pauciflora
montana
standleyana
aracaensis
hirsuta
glabra
macrophylla
velutina
anisophylla
capitata
duckei
glabrescens
plicata
igapoana
coriacea
acrensis
sessiliflora
peruviana
dudleyi
macrocarpa
resinosa
spruceana
occulta
plicatiformis
guianensis
SHRUBLAND
LOW.FOREST
TALL.FOREST
SHRUBLAND
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SHRUBLAND
LOW.FOREST
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groups of closely related species. One group corresponds to *Pagamea coriacea*, *P. acrensis* and *P. igapoana,* which form a clade according to the ITS dataset, although these species differ in their preference for habitat structure (Fig. 6C). The other group corresponds to *P. occulta* and *P. spruceana,* also closely related. The sister-pair *P. bahiana* and *P. harleyi* are both found in low riverine forests, but *harleyi* is also found in dry open shrublands. *Pagamea dudleyi* and *P. macrocarpa,* sister species in the ITS analyses, both occur in dry habitats, but *dudleyi* prefers low open vegetation, while *macrocarpa* is found mostly in tall forests. Several species prefer tall forests, both in dry and riverine systems (Fig. 6C). Within species variation correlates, in some cases, with geography. *Pagamea aracaensis,* for example, has two disjunct populations that differ morphologically (see Chapter 3) and ecologically. One is made up of shrubs in the paleo-dune fields surrounding Aracá tepui in Central Amazon (see Carneiro et al. 2002), the other, much further south, of trees from tall dry forests.

These patterns appear to suggest greater phylogenetic conservatism in preference for flooding than habitat structure, i.e. with fewer evolutionary shifts in terms of preference for the former than for the latter. To test this hypothesis, I first calculated for each tip on the ITS phylogeny the mean habitat structure rank and mean flooding rank, and

← **Figure 6**. Habitat types and species. **A**. Relationship between plant height and habitat type. **B**. Nine habitat types (H1-H9) defined by the relationship between vegetation structure (canopy height) and flooding rank, used to test the association between species and habitat in C. **C**. Association between species and habitat type. A black bar above the baseline indicate greater observed than expected frequencies, otherwise a white bar below the baseline is shown. The height of the bar is proportional to the signed contribution to the Pearson's chi^2.

tested for phylogenetic dependence using the orthogram method of Ollier et al. (2005). I also tested for phylogenetic dependence in two other variables, mean shade index and mean altitude. All four variables showed a significant departure from phylogenetic independence (Table 2). More nodes in the phylogeny accounted for a significant amount of variation in both habitat structure and shade index than of flooding level or altitude (Fig. 7A-D). In addition, three nodes had a significant effect for both habitat structure and shade index, while there were no nodes at which either of these traits and flooding level were significant. Altitudinal variation was the most conservative trait, with only four nodes having a significant effect, the Thyrsiflora clade comprising most of the species found at high elevations (node labeled 23 in Fig. 7E). Note that *Pagamea capitata* in the Guayana Shield occurs from sea-level to 2500 m.a.s.l, but the mean altitude for the single tip from this region is around 500 m and the phylogenetic effect was, as consequence, not significant. Two additional species not sampled for this study are also found above 1500 m elevation in the Guayana Shield. Both these species are likely members of the Macrophylla clade according to morphological traits that are putative synapomorphies for this clade (see Chapter 1), and may represent one or two additional shifts from lowland to highland environments. The other high-altitude (> 1000 m) species are found in the Andes (*P. macrocarpa* and *P. dudleyi*), where also *P. thyrsiflora* is found, or in the Atlantic Shield of Brazil (*P. glabrescens*).

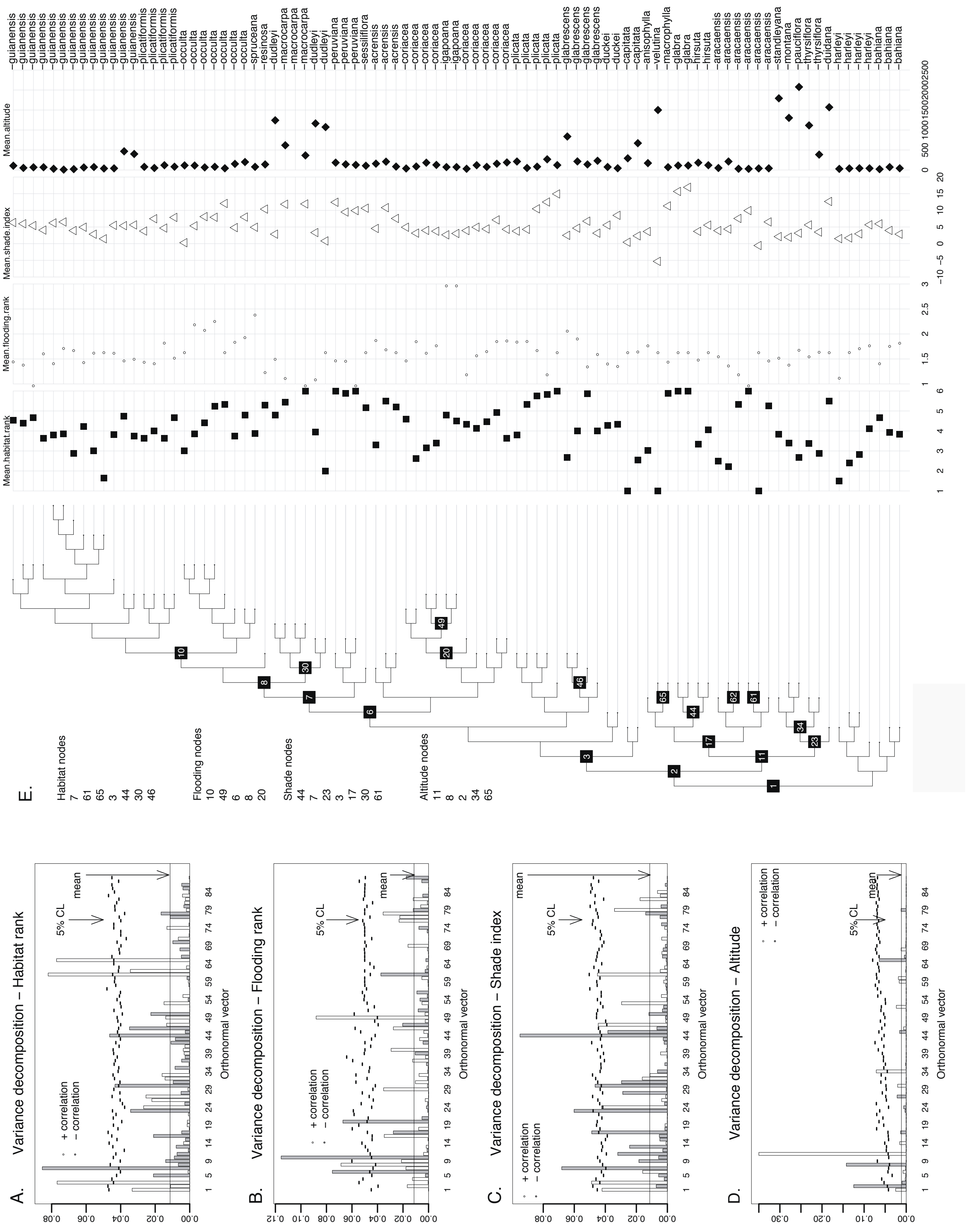
Competitive exclusion may be an important process in the nutrient-poor system in which *Pagamea* is found (e.g. Commes and Grubb 1998), and it may be a constraint for species coexistence. If this is true, recently diverged species that are sympatric should be ecologically divergent. To test whether sympatry requires ecological divergence, I first plotted the mean ecological distance between the daughter clades for all nodes in the ITS phylogeny against both their degree of sympatry and their age of divergence. These plots provide no evidence that ecological divergence increases with the degree of sympatry (Fig. 8A), nor is there a relationship between ecological divergence and node age for sister-clades that are sympatric (Fig. 8B). However, the degree of sympatry estimated by range overlap may not correspond to fine-scale co-occurrence, and the mean ecological distance between clades may be misleading because of spatial variation, i.e. local differences even when the average is the same. The patterns of habitat differences described above for closely related species suggest that, at least in some cases, they are ecologically different, and field observations suggest that species of *Pagamea* tend to show preference for different habitats when in the same locality. For example, at Jauacanã in the Upper Rio Negro region, I observed *P. spruceana* in highly flooded open habitat, *P. igapona* in highly flooded forest, *P. coriacea* in moist shrubland, *P. hirsuta* in dry low forest and *P. acrensis* and *P. plicata* in tall dry forest.

If species are in different habitats when in the same locality, then the ecological distances between individuals of the same species may be smaller than that between a species and the other species from the same site, if species are ecologically constant. Therefore, for each site in which two or more species were found, I first calculated the mean ecological distance within each species and the mean ecological distance between

Table 2. Results for the four statistics testing the association between phylogeny and ecology: habitat rank, flooding rank, shade index and altitude. **R2Max** measures the maximum variance explained by a single topological vector, i.e. maximum coefficient of association (r^2) between trait and vector, and therefore will peak when a single node on the tree accounts for most of the variance in the trait being analyzed; **Dmax** is derived from the cumulative orthogram (cumulative amount of variance from root to tips – topological vectors are ordered in the analyses from root to tips), and it tests for "diffuse phylogenetic dependence", i.e. when variance in trait is partitioned among several nodes; the **SCE** tests the "average local variation of the orthogram values", it measures the difference in variance explained by "closely-related" vectors; the **SkR2k** statistics indicates whether the variance distribution is skewed towards the root (negative values) or the tips (positive values) of the phylogenetic tree (see Ollier et al. 2005 for details on statistics; tests performed on 999 permutations).Test statistics with positive values means P(X>=obs) and negative values P(X<=obs).

Tree	Variable	R2Max	SkR2k	Dmax	SCE
ITS	Mean habitat rank	0.085 (P>0.192)	- 36.111 (P=0.02)	0.168 (P=0.049)	0.909 (P=0.048)
ITS	Mean flooding rank	0.116 (P=0.332)	- 34.38 (P=0.007)	0.248 (P=0.01)	1.622 (P=0.019)
ITS	Mean shade index	0.095 (P=0.2)	-33.115 (P=0.003)	0.246 (P=0.004)	1.805 (P=0.004)
ITS	Mean altitude	0.459 (P=0.001)	-17.432 (P=0.001)	0.629 (P=0.001)	11.202 (P=0.001)

→ **Figure 7**. Variance in ecological variables explained by different nodes in the ITS tree. **A-D**. Variance in ecological trait value explained by the different orthonormal vectors representing nodes in the ITS tree. The tree is fully dichotomous and each orthonormal vector represents a comparison between the daughter clades of each node, with the lower clade (in the figure) having negative values and the upper clade having positive values. Vectors are orthogonal and therefore uncorrelated. The amount of variance in the trait explained by each vector is obtained by correlating the trait with the vector, and positive or negative correlations are indicated by white or gray bars respectively. Vector are ordered from root (#1) to tips, i.e. by decreasing number of nodes within the daughter clades. The 5% confidence limit interval was obtained by permutation of the trait values among tips in the phylogeny (999 permutations). **E**. ITS tree with nodes numbered according to the corresponding orthonormal vectors. Only nodes explaining a significant amount of variation in the ecological traits are shown, and the nodes for each trait are indicated. The actual mean trait value for each tip is shown on the right.


A.
Variance decomposition – Habitat rank
B.
Variance decomposition – Flooding rank
C.
Variance decomposition – Shade index
D.
Variance decomposition – Altitude
+ correlation
− correlation
5% CL
mean
Variance
Orthonormal vector
E.
Habitat nodes
7
61
65
3
44
30
46
Flooding nodes
10
49
6
8
20
Shade nodes
44
7
23
3
17
30
61
Altitude nodes
11
8
2
34
65
Mean.habitat.rank
Mean.flooding.rank
Mean.shade.index
Mean.altitude

a species and each of all the other species found at the same site. I then subtracted the two mean distance values for each pairwise comparisons between a species and all other species, obtaining a measure in which negative values indicated more ecological variation within species than between species, and positive values indicating greater ecological difference between species than within species.

There were 149 sites, defined as a cluster of samples found within 100 km, in which a species had at least two individuals and where at least one other species was also found. There were 543 comparisons for these sites, and the ecological distance between species was significantly greater than the within species distance for 207 comparisons (38%; one-tail t-test, $P<0.05$). Most species at each site showed positive values in the difference between the two means (Fig. 8A), indicating greater ecological variation in relation to individuals of other species than when compared to individuals of its own species. These patterns suggest that species, when in the same site, tend to occur in different habitats. These comparisons show no particular pattern when plotted against age of divergence (Fig. 8B), with the greatest ecological differences representing old divergences.

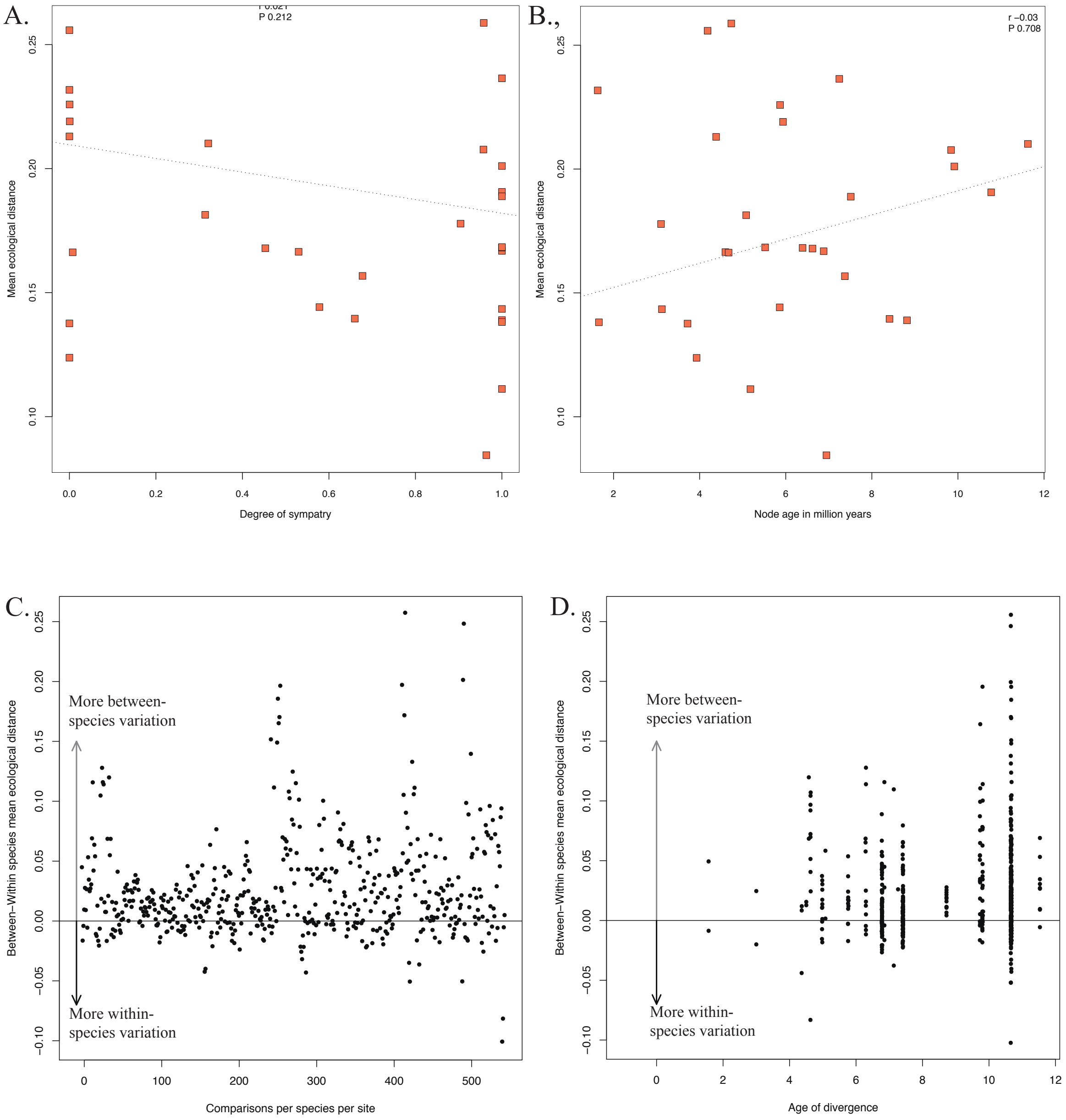


Figure 8. Relationship between ecological similarity and sympatry. **A**. The mean ecological distance between all pairs of sister-clades in the ITS phylogeny plotted against their degree of sympatry. **B**. The same ecological distance but plotted against node age (see also Fig. 3). **C**. The difference in mean ecological distance between and within species at different sites. Each dot in the plot represents a pairwise comparison of the ecological similarity between specimens of two species found within 100 km of each other. If the dot is above the line it indicates that the ecological distance between species is greater than that found within species, otherwise the dot is placed below the line. **D**. The same, but in relation to the age of divergence between each pair of species according to the ITS dataset.

DISCUSSION

The Gaertnera-Pagamea divergence

The timing of divergence obtained for the split between *Pagamea* and *Gaertnera* is estimated to have occurred during the middle Miocene (~ 12 +/ 4 my ago). The two sets of calibrations used in this study, the molecular ages estimated by Bremer et al. (2004) and the first occurrence of Rubiaceae pollen in the fossil record (Roth and Dilcher 1979), produced very similar estimates (both with mean of 12 my BP), which is surprising given that fossils tend to postdate the actual time of divergence and the assignment of fossils to nodes in phylogenetic trees is usually problematic. The *Faramea* pollen fossil from the early Eocene (~ 40 my; Graham 1985) resulted in much older estimates for the divergence of *Pagamea* and *Gaertnera,* and increased the error in the age estimates. This suggests that the identification or the dating of this fossil as *Faramea* may be incorrect. However, this pollen has distinctive diporate form that makes its assignment to *Faramea* unambiguous, and it was found in a well-studied site in Panama for which age estimates have great confidence (A. Graham, pers. comm. 2006). Therefore, the congruence in age estimates for the analyses that did not include this *Faramea* fossil may only be a coincidence, and reflect the problems associated with dating molecular phylogenies in general, and in particular when the fossil record is poor and the rate of molecular evolution does not behave in a clock-like fashion. Fossils of Rubiaceae indicate that the family was already very widespread during the Eocene (37-

54 my BP), with records from Australia, China, North America, Central America and Africa (Graham in press), indicating that the family originated earlier than its oldest unambiguously identified fossil record. Overall, these analyses indicate that *Pagamea* and *Gaertnera* diverged as early as the Early Miocene (~ 20 million years ago) and as late as the Middle Miocene (~ 12 million years ago). Hence, dating the divergences within *Pagamea* using 12 million years as a calibration for the split between *Pagamea* and *Gaertnera* are likely to yield underestimates of divergences times[1].

A Miocene divergence for *Pagamea* and *Gaertnera,* however dated, implies either long distance dispersal across the Atlantic or that the ancestors of these clades have migrated through the Tertiary North Atlantic land-bridge, during times when (sub)tropical forests were found at high latitudes (Tiffney 1985; Renner *et al*. 2001; Davis *et al*. 2002, 2004). A Gondwanan vicariant event is clearly not possible, because it would imply that these genera diverged around 90 million years ago (Parrish 1993), predating the oldest fossil of Rubiaceae (~ 50 million years; Graham in press) and molecular estimates for the age of the Gentianales as whole (~ 76 my BP; Bremer et al. 2004). Although the hypothesis of migration through a boreotropical land-bridge has support for many tropical disjunctions, such as in Malpighiaceae (Davis et al. 2002, 2004), Lauraceae (Chanderbali et al. 2001), and Melastomataceae (Renner et al. 2001, Renner and Meyer

[1] I have just recently talked to A. Graham who gave me a list of other fossils of Rubiaceae to use as additional calibration ages, and I plan to do so in the future as time is running short. However, I don't think my conclusions will change much, since I have basically disregard actual divergence times in *Pagamea*. Relative ages are unlikely to change.

2001), in these cases fossil records in Europe or North America also strengthen the argument. *Pagamea* is neither found in Central America nor in the Caribbean islands, but it is restricted to South America; the North Atlantic land bridge was present only until the early Oligocene (~ 33 my BP; Tiffney 1985), well predating the age estimates for divergence of the two. Therefore, dispersal across the Atlantic is the most likely scenario explaining the split between *Pagamea* and *Gaertnera*, because since 90 my ago the Atlantic has been a major barrier between Africa and South America (Tiffney 1985). Molecular phylogenetic dating supports scenarios of Trans-Atlantic dispersals, both ancient and recent, for lineages of plants, rodents, monkeys and lizards (see Renner 2004 for a review and references).

The direction of dispersal across the Atlantic remains unclear, because the placement of Gaertnereae in Rubiaceae is still undefined (Andersson and Rova 1999; Bremer and Manen 2000; Robbrecht and Manen 2006). Furthermore, all the lineages to which this clade is related occur in both continents (see Robbrecht and Manen 2006), and any ancestral area reconstruction will likely be ambiguous. However, some lines of evidence suggest that dispersal may have been from Africa to South America. First, the general pattern of dispersal across the Atlantic suggests that only wind-dispersed lineages have dispersed from South America to Africa during the Tertiary, while dispersals from Africa to South America involved sea currents (Renner 2004; see also Parrish 1993). *Pagamea* and *Gaertnera* are both dispersed by birds, but seeds may have also rafted across the Atlantic in “floating islands”, which may have may the voyage in very short periods of time (Renner 2004). Second, the placement of the Harleyi clade as sister to the rest of *Pagamea* is in agreement with this hypothesis. The Harleyi clade is endemic to the Atlantic coast of Brazil along a latitudinal range that coincides with that of sea currents arriving from Africa (South Equatorial Current and Brazil Current in Renner 2004, fig. 1), while currents in the opposite direction occur much further north. The direction of these currents has apparently not changed since the breakup of West Gondwana (Parrish 1993). In addition, *Pagamea* is also an edaphic specialist and species of the Harleyi clade occur on marine sand deposits at sea level, a trait that could have facilitated the establishment of the first migrant seeds. However, unlike *Pagamea, Gaertnera* is not an edaphic specialist (Malcomber, S., pers. comm. 2005), several species are found on sandy soils along the coasts of Africa (Cameroon and Equatorial Guinea), Madagascar and South East Asia, according to the TROPICOS database (www.mobot.org). Relationships in *Gaertnera* are still unclear, although there is some support for a West African species, *G. cooperi*, as being sister to all other *Gaertnera* (Malcomber 2002). *Gaertnera cooperi* is found mainly in Liberia and Ivory Coast, and label data suggest it occurs in moist environments (riverine forest), but is unclear whether these habitats are predominantly on sandy soils. Therefore, it remains unclear whether specialization to nutrient-poor sandy habitats was a trait of the ancestral lineage leading to *Pagamea* and *Gaertnera*. This provides and interesting, though speculative, scenario for the Trans-Atlantic divergence of *Pagamea* and *Gaertnera*.

The timing of speciation within *Pagamea****?***

In addition to the lack of good fossils for the calibration of phylogenetic trees to obtain diversification times, another major source of error in phylogenetic dating is phylogenetic uncertainty (Rustschmann 2006). Phylogenetic relationships among species of *Pagamea* are, in part, still unclear because chloroplast (*rps16* intron and *rpl20-rsp12* spacer) and nuclear (ITS) markers have somewhat different histories, and also because many internal branches on individual and combined phylogenetic trees are short and poorly supported (Chapter 1). The incongruences between ITS and chloroplast trees are mainly caused by species that do not form a monophyletic group according to the chloroplast, but which are monophyletic according to ITS data: *P. guianensis*, *P. occulta*, *P. plicatiformis* and *P. acrensis*. In addition, *P. dudleyi* has different placements in the two trees. In all these cases, the chloroplast lineages that are incongruent with those suggested by ITS data are restricted to particular geographical localities, these usually situated at the periphery of each species range (Chapter 1).

These incongruent phylogenetic patterns and the age estimated in this study suggest a scenario of retention of different ancestral polymorphisms for these species. Incongruence between phylogenetic datasets derived from the different genomes in plants has been attributed to either hybridization (e.g., Soltis et al. 1996; Hardig et al. 2000) or lineage sorting (Wendel and Doyle 1998; Linder and Rieseberg 2004; Jakob and Blattner 2006). The within species differences found in this study apparently do not indicate hybridization, at least not recent hybridization, because the chloroplast lineages are always monophyletic and unique to each species, and in no cases does a species share a chloroplast sequence with another species. The age estimates for the MRCAs of all accessions in the chloroplast and ITS phylogenetic hypotheses indicate that the ages of all those accessions having different positions in the chloroplast/combined and the ITS trees are all greater for the chloroplast data [6-8 my (chloroplast) *vs*. 4-6 my (ITS)]. Otherwise, estimates for the MRCAs that are older or younger than this time window are largely congruent between the two datasets, but with the ages from ITS tree usually older than those from the chloroplast tree. That older nodes are free from the influence of lineage sorting can be explained by the loss of polymorphism with time and by fixation of lineage-specific alleles (Wendel and Doyle 1998). On the other hand, the recent speciation events whose age estimates are congruent between the two datasets all represent species with small ranges, in particular members of the Macrophylla clade (Fig. 4), and species with small ranges would have less opportunity to retain ancestral polymorphisms. The fixation rate of chloroplast lineages in *Pagamea* is likely to be high because the white-sand habitats are usually small and isolated (Huber 1995; Prance 1996). Therefore, in widespread species, different chloroplast lineages may become fixed in different “islands”, and persistence time may increase in older lineages. Jakob and Blattner (2006) have shown that ancestral chloroplast types have survived for at least 4 my in Neotropical *Hordeum* (Poaceae), predating most speciation events. Furthermore, the fact that different chloroplast lineages within species are always in different localities, and usually at the periphery of the species range (Chapter 1), points to retention of ancestral polymorphisms in different populations.

This interpretation suggests that the ITS topology is a better estimate of species relationships, which is in agreement with the fact that the ITS tree has a better fit to morphological, geographical (see Chapter 1), and ecological variation.

Age estimates indicate that all speciation events in *Pagamea* took place before the Pleistocene, in agreement with several studies of divergence times in other lineages (e.g. Zamudio and Greene 1997; Silva and Patton 1998; Clough and Summers 2000; Glor et al. 2001; Costa 2003; but cf. Richardson et al. 2001; Monteiro et al. 2003; Ribas and Miyaki 2004). Vicariance events associated with Quaternary climatic changes have been the traditional explanation for diversification in tropical South America (see Haffer 1997 for a review), but because such climatic cycles are caused by changes in the Earth orbital cycles (Milankovitch cycles), a Tertiary timing of speciation events does not refute the so called “forest refuge hypothesis” (Haffer 1969, 1997) since climatic cycles were also occurring during that time. Nonetheless, the extent of forest fragmentation during periods of aridity is still controversial and recent studies of within-species variation suggest that climate change in the Amazon had little effect in fragmenting populations during the Pleistocene (Aide and Rivera 1998, Cavers et al. 2003, Dick et al. 2003, Novick et al. 2003, see also Lessa et al. 2003).

Lineage-through time plots and speciation models indicate a decrease in net speciation rate through time, with a logistic density dependent speciation model (DDL) being the best fit to data. This suggests that speciation in *Pagamea* is close to saturation, i.e. speciation rate decreased because of the filling of available niches (e.g. Zink and Slowinski 1995). Although models of multiple rate variation equally fit the data, both models show a trend of decreasing rate of speciation with time, and rate constancy is strongly rejected. Multiple shifts in speciation rate may suggest a cyclic pattern, but in this case shifts in the rate of speciation imply decreases rather than increases in rate. Multiple increases in the rate of speciation would be expected if cyclic factors like forest fragmentation caused by climatic changes had promoted divergence in *Pagamea*. The single increase in speciation rate at ~ 3 million years ago (ITS data) is difficult to understand as it relates to only two, geographically-unrelated, speciation events.

A pattern of decreasing rate of speciation through time could also arise by increasing extinction rates or by incomplete sampling (Pybus and Harvey 2000). In addition, it may also reflect our ability to recognize species at early stages of divergence, given that it may take time for morphological, ecological and sequence differences to appear after speciation. I cannot rule out any of these alternative scenarios. My sampling includes most known species of *Pagamea* (the missing species appear to belong either to the Macrophylla or the Thyrsiflora clades. Based on their morphology, there is no reason to suspect that they represent recent speciation events). However, the Amazon flora is still very poorly collected and sampling is also localized (Nelson et al. 1990; Prance et al. 2000), so more species probably remain to be discovered. Two lines of evidence suggest extinction has not played a major role, at least in the Amazon region. The first is that ancient chloroplast lineages have persisted within species. The second is the positive and significant relationship between geographical area and fecundity. One would not expect such a relationship if extinction had shaped the geographical range of species, unless extinction was not random, with low fecundity species being affected more strongly by extinction. Indeed, low-fecundity species are apparently also rare, at least locally. However, the models of speciation that included an extinction parameter were worse fits to the data. Extinction may have played an important role along the Atlantic Coast of Brazil, where the Harleyi clade is endemic. Species in this region are found from sea level to 110 m, with a mean of 40 m, and are restricted to white-sand marine deposits along the coast. The Harleyi clade may be sister to all other *Pagamea,* yet has produced only two species (*vs.* 30). Although this number may be related to available space (species-area relationship), during the last 10 million years there were four sea-level rises of more than 80 m, the last one occurring around 400 thousand years ago (Haq et al. 1987). Therefore, sea-level rise may have caused the extirpation of local populations (and species) in this region. However, sea level rises that may have also caused flooding of large areas in Central Amazon may have promoted speciation (see Marriog 1997; Nores 1999; Hall and Harvey 2002); in any event, it is unlikely to have caused major extinction of *Pagamea,* because white-sand habitats in the area that was flooded is apparently scarce.

The geography of speciation

Understanding the geography of speciation in a clade confined to a single continent and with a more or less continuous distribution is difficult, in particular when relying on a species-level phylogeny and on the current geographical distribution of its member species, which are estimated to have diverged before 1.5 my ago. If for no other reason, one would not expect that the ranges of species have remained unchanged since the time of speciation (see Losos and Glor 2003), or that extinction is irrelevant, even in tropical South America (e.g. Haffer 1969, 1997; Bush 1994). The method of Barraclough and Vogler (2000), used in this study, accounts for changes in the range of species by looking at the range size and overlap of sister-clades through time. It is not free from limitations, however, and simulations show that when ranges change greatly, it may be impossible to infer the geographical mode of speciation (Barraclough and Vogler 2000; see also Losos and Glor 2003).

In *Pagamea,* the degree of sympatry of sister-clades through time indicates that range changes since the time of speciation has been high. Even the recent divergences that are today largely sympatric, namely *P. igapona vs. P. coriacea* and *P. spruceana vs. P. occulta*, appear to have originated in allopatry, because *igapoana* and *spruceana* are not immediately related to the sympatric samples of their progenitor species, the paraphyletic *P. coriacea* and *P. occulta*, respectively. That divergence in *Pagamea* is mostly allopatric should also be expected by the fact that populations are in general disjunct because of the scattered and isolated distribution of the white-sand habitats (Huber 1995; Prance 1996). However, in such habitat systems, isolation may be more apparent than real. Conhaft (2000), for example, found that a bird species in the genus *Hemitriccus*, a specialist in these white-sand habitats, showed less genetic structure at similar spatial scales than its closest relatives, which are restricted to the more continuous tall terra-firme forests. Thus, this white-sand specialist shows greater vagility than its terra-firme relatives. The high degree of sympatry for the daughter clades of most nodes in the *Pagamea* phylogeny is agreement with this hypothesis; *Pagamea* is vagile. The few nodes whose daughter clades are completely allopatric (Fig. 3A) belong to the Macrophylla clade, whose species have low dispersal ability as inferred by the measure of fecundity used in this study. Hence, because of the high level of range changes, the possibility of sympatric speciation in *Pagamea* cannot be ruled out (see also Losos and Glor 2003).

Notwithstanding, the general pattern of the degree of range size symmetry for nodes in the *Pagamea* phylogeny strongly supports the hypothesis of peripatric speciation as the predominant mode of speciation in this genus. This is interesting because of the scattered and isolated distribution of the habitats in which *Pagamea* occurs. Peripatric speciation is a form of allopatric speciation in which a small isolated population becomes a new species. Because the population is small, theory predicts an important role for genetic drift in peripatric speciation (Coyne and Orr 2004, pg. 105). Genetic drift following a colonization event to a new white-sand "island" can lead to the fixation of novel alleles that may result in reproductive isolation between ancestor and descendant species (ibid.). In fact, the best examples of peripatric speciation come from oceanic islands and archipelagos (see Coyne and Orr 2004 for a review). In the *Pagamea* phylogeny, the most recently divergent species have highly asymmetrical range sizes (Fig. 3B), which is consistent with peripatric speciation. Two of these divergences, in particular, point to peripatric speciation. *Pagamea igapona* and *P. spruceana* have very small ranges and both make their ancestor species, which have very large ranges, paraphyletic (Fig. 4). Although they are currently sympatric with their ancestor species, phylogenetic relationships suggest they originated in allopatry, probably via recent peripatric speciation. In addition, in the case of *P. igapoana*, speciation is correlated with a shift to a highly flooded environment (Fig. 7), while that of *P. spruceana* is correlated with a morphological shift, since it has capitate inflorescences unlike those of its closest relatives (in *Pagamea*, capitate inflorescences are found only in the distantly related *P. capitata* and *P. harleyi*; Chapter 3). Such patterns suggest that these speciation events, at least, might have been caused by an interaction between drift and selection (i.e. a founder effect; see Coyne and Orr 2004, p. 106). The signal at older divergences may have been obscured by the frequent range changes discussed above. In this case, it is expected that range size asymmetry decreases with increasing node age (Barraclough and Vogler 2000). Although this is true for some older nodes, others display high range size asymmetry (Fig. 3B). For these nodes, the difference in range size between sister-clades may have been maintained (or even increased) after speciation, as a consequence of differences in the dispersal ability of species. Overall, this study supports peripatric speciation as the predominant mode of speciation in *Pagamea*.

Biogeography

There are few common patterns between age estimates and geography in *Pagamea* that would allow the inference of vicariance caused by a common historical factor (see Haffer 1997 for a review). In addition, with the high levels of range change detected in this study, and the errors likely associated with actual age estimates (see above), any correlation between divergences and historical factors can be only speculative. However, one common pattern is the recolonization of the Atlantic region by both *P. guianensis* and *P. glabrescens.* The Atlantic region is currently separated from the Amazon by the Cerrado and Caatinga biomes in central and northeast Brazil, which form a strong climatic barrier. However, forest connections are known to have been established at different times since the late Tertiary (see Costa 2003). It is interesting that these recolonization events have occurred at similar times, at 2.2 +/- 0.88 and 2.6 +/- 1.3 million years ago, respectively. Nonetheless, the routes of dispersal for these groups might still have been different. Three main biogeographical routes connecting the Amazon and the Atlantic forests have been proposed (see Costa 2003 and refs): one major route through the Paraná river basin; a secondary route to the northeast along the Atlantic coast around the horn of Brazil; and a minor route via riverine forests through the Cerrado of Central Brazil. Given its current distribution, *Pagamea glabrescens* appears to have migrated through the Cerrado of Central Brazil. Indeed, this species is currently found in riverine forests in this region, although today it is restricted to areas of high precipitation, like the mountains of the Atlantic shield. *Pagamea guianensis*, on the other hand, is not found in Central Brazil, and it may have migrated south through the coastal route.

The role of ecology in speciation

The significant association between habitat types and species suggest that habitat specialization has played a role in diversification of *Pagamea* and may be important for species coexistence, since species also tend to be in different habitat types when in the same local area. Although there is variation within some species, such variation is correlated with geography. Since there are fewer shifts in altitude and flooding regime than either habitat structure or shade tolerance, the former factors show greater phylogenetic conservatism than the latter. Sister-species may show differences in their preference for open or closed habitats, but they are usually similar in their preference for either flooding regime or altitude.

Seedlings and adult trees in Amazonian floodplain environments may be continuously submerged for up to seven months in some regions, and taxa show different adaptations to these conditions (Parolin et al. 2004). That adaptation to a flooding environment is a more difficult transition that to a different light condition is also indicated by species distribution in specific zones along flooding gradients within Amazonian floodplain systems (Parolin et al. 2004), and by a decrease in diversity with increasing flooding levels (Ferreira 2000). Within *Pagamea*, there are two main shifts from dry to flooded environments, one associated with the clade including *P. coriacea*, *P. acrensis* and *P. igapoana*, and another with the clade including *P.occulta* and *P.spruceana*. Another important shift is that of *P. igapoana* to a highly flooded environment, in contrast to *P. coriacea.* All species in highly flooded environments are found in black-water, nutrient-poor, floodplain systems of the rio Negro basin. This relationship between flooded black-water habitats with drier, white-sand habitats, is found in several taxa that have adapted to the stressful conditions of these habitat types (i.e nitrogen and phosphorus deficiences, and water stress; Herra and Jordan 1981; Tiessen et al. 1994), such as Rapateaceae, Humiriaceae, *Moronobea* (Clusiaceae), and *Retiniphyllum* and *Henriquezia* (Rubiaceae; Steyermark 1986; Kubitzki 1989; Berry et al. 1995).

Altitudinal shifts have been postulated to be important in generating diversity in taxa adapted to these nutrient-poor environments along the altitudinal gradient of the Guayana Shield (Steyermark 1986; Kubitzki 1989), with glacial cooling promoting such shifts (Huber 1988). *Pagamea* has been considered to be a lowland genus that occasionally colonized high-altitude environments (Steyermark 1986), which is in agreement with the findings of this study. However, contrary to earlier interpretations (Steyermark 1986; Kubitzki 1989), *Pagamea* has not adapted to the white-sand environments in the Guayana shield region, since it is quite likely that the ancestral lineage leading to *Pagamea* and *Gaertnera* was already a white-sand taxon. The higher diversity of *Pagamea* in the Guayana shield is, therefore, probably related to the greater area of white-sand habitats, and the greater environmental heterogeneity within these habitats, both in relation to flooding and altitude (Kubitzki 1989; Huber 1995; Prance 1996).

At least three independent lineages of *Pagamea* colonized the Guayana highlands. The clade comprising most of the high-altitude species of *Pagamea*, the Thyrsiflora clade, appears to represent a single colonization of this high-altitude environment with subsequent spread throughout the shield. Age estimates for this clade indicate that it had spread throughout the Guayana highlands before 1.63 +/- 1.1 million years ago (the split between *P. pauciflora* and *P. montana*), and that species from two nearby tepuis (*P. pauciflora* from Chimantá and *P. standleyana* from Ayuán) diverged around 3.12 +/- 1.5 million years ago, predating changes in the altitudinal range of species related to Pleistocene glacial cooling (Huber 1988; Bush 1994). An additional colonization of high elevations in the Guayana shield happened within the Capitata clade (*P. capitata)*, which occurs along the entire altitudinal gradient in this region. Whether lowland and high-altitude populations of this clade represent different species remains unclear. The Macrophylla clade also occurs at high elevations in the Guayana shield; furthermore, morphology suggests there may have been two additional independent shifts (no molecular sampling for these have been obtained).

Adaptations to a high-altitude environments in other regions happened at least twice in *Pagamea*. Although *Pagamea thyrsiflora* is also found at high elevations in the Andes, it can be considered as being pre-adapted to these conditions as it is found at a wide range of altitudes in the Guayana shield. The other two lineages to colonize high-altitude environments, *P. macrocarpa* and *P. dudleyi* in the Andes, and *P. glabrescens* in the Atlantic shield of Brazil, are members of a large clade that has not colonized high-altitude environments in the Guayana Shield, even though members of this clade occur in the surrounding lowlands.

Finally, the fact that species in the same locality tend to occur in different habitats suggests that competition may have played a role in habitat specialization in *Pagamea,* and may preclude fine-scale sympatry. Competition is also expected to be more intense in resource-limited environments like the white-sand habitats to which *Pagamea* is restricted, and is one hypothesis explaining the low biological diversity of these habitats (e.g. Coomes and Grubb 1998).

CONCLUDING REMARKS

The results of this study suggest that *Pagamea* colonized South America during the Miocene after long distance dispersal from Africa. The genus arrived at the Atlantic coast of central Brazil and soon after spread to the Amazon region where most of its diversity was generated. Speciation took place mainly during the Tertiary, which is in agreement with recent findings from molecular phylogenies that have challenged the traditional view that climatic changes during the Pleistocene was important in generating diversity in tropical South America. The results also point to an important role for peripatric speciation in generating diversity in *Pagamea*. Peripatric speciation has been considered to be a rare mode of geographical speciation, in particular within continental areas (Coyne and Orr 2004). However, a predominant role for peripatric speciation in *Pagamea* fits with its preference for a habitat type that has an island-like distribution within continental South America, and in which genetic drift may be a strong force leading to speciation. Patterns of range overlap and symmetry between sister-clades through time also indicate higher levels of range change that, at least in part, are related to the dispersal ability of species. The findings of this study also suggest that, despite its habitat specificity, *Pagamea* has diversified into the whole range of environmental variation within white-sand habitats, and along altitudinal gradients in the Andes and the Guayana Shield in particular. Finally, fine-scale specialization within white-sand habitats seem also to be important for the coexistence of species of *Pagamea*. This study is, to date, the most detailed account of the diversification of a lineage from white-sand systems in tropical South America.

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CHAPTER 3

Revision of *Pagamea* Aubl. (Rubiaceae)

INTRODUCTION

Pagamea Aubl. (Rubiaceae) is a genus of shrubs and trees that is restricted to tropical South America. In a previous study (Chapter 1), I combined phylogenetic analyses of molecular data from both chloroplast and nuclear genomes with phenetic analyses of morphological characters, in an explicit geographical context, to delimit species in *Pagamea*. I think about species in the context of a lineage-based concept (de Queiroz 1998), in which "substantial" reproductive isolation becomes a guiding rather than an absolute criterion for delimiting species, so giving flexibility to the Biological Species Concept (see Coyne and Orr 2004). Species are but a part of the continuous process of evolution, and diversification occurs only after reproductive isolation has been established. But if our interest is evolution, then we should look at all the stages of this continuous process. In each group there are likely to be different stages of the speciation process (de Queiroz 1998), and we may want to recognize all of them, monophyletic, paraphyletic, those that are morphologically different but are allopatric, those that are morphologically cryptic but sympatric, those that are distantly related but morphologically convergent. Understanding all these types of species permits the comprehension of the processes generating species, be they associated with particular paleo-ecological change (e.g. Haffer 1997), a particular configuration of the landscape (Chapter 2), or biological interactions (e.g. hybridization), etc. Our ability to delimit species, in practice, depends on the amount and kind of information we can obtain, and new information will likely change the way we understand species.

The method I employed for species delimitation in *Pagamea* (Chapter 1) is not free from limitations, but I think is a necessary first step if one wants to understand plant speciation in general, and in tropical South America in particular. Molecular data combined with an explicit understanding of morphological variation, using sympatry as indirect evidence of reproductive isolation, even if partial or temporary, suggested 29 species in *Pagamea* (Chapter 1). Results indicate different types of species, some are monophyletic, or paraphyletic, or sympatric almost cryptic species, or sister species that are morphologically very different but are allopatric. Molecular variation was not great in three sequenced markers (Chapter 1), despite the fact that most species appear to have originated before the beginning of the Pleistocene (Chapter 2). Chloroplast and nuclear markers were also incongruent for part of the molecular phylogeny (Chapter 1). The ITS phylogeny best describes patterns of morphological, ecological and geographical variation, and is the best hypothesis of species-level relationships (Chapter 1, 2), and the chloroplast phylogeny shows a pattern that is congruent with the hypothesis of differential sorting of ancestral polymorphism among species. In one case, at least, there is also a possible scenario of hybridization (Harleyi clade; Chapter 1, 2). Results of Chapter 1 and 2 raise more questions than give precise answers about species in *Pagamea*, but they provide a powerful framework to look at intraspecific and interspecific patterns of variation among closely related species and give directions for further studies.

Some species delimited in Chapter 1 and 2 have not yet been formally named, while others have a different circumscription from previous studies (Steyermark 1965, 1974). There are also species recognized earlier that could not be sampled for molecular data. There are also interesting patterns of intraspecific morphological variation that are important in the discussion of speciation in *Pagamea*. Here, I provide a taxonomic treatment for the species of *Pagamea*, including the best hypothesis of phylogenetic relationships among species, keys and tips for species identification, and a discussion on intraspecific geographical patterns of morphological variation. All told, I recognize 32 species, the species delimited in Chapter 1 and *Pagamea jauaensis*, *P. diceras* and *P. puberula* that were not sampled for molecular data.

PHYLOGENETIC POSITION

Pagamea is sister to the genus *Gaertnera* L., which includes 68 species and has undergone a rapid radiation throughout the paleotropics (Malcomber 2002). These two genera form the tribe Gaertnereae, a member of the supertribe Psychotriidinae, a predominantly woody clade of core Rubioideae (Robbrecht and Manen 2006). Phylogenetic evidence of chloroplast markers suggest that Gaertnereae are sister to the other Psychotriidinae (Andersson and Rova 1999; Bremer and Manen 2000; Robbrecht and Manen 2006), but support is low and there is some conflicting evidence (see Robbrecht and Manen 2006). Gaertnereae have a few morphological synapomorphies, including a sheathing (amplexicaul) stipule, a secondarily superior ovary, which changes from inferior to superior during development (Igersheim et al. 1994), xylem with parenchyma bands, and compound pollen apertures with crescent-shape costae (Jansen et al. 1996). Morphological synapomorphies for *Pagamea* are still unclear. *Gaertnera* has partially fused corolla lobes (Malcomber 2002), a character that is apparently not found in *Pagamea* (Chapter 1). In general, *Gaertnera* has terminal inflorescences and glabrous corolla lobes, and *Pagamea* axillary inflorescences and corolla lobes densely covered by white hairs, but neither characters is not fixed in either genus. There are also some quantitative wood anatomical and palynological differences between the two genera (Jansen et al. 1996), but only a few species have been examined, and variation is overlapping. *Pagamea* and *Gaertnera* are found in different continents, and their divergence is estimated to have occurred during the Early to Middle Miocene, representing a trans-Atlantic dispersal event (Chapter 2).

TAXONOMIC TREATMENT

PAGAMEA Aubl., Hist. Pl. Guiane 112, t. 44. 1775.—TYPE: *P. guianensis*, GUYANE FRANÇAISE, sommet de la montagne Serpent, à l’habitation appellée Gallion, FL-old, *Aublet* s.n. (Holotype: !BM).

Shrubs or trees. Leaves opposite, petiolate, membranous to coriaceous, glabrous to densely pubescent. Stipules cylindrical or conical, amplexicaul, with 4–8 apical setae, these usually reduced when the stipule is conical; usually only the terminal (youngest) stipule present, lower deciduous, but the base frequently persistent. Inflorescences axillary (pseudoterminal; an apparently terminal head formed by a cluster of axillary inflorescences), pedunculate (sessile), compound cymose (reduced to 1–3 flowers), congested, many-flowered, capitate, spicate, thyrsoid, or paniculate; bracts reduced, simple (lobed or leaf-like). Flowers small, distylous, homostylous or unisexual, sessile (pedicellate). Calyx cup-shaped, truncate to lobed, lobes 4–6. Corolla white, cream-colored or greenish, rotate, campanulate or tubular, 2–4.5 (–10) mm long and 1–1.5 (–3.5) mm diameter at the base, the tube always glabrous inside, the lobes 4(–5), valvate, densely pubescent adaxially (glabrous) with hairs usually longer at the base. Stamens 4 (–5), exserted, inserted near top of the corolla tube; anthers oblong to lanceolate, dorsifixed near the base. Ovary secondarily superior, 2-locular; ovules solitary in each locule, ascending, the placentation basal or axile near the base. Fruit a fleshy drupe, globose to ellipsoid, 3.5–13 mm long, shiny black, purple-black or reddish at maturity, partially inserted in a cup-shaped calyx or completely exserted, the calyx shallow, plate-like, red (orange) at maturity. Pyrenes 2, hard, obovate to obdeltoid, with one seed each.

Distribution – Pluvial tropical South America, in three main disjunct areas: (1) Atlantic forest of Brazil, Central Brazil Highlands; (2) Amazon region, Andes, Orinoco basin, Guyana Highlands; and, (3) the Chocó region of Colombia (Fig. 1). Species occur from

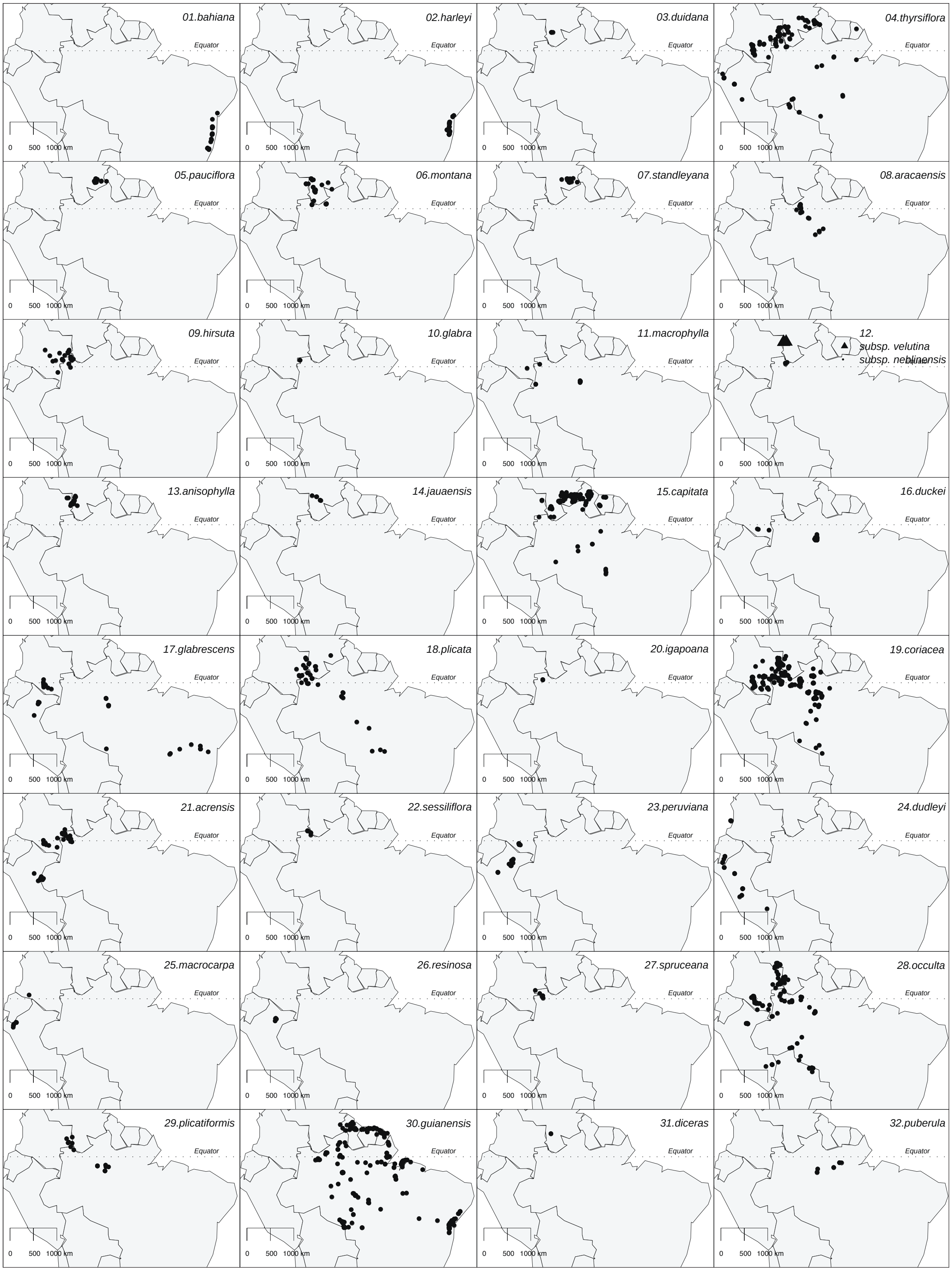

Figure 1. Geographical distribution of recognized species. Phylogenetic order (see Fig. 3).

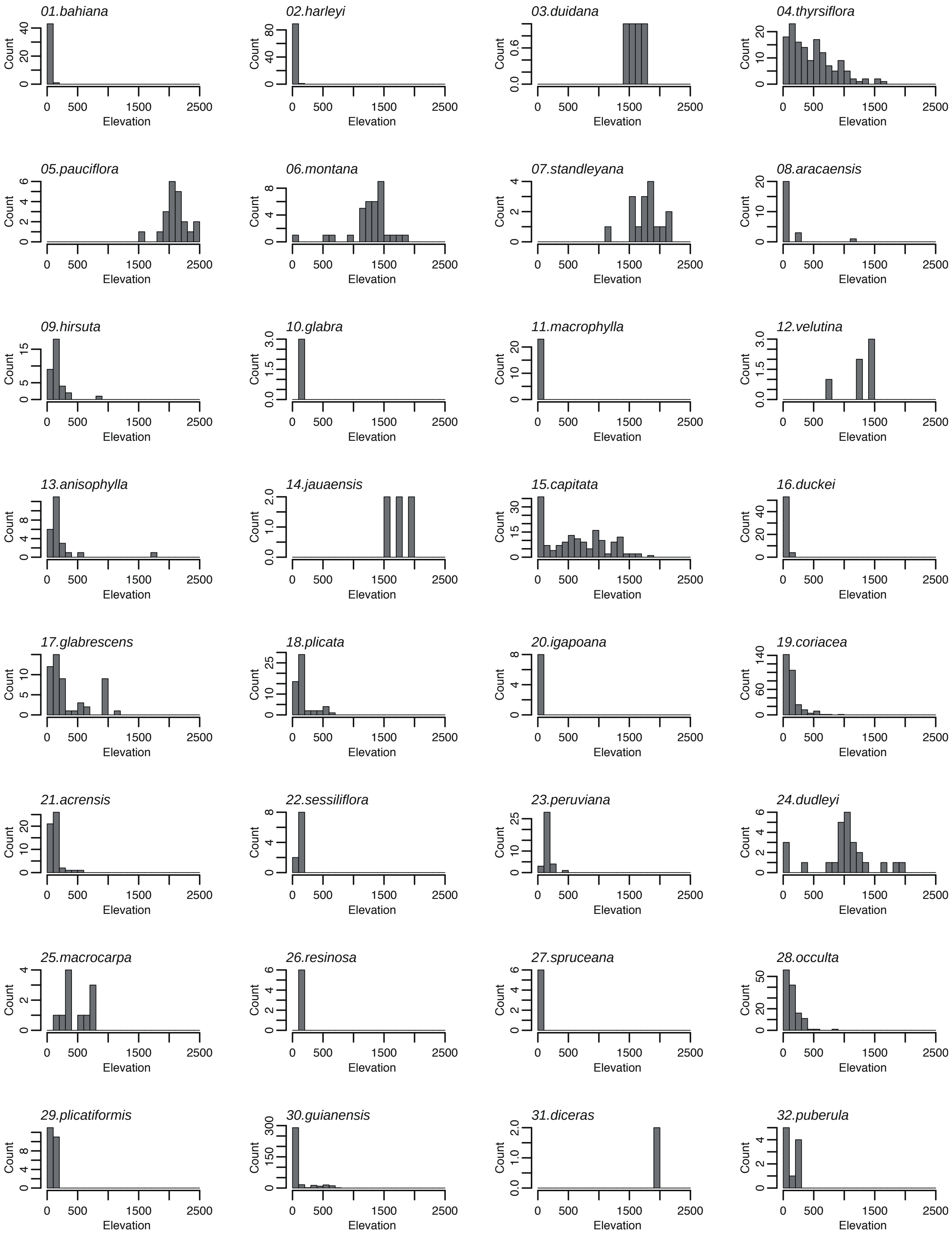

Figure 2. Altitudinal distribution of species. Phylogenetic order (see Fig. 3)

sea level to 2400 m in the Guyana Shield and the Andes (Fig. 2).

Habitat – *Pagamea* is an edaphic specialist lineage. Species are found only on very acidic, oligotrophic soils, on both white-sand and sandstone formations (Chapter 2). Within this general habitat, there is considerable environmental heterogeneity, in particular on the Guayana Shield, where the diversity of *Pagamea* is highest. Species of *Pagamea* occur in all habitat types found on such soils: savannas, dense scrublands, low forests and tall forests, whether flooded or not. There is, however, more phylogenetic conservatism in preference for degree of flooding and in altitude than for forest structure (Chapter 2). There is intraspecific variation in preference for vegetation structure and in shade tolerance, but different species when in the same site tend to occur in different habitat types (Chapter 2).

Species relationships – *Pagamea* comprises eight major clades according to the ITS data (see Chapter 1 and 2): Harleyi, Thyrsiflora, Macrophylla, Capitata, Duckei, Plicata, Coriacea and Guianensis (Fig. 3). The Guianensis clade is here divided into two groups, a clade forming the Guianensis complex, and a grade conforming to all species endemic to Western Amazon (Peru, Ecuador, both lowlands and the Andes, and the Chocó region of Colombia) and one species (*Pagamea sessiliflora*) endemic to the Negro-Casiquiari-Orinoco region. The Western Amazon grade is not rejected as monophyletic (AU and SH tests, $P > 0.084$). Of the remaining clades, Capitata and Duckei, include a single species, and the Coriacea clade has no support, although it is bounded by well-supported nodes (Fig. 3). Most species for which at least two individuals from different localities were sampled for molecular data (Chapter 1), are either supported as monophyletic, or their monophyly is not rejected (see Table 1). Two species, *P. coriacea* and *P. occulta*, are paraphyletic in relation to species, *P. igapoana* and *P. spruceana*, respectively. The latter have a much smaller geographical distribution than the former, and they are completely sympatric (Chapter 1, 2). Within the Guianensis and Macrophylla clades, species relationships remain unclear, although some relationships indicated by the ITS correlate with geography, morphology and/or ecology (Chapter 1, 2). Two other species, *P. jauaensis* and *P. diceras*, have not yet been sampled for molecular data, and three morphotypes are known from single specimens whose taxonomic status and phylogenetic placement remain unclear. Morphology supports the placement of *P. jauaensis* in the Macrophylla clade, and breeding system and geographical distribution suggest a relationship with *P. anisophylla* (see discussion under *P. anisophylla*).

Phylogeny and morphology – Morphology does not vary independently of phylogeny and the clades listed above occupy somewhat different portions of morphological space (Chapter 1). Variation is quantitative and overlapping and here I report it only for comparisons between closely related species.

The Macrophylla clade, with 7 species, is the only clade with obvious morphological apomorphies: a conical stipule that splits laterally, with leaves convolute-folded inside, and which may have marks parallel to the midrib after unfolding, the flower calyx densely covered inside by silvery appressed hairs. All other species of *Pagamea* have a cylindrical stipule with plicate-folded leaves emerging from the top, and the calyx is

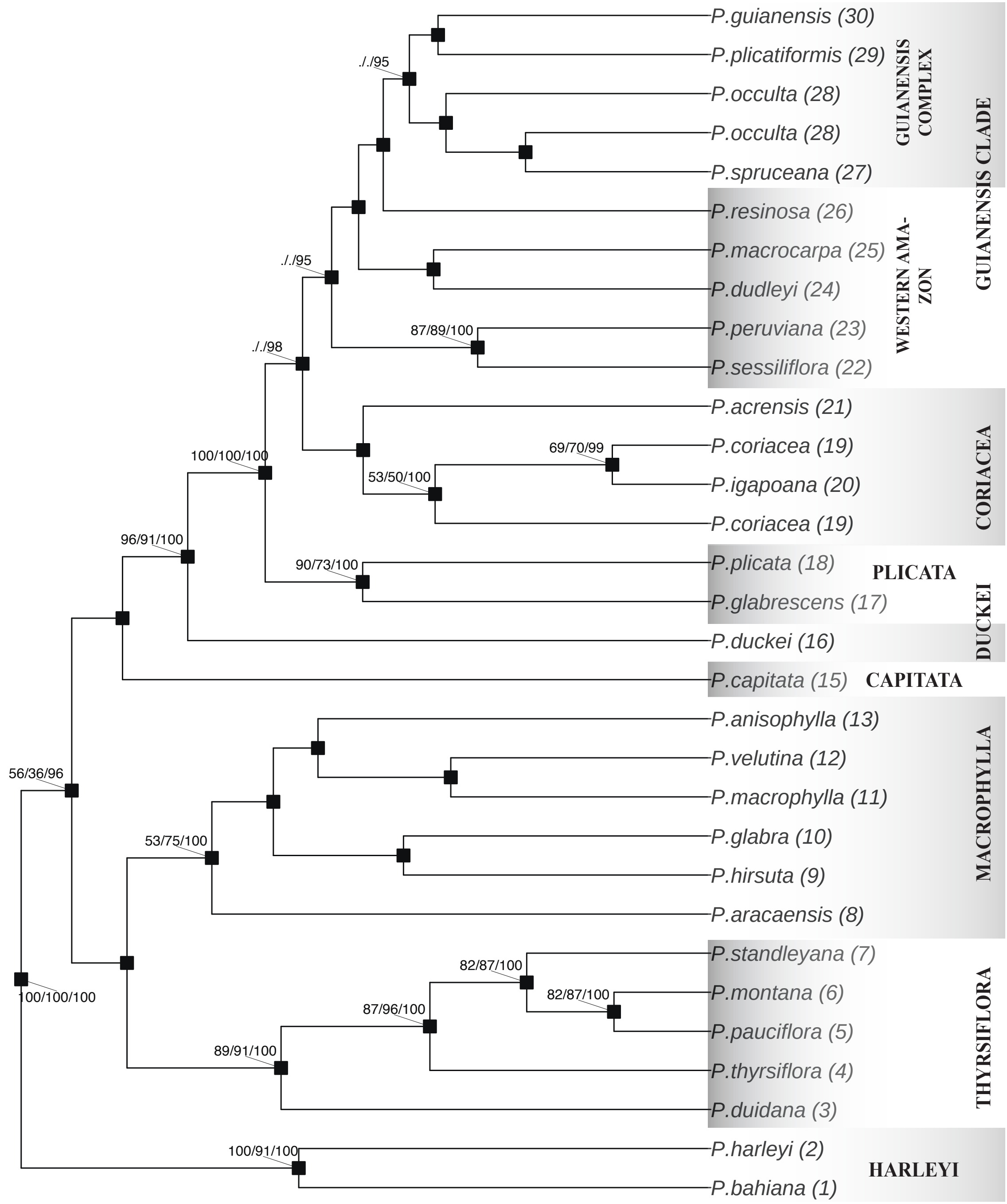

Figure 3. One of the best ML trees for the ITS dataset, and including only one sample per species for monophyletic species (see Table 1 for species monophyly). For the paraphyletic *P. coriacea* and *P. occulta* two accessions were included to emphasize the pattern (see Chapter 1 for a larger tree) . Support for nodes: MP-bootstrap/ML-bootstrap/Bayesian PP; only nodes with good (70% boostrap or 95% bayesian pp) support are shown. Number after species indicate order in treatment.

Table 1. Species monophyly according to both nuclear (*ITS*) and chloroplast (*rps16* and *rpl20-rps12*) datasets: **S** = when relationship is supported by either ML, MP boostrap (>= 70%) or by Bayesian posterior probabilities (>=95%); **NS** = monophyletic but support below these critical values; **NR** = monophyly not rejected according to both AU and SH tests (see Chapter 1). **n** = number of accessions for each dataset; **max geo dist** = maximum geographical distance between molecular accessions / maximum geographical distance among all collections of each species.

SPECIES		**ITS DATASET**			**CHLOROPLAST DATASET**		
		Monophyly	**n**	**max geo dist**	**Monophyly**	**n**	**max geo dist**
1	*bahiana*	monophyletic S	3	165/815 km	polyphyletic with *harleyi*	4	165/815 km
2	*harleyi*	monophyletic S	4	352/423 km	polyphyletic with *bahiana*	6	393/423 km
3	*duidana*		1	0/36 km		1	0/36 km
4	*thyrsiflora*		2	264/8742 km	monophyly NR	6	1741/8742 km
5	*pauciflora*		1	0/269 km	monophyletic S	2	63/269 km
6	*montana*		1	0/649 km	monophyly NR	4	17/649 km
7	*standleyana*		1	0/345 km		1	0/345 km
8	*aracaensis*	monophyletic NS	6	683/736 km	monophyly NR	6	684/736 km
9	*hirsuta*	monophyletic S	2	179/672 km	monophyletic S	3	179/672 km
10	*glabra*	monophyletic S	2	0/0 km	monophyletic S	2	0/0 km
11	*macrophylla*		1	0/1204 km	monophyletic S	2	3/1204 km
12	*velutina*		1	0/56 km		1	0/56 km
13	*anisophylla*		1	0/282 km	monophyletic S	2	82/282 km
15	*capitata*	monophyletic S	2	1482/7572 km	monophyletic S	5	1874/7572 km
16	*duckei*	monophyletic S	2	27/1333 km	monophyletic S	3	36/1333 km
17	*glabrescens*	monophyly NR	4	3656/3914 km	monophyletic S	9	3683/3914 km
18	*plicata*	monophyletic S	5	1052/2671 km	monophyly NR	5	1052/2671 km
19	*coriacea*	monophyletic SC	9	1220/2399 km	paraphyletic by *igapoana*	20	1587/2399 km
20	*igapoana*	monophyletic NS	2	0/0 km	monophyletic NS	2	0/0 km
21	*acrensis*	monophyletic S	3	1096/1265 km	2 allopatric clades	4	1097/1265 km
22	*sessiliflora*		1	0/119 km		1	0/119 km
23	*peruviana*		3	405/785 km	monophyly NR	5	405/785 km
24	*dudleyi*	monophyletic NS	2	434/2086 km	monophyletic S	3	1156/2086 km
25	*macrocarpa*	monophyletic S	4	91/785 km	monophyly NR	5	126/785 km
26	*resinosa*		1	0/56 km	monophyletic S	2	0/56 km
27	*spruceana*		1	0/242 km	monophyletic NS	2	54/242 km
28	*occulta*	paraphyletic by *spruceana*	7	1535/2731 km	2 allopatric clades	9	1871/2731 km
29	*plicatiformis*	monophyly NR	4	199/1107 km	2 allopatric clades	8	199/1107 km
30	*guianensis*	monophyly NR	12	3257/7271 km	2 allopatric clades	17	3257/7271 km
31	*diceras*		0			0	
32	*puberula*		0		monophyletic S	2	538/578 km

either glabrous or with erect hairs inside. In addition, species of the Macrophylla clade have flower/fruit calyces with lobes at most very short in proportion to the calyx tube, or absent. In fruit, this calyx encloses the drupe for almost half its length, while in most other species the calyx is shallow or with long lobes. Many members of the Macrophylla clade have also brochidodromous venation, which is otherwise only found in the Coriacea clade.

Breeding system variation correlates with phylogeny (Chapter 1). *Pagamea* has been considered a distylous genus (Steyermark 1965, 1973). Floral morphology, however, suggests that some clades that are predominantly homostylous. Most of the distylous species may actually be dioecious, as suggested by the observation that specimens with fruits tend to correspond with “longistylous” morphs. “Staminate” plants have extremely reduced styles, with closed, non-papillose stigmatic lobes, whereas “pistillate” plants have anthers that are shrunken, densely packed with raphides and lack pollen (Chapter 1). The Harleyi, Thyrsiflora, Macrophylla and Capitata clades are predominantly homostylous, and there seems to be one major transition to dioecy, at the node leading to the remaining five clades (Duckei and sister-group; see Fig. 3). Within this major clade, *P. coriacea* has all types of flowers. However, homostyly, at least in *P. capitata*, may be a cryptic distylous breeding system, because in a population in the Gran Sabana of Venezuela there is dimorphism in relation to pollen production, pollen size and stigma size (O. Hoecke, pers. comm. 2006).

Phylogeny and ecology – The Thyrsiflora clade includes most species found at high (>

1000 m) altitudes in the Guayana Shield. Two other clades, Capitata and Macrophylla, include some species from high elevations in this area, and may represent two or three additional highland colonization events (Chapter 2). The Thyrsiflora clade and a pair of species from the Guianensis clade have also colonized high altitudes in the Andes, and the Plicata clade is the only one found at high altitudes in the mountains of Central Brazil.

Biogeography – Most species of *Pagamea* originated during the Late Miocene to Pliocene, and all divergences between species are estimated to have occurred before the Pleistocene (> 1 my old; Chapter 2). The Harleyi clade is sister to the rest of the genus, and is endemic to the Atlantic Coast of Brazil, while its sister-group occurs mainly in the Amazon and Guayana region. This divergence took place as long as 9 million years ago, but two species of the Amazonian lineage have independently returned to the Atlantic region about 2 million years ago (Chapter 2). There is likely one major colonization of the Western Amazon (Peru and Ecuador), although only two species, *P. dudleyi* and *P. macrocarpa* have colonized high elevations in the Andes. *Pagamea dudleyi* may have crossed the Andes into the Chocó region (see note under *P. dudleyi*).

Peripatric speciation is supported as the predominant mode of speciation in *Pagamea* (Chapter 2). Such a mode of speciation may be associated with the island-like distribution of its preferred habitat, which are naturally fragmented, both on high (tepuis of the Guayana Shield; Huber 1995) and low (caatingas or campinas of the Amazon basin; Prance 1996) altitudes. Furthermore, the considerable geographical structure to the morphological variation in some species (see species notes). Lastly, species appear to differ in dispersal ability (i.e. fecundity, flower production; see Chapter 2), and vagile species so defined have, as a rule, larger ranges.

Uses – *Pagamea plicata* is used by indian communities in the Upper Rio Negro region for a red pigment extracted from the inner bark, which is used to paint fibers of Marantaceae (Nakazono *et al*. 2004) for making baskets and other artifacts. The inner bark of *P. plicata* appears to be redder and produce more sap in populations from the Upper Rio Negro, while plants around Manaus, as well as its sister species, *P. glabrescens,* have a red, but not so sappy, inner bark (pers. observations). Also in the Upper Rio Negro, *Pagamea macrophylla* is used as an ingredient in ritual snuffs , but whether or not the plant contains any psychoactive principles is unknown (de Smet 1985).

Identification tips – The genus is very easy to recognize by its opposite leaves, sheating stipules and superior ovary, unlike any other Rubiaceae in South America, in particular, those growing on white sands and similar habitats. The leaves are usually clustered on top of orthotropic branches, in some species more densely so than others, and the plant has a candelabrum appearance. Some shrubs have multiple stems. The outer bark of the trunk of both shrubs and trees is greyish in color and deeply sulcate.

Key to the species of *Pagamea*

1. Terminal stipule conical, splitting laterally, the leaf blade convolute inside; calyx

densely covered inside by appressed silvery hairs

2. Both surfaces of lamina hirsute, pilose or pubescent, hairs usually dense

   3. Lamina obovate, with 7–10 pairs of secondary veins; trichomes 2–4.5 mm long; inflorescence 7–12 cm long, peduncle 5–7 cm long; ovary glabrous.......09. ***hirsuta***

   3. Lamina elliptic, with ca. 6 pairs of secondary veins; trichomes 1–1.5 mm long; inflorescence 6–7 cm long, peduncle 3–4 cm long; ovary pubescent at apex ....……..........................……..................................…..... 12. ***velutina***

2. Lamina glabrous or nearly so, if with hairs, these minute (< 0.5 mm long) or, if longer, then sparse

   4. Leaves > 12 cm long

      5. Lamina with 15-20 pairs of secondary veins ………………………...10. ***glabra***

      5. Lamina with 5-10 pairs of secondary veins

         6. Leaves 13-15 cm long, the lamina 3.5-5 cm wide, usually with domatia on the vein axil abaxially [above 1000 m altitude on the Guayana Shield] ....……..................................….. 12. ***velutina***

         6. Leaves 14-26 cm long and 5-10 cm wide; lacking domatia [lowlands of Central Amazon] ....……..……………………….........11. ***macrophylla***

   4. Leaves < 12 cm long

      7. Lamina with 8-17 secondary veins; flowers bisexual, homostylous ....08. ***aracaensis***

      7. Lamina with 3-7 secondary veins; flowers unisexual, strongly heterostylous

         8. Petiole 6-11 mm long; calyx tube 1.8-3 mm long, the lobes 0.2-0.6 mm long [high-altitude of the Guayana Shield] ....……………..........14. ***jauaensis***

         8. Petiole 10-22 mm long; calyx tube 1-2 mm long, the lobes 0-0.2 mm long

[lowlands of the Guayana Shield] …………………………..13. ***anisophylla***

1\. Terminal stipule cylindrical, not splitting laterally, the leaves emerging from top, plicate-folded inside; calyx glabrous inside, or if with hairs, these not silverish

9\. Lamina bullate, adaxially with the secondary veins conspicuously impressed and usually pubescent; the veins strongly prominent abaxially; abaxial surface densely or sparsely pubescent

10\. Calyx lobes > 2 mm long, usually twice as long as the tube of calyx [inflorescences < 5 cm long; lamina membranous and > 4 cm wide] ......16. ***duckei***

10\. Calyx lobes < 1.5 mm long, at most as long as the tube of calyx

11\. Inflorescences up to 6.5 cm long; lamina chartaceous or membranous and < 3.5 cm wide ………………………………………………...29. ***plicatiformis***

11\. Inflorescences 5-20 cm long; lamina strongly coriaceous and > 3.5 cm wide

12\. Secondary axes of inflorescences 1-4 cm long; calyx lobes 0.3-1 mm long, the tube 0.8-1.6 mm long, usually glabrous outside; secondary veins and midrib glabrous adaxially; ovary glabrous ..………………..17. ***glabrescens***

12\. Secondary axes of inflorescences 0-1 cm long; calyx lobes 0.6-1.8 mm long, the tube 1.2-2 mm long, usually pubescent outside; secondary veins and midrib pubescent adaxially..…..................………………........18. ***plicata***

9\. Lamina adaxially not bullate or plicate, the veins usually glabrous; the abaxial surface glabrous or pubescent

13\. Lamina abaxially pubescent, hairs usually dense

14\. Ovary densely pubescent; calyx pubescent outside and usually with hairs inside; midrib of lamina pubescent adaxially ……..........................32. ***puberula***

14\. Ovary glabrous or with minute hairs; calyx glabrous or nearly so on both surfaces; midrib of lamina glabrous adaxially ....…………...28. ***occulta***

13. Lamina abaxially glabrous or nearly so

15. Inflorescence of an apparently terminal head formed by a cluster of sessile axillary inflorescences ………………………….....................22. ***sessiliflora***

15. Inflorescence axillary and pedunculate

16. Inflorescence units capitate, the lateral axes, when present, about as long as the main axis

17. Stipules persistent on all nodes with leaves; ovary densely pubescent apically; lamina ovate, the apex acute ....15. ***capitata***

17. Stipules soon caducous, or only the base persistent; ovary glabrous; lamina other than ovate

18. Inflorescence without lateral branches; plant dioecious [Upper Rio Negro basin] …………………………………...........27. ***spruceana***

18. Inflorescence with lateral branch > 1 cm long; flowers perfect, homostylous [Atlantic coast of Brazil] …………………......02. ***harleyi***

16. Inflorescence not capitate, with the main axis above longer than the lateral axes

19. Venation brochidodromous, i.e. veins loop-connected

20. Lamina < 2.5 cm wide …………………………………20. ***igapoana***

20. Lamina > 3 cm wide ....……………………………...19. ***coriacea***

19. Venation eucamptodromous, i.e. veins free

21. Petiole > 2.5 cm long **OR** > 3 mm thick

22. Calyx lobes 1-2.5 mm long, equal or up to twice as long as the calyx tube; lamina chartaceous, 18-32 x and 6-13 cm..........………

……………………...........…………………………23. ***peruviana***

22. Calyx lobes < 1 mm long, shorter than the calyx tube; lamina coriaceous, usually < 18 cm (-26) x < 6 (-8) cm

23. Petiole less than 1/6 or 1/7 of the length the blade; veins usually strigose abaxially, strongly raised ....17. ***glabrescens***

23. Petiole more than 1/5 of the length of the blade; veins usually glabrous abaxially, flat or only slightly raised ......……………………….... .....…………….........19. ***coriacea***

21. Petiole < 2.3 cm long **OR** < 3 mm thick

24. Leaves > 12 cm long

25. Lamina more than 4 times longer than wide (14-17 x 2.6-3.6); the blade and the terminal stipule with resinous marks [Iquitos area] ....26. ***resinosa***

25. Lamina wider, less than 4 times longer than wide (usually < 15 long); the blade and terminal stipule without resinous marks.

26. Inflorescence 6-10 cm long, the peduncle > 4 cm long; with 2-3 internodes along the main axis ....28. ***occulta***

26. Inflorescence 2-7 long, the peduncle < 4 cm long; with 0-2 internodes along the main axis

27. Calyx tube < 1 mm long, the lobes < 0.7 mm long [Eastern Amazon and Guianas] ....………30. ***guianensis***

27. Calyx tube (0.8) 1-1.8 mm, the lobes 0.5-2 mm long [Western Amazon, Andes and Chocó]

28. Inflorescences 2-7 cm long; the peduncle 1.5-4 cm

long; leaf-blade with 4-10 veins; fruit calyx ca. 5 mm in diameter; drupe 5.3-10 mm x 4.5-9 mm ..24. ***dudleyi***

28. Inflorescences < 2.6 cm long; the peduncle 1.8-2 cm long, leaf-blade with 7-12 veins; fruit calyx > 8 mm in diameter; drupe 9-14 mm x 6-11 mm wide ....25. ***macrocarpa***

24. Leaves < 12 cm long

29. From above 1000 m in the Guayana Shield region

30. Flowers or fruits clusters not separable in the distal part of main axis, internodes not distinguishable ....31. ***diceras***

30. Flower or fruit in clusters separated by internodes, or inflorescences single-flowered

31. Leaf-blade margin strongly revolute …......05. ***pauciflora***

31. Leaf-blade margin flat

32. Calyx tube up to 1 mm long …………..04. ***thyrsiflora***

32. Calyx tube 1.2-3 mm long

33. Without domatia on the leaf-blade abaxially...06. ***montana***

33. Domatia present abaxially, even when secondary veins are inconspicuous

34. Petiole 5-8 mm long, densely pubescent; midrib of lamina adaxially densely pubescent; calyx lobes absent or up to 0.6 mm long ....03. ***duidana***

34. Petiole 2-7 mm long, glabrous or nearly so;

midrib of lamina glabrous adaxially; calyx lobes 0.4-1.8 mm long

35. Leaves 3-5.5 cm long; entire inflorescence (1) 2-3 cm long, with 5-60 flowers; calyx lobes 0.4-0.9 mm long [Western Guayana Shield] ……..…………….…….... 06. ***montana***

35. Leaves 1-4 cm long; entire inflorescence 0.4-1.8 cm long, with up to 12 flowers; calyx lobes (0.4) 0.8-1.8 mm long [Eastern Guayana Shield] ……….…………........... 07. ***standleyana***

29. From the lowlands or other regions

33. Flower individually separated and/or pedicellate

34. Peduncle 1/2 the length of the inflorescence or longer [Atlantic coast of Brazil] ....01. ***bahiana***

34. Peduncle < 1/2 the length of the inflorescence [Amazon].04. ***thyrsiflora***

33. Flowers sessile, densely clustered [the following species largely overlap in morphology, but are distinct where they co-occur]

35. Atlantic Coast from Bahia (Brazil) to Guiana ....30. ***guianensis***

35. Central and Western Amazon and Upper Rio Negro/ Orinoco [Bolivia, Colombia, Ecuador, Venezuela and Brazil]

36. Leaves 4-8 x 1.5-2.5 cm

37. Tertiary veins conspicuous; midrib and usually the secondary veins densely strigose abaxially [look towards the leaf apex] ....………...30. ***guianensis***

37. Tertiary veins inconspicuous; midrib glabrous abaxially .....…...............……………......21. ***acrensis***

36. Leaves 7-12 x 2-2.5 cm

38. Petiole 0.5-1(-1.2) cm long; leaf blades 3-8 x 1-2.6 cm wide; tertiary venation strongly conspicuous; petiole, midrib and secondary veins abaxially densely strigose [look towards the leaf apex] ....30. ***guianensis***

38. Petiole 1-2.5 cm long; leaf blades 6-10 x 1-2-4.5 cm; tertiary veins obscure or slightly visible; petiole, midrib and secondary veins glabrous or only sparsely strigose abaxially;

39. Petiole glabrous AND inflorescence < 4 (-5) cm long [Andes and Chocó] ....24. ***dudleyi***

39. Petiole densely pubescent OR, if glabrous, then inflorescence > 5 cm long [lowlands] ....28. ***occulta***

SPECIES

The taxonomic treatment is organized following clades and species order in Figure 3, from bottom to top. Three additional species are included: *Pagamea jauaensis* (14), hypothesized as sister to *P. anisophylla* (13); and two unplaced species, *P. diceras* (31) and *P. puberula* (32). See notes under these species for discussions on species limits and intraspecific patterns of variation. Geographical distribution, altitudinal distribution and phenology, i.e. counts of flowering and fruiting specimens through time, are summarized for all species in Figures 1, 2 and 4, respectively.

Descriptions include characters used for delimiting species (Chapter 1), and additional descriptors of shape and pubescence. For each species, measurements are summarized as the ***mean +/- standard deviation (min-max)*** of collections listed in Appendix A (see Table 2 for characters).

Harleyi clade

This clade is sister to the rest of the genus (Chapter 1, 2; Fig. 3), and includes two species that are endemic to the Atlantic Coast of Brazil (Fig. 1).

01. ***Pagamea bahiana*** Vicentini, sp. nov. —TYPE: Brazil, Bahia, Alcobaça, Rodovia BR 255 ca. 6 km a NW de Alcobaça, 17° 31' 10" S and 39° 11' 44” W, 17 Sep 1978, FL/ buds, *Mori 10604* (Holotype: !CEPEC; Isotypes: !NY, !US).

Pagamea bahiana and *P. harleyi* are sister clades according to the ITS molecular marker, polyphyletic according to the chloroplast genome. Calyx lobes in *P. bahiana* are shorter than those in *P. harleyi*. The inflorescence of *P. bahiana* is cymose, and have few isolated flowers; the main axis is usually longer than the lateral ones, and branches are

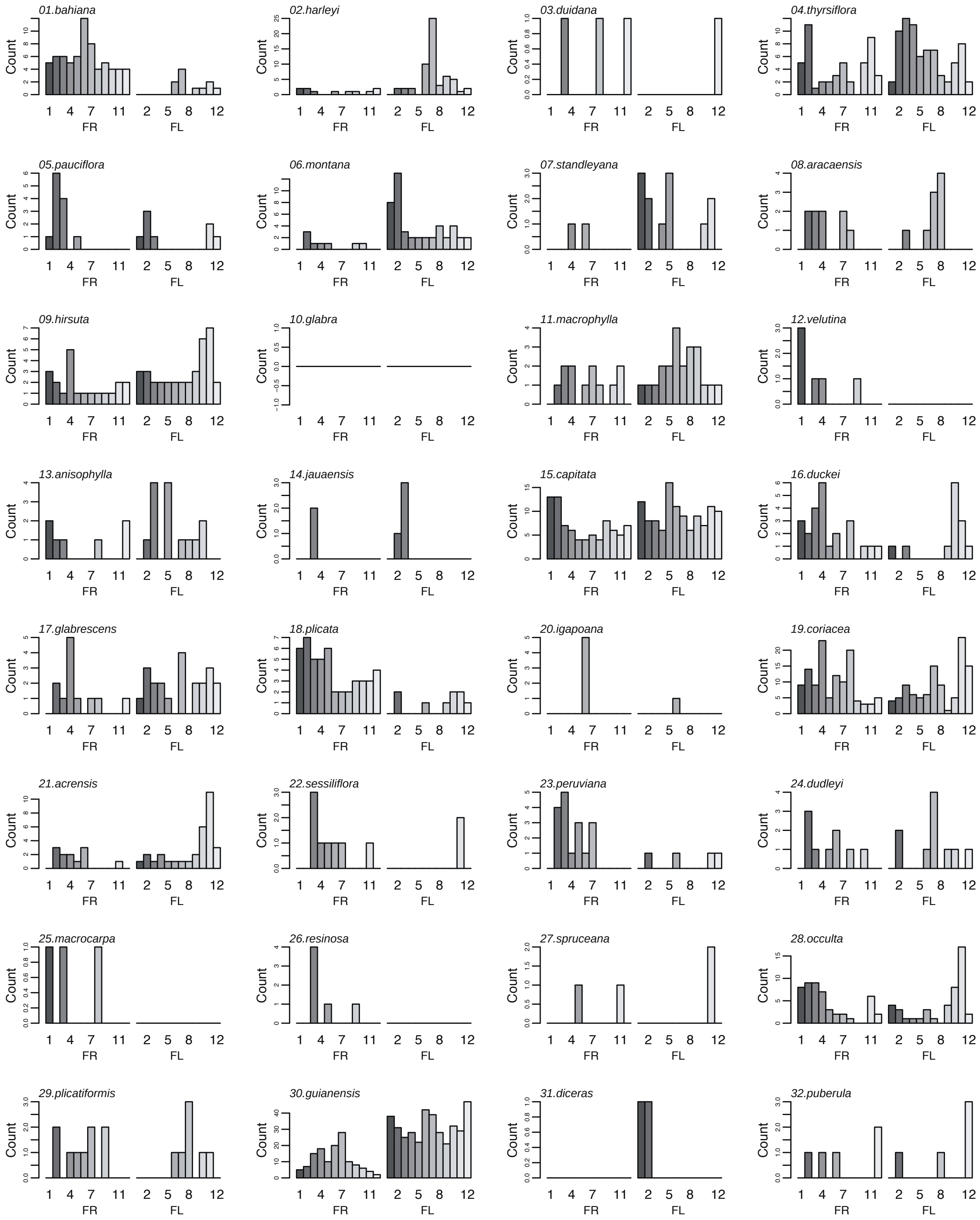

Figure 4. Flowering and fruiting time of species. Counts of specimens by month. Phylogenetic order (see Fig. 3). *Pagamea glabra* is only known from three sterile specimens from a single population.

Table 2. Description of characters used in multivariate analyses.

Label	Type	Description
LEAFLEN	mm	Average leaf length
LEAFWID	mm	Average leaf width
PETIOLEN	mm	Average petiole length
VENADENS	ratio	Average venation density (number of secondary veins/lamina length)
	ratio	Average domatia densisty (number of domatia)/(number of secondary veins)
LFSHAPE1	ratio	Average (lamina length to maximum width)/ (lamina length)
LFSHAPE2	ratio	Average (lamina width)/(lamina length)
LFSHAPE3	ratio	Average (petiole length)/(leaf length)
REVPROP	ratio	Average (revolute size/leaf width)
INFLPEDU	mm	Average inflorescence peduncle length
INFLLEN	mm	Average inflorescence total length
INFLBRAN	mm	Average inflorescence 1st branch length
INFLSH1	ratio	Average inflorescence (peduncle length)/(total length)
INFLSH2	ratio	Average inflorescence (1st branch length)/(main axis length)
INFLSH3	ratio	Average inflorescence (main axis 1st internode length)/(main axis length)
INFLSH4	ratio	Average (1st branch 1st internode length)/ (1st branch length)
INFLNO1	count	Average number of nodes on main axis
INFLNO2	count	Average number of nodes on 1st lateral branch
NFLOWERS	count	Average number of flowers per inflorescence
CALYXLOB	mm	Average length of flower calyx lobes
CALYXTUB	mm	Average length of flower calyx tube
CALYXRAT	ratio	Average (calyx lobes length)/ (calyx tube length)
PETIPUB	score	Principal Coordinate Analyses scores on a single axis representing the correlation of two ranks describing petiole indumentum (density and length)
PUBABAX	score	Principal Coordinate Analyses scores on a single axis representing the correlation of six ranks describing indumentum abaxially (density and length on lamina, veins and midrib)
PUBADAX	score	Principal Coordinate Analyses scores on a single axis representing the correlation of six ranks describing indumentum adaxially (density and length on lamina, veins and midrib)
INFLPUB	score	Principal Coordinate Analyses scores on a single axis representing the correlation of two ranks describing inflorescence peduncle indumentum (density and length)
CALXYPUB	score	Principal Coordinate Analyses scores on a single axis representing the correlation of two ranks describing indumentum inside the calyx tube (density and length)
OVARYPUB	score	Principal Coordinate Analyses scores on a single axis representing the correlation of two ranks describing indumentum on ovary (density and length)

not subtended by leaf-like bracts; the inflorescence of *P. harleyi* is capitate or the units within it are capitate, the flowers being densely clustered and usually subtended by leaf-like bracts.

Shrub or tree 3.9 ± 2.1 (1.3-12) m tall. *Twigs* 2.2-4 mm thick. *Stipules* cylindrical, 9.6 ± 2.1 (6.9-12.6) mm long, caducous or only the base persistent. *Leaves*: petiole 0.9 ± 0.3 (0.3-1.6) cm long, glabrous (densely strigose abaxially); lamina elliptic, chartaceous to coriaceous, 7 ± 1.5 (3.6-10.8) cm x 2.1 ± 0.5 (1-3.5) cm, glabrous on both sides, the margin flat; the midrib with 3.9 ± 1.4 (0-6) domatia abaxially, glabrous (densely strigose); the venation eucamptodromous, conspicuous, the veins arching, 5.7 ± 0.9 (4-8) pairs, these glabrous on both sides. *Breeding system* homostylous. *Inflorescences* cymose; peduncle 1.9 ± 0.9 (0.4-4.3) cm long, glabrous or nearly so; main axis 1 ± 0.6 (0-2.8) cm long, with 1.9 ± 0.7 (0-4) internodes; secondary axis 0.3 ± 0.3 (0-1.5) cm long, with 1.2 ± 0.5 (0-3) internodes; 11.3 ± 15.3 (3-61) flowers per inflorescence. *Flower calyces* glabrous outside, glabrous or sparsely pubescent inside, the lobes 0.4 ± 0.2 (0-0.7) mm, 0.3 ± 0.2 (0-1.1) times the length of the calyx tube. *Ovary* glabrous (sparsely hairy). *Fruits*: calyces orange, the drupe black, ellipsoid, 6 ± 0.6 (5-7) x 4.8 ± 0.5 (3.9-6) mm.

Vernacular – Caçutinga.

Distribution and habitat – This species is endemic to coast of the states of Espírito Santo and Bahia, Brazil. It is restricted to periodically flooded areas in restinga forests;

it has not been found in the more open shrubland vegetation (restinga aberta). Lowlands, 0-80 m elevation.

Notes –The reciprocal monophyly of *P. harleyi* and *P. bahiana* is supported by ITS data (Fig. 3) but not by chloroplast data (Table 1). These species are sympatric in the region between Porto Seguro and Salvador (Bahia), but *P. bahiana* is also found south of Porto Seguro in the state of Espírito Santo. Specimens of *P. bahiana* from the localities where it is found alone are more distinct from *P. harleyi* than those from the region of sympatry (Chapter 1). This pattern, coupled with the fact that these species are reciprocally monophyletic only according to the ITS data, suggests hybridization between the two in the region where their ranges overlap (Chapter 1). However, I found individuals of the two species growing side-by-side in the field and they could be readily distinguished. These patterns indicate that the two are different species, despite the possibility that reproductive isolation between them is incomplete.

Pagamea bahiana and *P. harleyi* can be distinguished by their calyx lobes, which are much shorter in *P. bahiana* than in *P. harleyi* (Table 3). The inflorescence of *P. harleyi* is also capitate or the units within it are capitate, the flowers being densely clustered and usually subtended by leaf-like bracts. The inflorescence of *P. bahiana* is cymose, and with fewer, isolated flowers; the main axis is usually longer than the lateral ones, and branches are not subtended by leaf-like bracts.

Because of its inflorescence structure and small leaves, *P. bahiana* usually has been identified as *P. guianensis,* which is also found in the Atlantic Coast of Bahia, Brazil. However, *P. guianensis* is clearly dioecious, while both *P. bahiana* and *P. harleyi* have perfect, homostylous flowers. When fruiting, the cupule of *P. bahiana* and *P. harleyi* is orange at maturity, while that of *P. guianensis* is bright red. The lobes of the calyx of *Pagamea guianensis* are also longer (0.6-1.5 *vs*. 0-0.8 mm) than those of *P. bahiana* (see Table 3).

02. ***Pagamea harleyi*** Steyerm.**,** Kew Bull. 38:317, 1983. —TYPE: Brazil, Bahia, Santa Cruz de Cabrália, 11 km S of Santa Cruz Cabrália, 16° 22' 0" S and 39° 1' 0" W, 17 Mar. 1974, FL, *Harley 17069* (Holotype: !CEPEC; Isotypes: !K, !MO, !NY, !P, !US). PLATE 1.

Shrub or tree 2.3 ± 1.2 (1-8) m tall. *Twigs* 4-6 mm thick. *Stipules* cylindrical, 17.3 ± 4.3 (9.6-26.4) mm long, caducous or only the base persistent. *Leaves*: petiole 1.4 ± 0.4 (0.7-2.8) cm long, glabrous (densely strigose to puberulent); lamina elliptic, coriaceous, 10.6 ± 2.6 (5.1-19.7) x 3.1 ± 0.6 (1.5-5.2), glabrous or nearly so on both sides, ± plicate, the margin flat; the midrib with 5.2 ± 1.3 (0-8) domatia abaxially, glabrous on both sides (densely strigose abaxially); venation eucamptodromous, conspicuous, veins arching, 6.6 ± 1.2 (4-11) pairs, these glabrous on both sides (densely strigose abaxially). *Breeding system* homostylous. *Inflorescences* capitate or subcorymbose; peduncle 4.3 ± 2.1 (0.9-12.1) cm long, glabrous to sparsely puberulent or strigose; main axis 0.7 ± 0.3 (0.2-2.1) cm long, with 1.4 ± 0.6 (1-3) internodes; secondary axis 0.5 ± 0.4 (0.1-2.3) cm long, with 1.3 ± 0.4 (1-2) internodes; 110 ± 23.3 (9-130) flowers per inflorescence. *Flower calyces* sparsely to densely puberulent on both surfaces, the lobes 1.4 ± 0.4 (0.4-7.9) mm, 1 ± 0.3 (0.3-2) times the length of the calyx tube. *Ovary* sparsely to densely hairy (glabrous). *Fruits*: calyces orange; the drupe black, ellipsoid, 6.9 ± 0.8 (5.7-8) x 5.7 ± 0.5 (5.2-6.5) mm.

Vernacular – Mangue-da-areia.

Distribution and habitat – This species is endemic to the coastal region of Bahia, Brazil, and is found in both forested (restinga alta) and open (restinga aberta, dunas) vegetation on white-sand soils . Lowlands, from sea-level to 80 m elevation.

Notes – *Pagamea harleyi* can be easily recognized by its somewhat plicate leaves and capitate to sub-corymbose inflorescence (see note under *P. bahiana*; Table 3).

Thyrsiflora clade

This clade includes five species, four of which are endemic to high elevations in the Guayana Shield and one, *P. thyrsiflora*, is widespread at mid to high elevations. All species have small leaves and inflorescences, often with few, pedicilllate flowers. The high-elevation species tend to have less flowers per inflorescences, but the flowers themselves are larger than those of the than those of the mid-elevation species, and they sometimes lack the typical white hairs that densely cover the inner side of the corolla in almost all other *Pagamea*.

03. ***Pagamea duidana*** Standl. & Steyerm., Fieldiana Bot 28:586, 1953. —TYPE: VENEZUELA, Duida tepui, 3° 36' 0” N and 65° 42' 0” W, 30 Dec 1928, FL, *Tate 567* (Holotype: !F; Isotypes: !NY, !US).

Table 3. The Harleyi clade and sympatric collections of *Pagamea guianensis*. Character differences between *P. bahiana* and the other two species shown when the mean value is different at P<0.05 (two-tailed t-test). Values shown are mean +/- standard deviation (min-max) averages per specimen (see Table 2 for characters).

Character	***bahiana***	***harleyi***	***guianensis***
PETIOLEN - mm	8.39 +/- 2.16 (3.25-11.5)	13.67 +/- 2.95 (7-20.33)	11.75 +/- 2.82 (7.4-19.83)
LEAFLEN - mm	66.85 +/- 11.66 (44-92.2)	101.1 +/- 18 (64.7-136)	74.11 +/- 11.15 (42.8-97.9)
LEAFWID - mm	20.22 +/- 4.08 (13.5-31.33)	29.6 +/- 4.48 (19.25-41.5)	n.s.
LFSHAPE1 - ratio	0.5 +/- 0.03 (0.44-0.58)	n.s.	0.44 +/- 0.03 (0.36-0.51)
LFSHAPE3 - ratio	0.13 +/- 0.02 (0.07-0.16)	n.s.	0.16 +/- 0.03 (0.12-0.23)
DOMADENS - ratio	0.66 +/- 0.24 (0-0.97)	0.81 +/- 0.12 (0.48-1)	0.52 +/- 0.23 (0-0.86)
INFLPEDU - mm	18.7 +/- 8.65 (6.88-38.5)	41.95 +/- 18.63 (9.5-92.67)	29.79 +/- 7.45 (17-57)
INFLLEN - mm	28.45 +/- 12.72 (9.38-57)	48.83 +/- 20.84 (11.5-100)	45.17 +/- 12.5 (27-83)
INFLBRAN - mm	2.95 +/- 2.67 (0-10.17)	4.57 +/- 3.85 (0.5-18.33)	1.52 +/- 2.01 (0-8.67)
INFLNO1 - count	1.87 +/- 0.7 (0.75-3.33)	1.4 +/- 0.54 (1-3)	n.s.
INFLNO2 - count	1.17 +/- 0.57 (0-2)	n.s.	0.6 +/- 0.67 (0-2)
INFLSH1 - ratio	0.67 +/- 0.12 (0.29-0.86)	0.85 +/- 0.05 (0.73-0.92)	n.s.
INFLSH2 - ratio	0.51 +/- 0.29 (0-1.02)	1.1 +/- 0.43 (0.11-2)	0.13 +/- 0.15 (0-0.52)
INFLSH3 - ratio	0.56 +/- 0.13 (0.33-0.91)	n.s.	0.49 +/- 0.1 (0.31-0.69)
CALYXLOB - mm	0.35 +/- 0.15 (0.13-0.79)	1.42 +/- 0.36 (0.68-2.13)	0.8 +/- 0.23 (0.45-1.29)
CALYXTUB - mm	1.27 +/- 0.12 (1-1.53)	1.41 +/- 0.22 (1.05-1.88)	1.1 +/- 0.11 (0.95-1.37)
CALYXRAT - ratio	0.28 +/- 0.12 (0.09-0.63)	1.03 +/- 0.19 (0.51-1.5)	0.73 +/- 0.19 (0.42-1.2)
NFLOWERS - count	19.31 +/- 13.42 (6.33-54)	42.82 +/- 22.99 (14-110)	39.62 +/- 25.27 (9-93)
PETIPUB - score	5.79 +/- 0.67 (3.11-6.04)	4.93 +/- 1.46 (1.01-6.04)	4.52 +/- 1.33 (1.01-6.04)
PUBABAX - score	17.85 +/- 1.12 (14.6-18.2)	15.52 +/- 2.42 (11.1-18.24)	n.s.
INFLPUB - score	0.72 +/- 1.03 (0-3.86)	4.24 +/- 1.37 (0-5.9)	2.3 +/- 1.17 (0-4.75)
CALXYPUB - score	1.25 +/- 1.48 (0-5.03)	2.67 +/- 0.48 (1.01-2.98)	0 +/- 0 (0-0)
OVARYPUB - score	4.59 +/- 0.9 (2.03-5.01)	3.24 +/- 1.31 (1.01-5.01)	3.32 +/- 1.81 (0-5.01)

Shrub or tree 1.7 ± 0.2 (1.5-1.8) m tall. *Twigs* 1.5 ± 0.6 (0.8-2.8) mm thick. *Stipules* cylindrical, 4.6 ± 1.5 (2-7) mm long, caducous or only the base persistent. *Leaves*: petiole 0.7 ± 0.2 (0.4-1.1) cm long, densely pubescent; lamina elliptic, membranous, 3.3 ± 0.7 (1.5-4.4) x 1.1 ± 0.3 (0.5-1.8) cm, glabrous on both sides, the margin flat to slightly revolute; the midrib with 2.1 ± 0.6 (1-3) domatia abaxially, sparsely to densely strigose on both surfaces; venation eucamptodromous, conspicuous, veins arching, with 3.6 ± 0.7 (2-5) pairs, these sparsely strigose abaxially, glabrous adaxially. *Breeding system* dioecious. *Inflorescences* cymose; peduncle 1.1 ± 0.3 (0.8-1.6) cm long, sparsely strigose; main axis 0.1 ± 0.1 (0-0.4) cm long, with 0.3 ± 0.2 (0-1) internodes; secondary axis absent; staminate plants with 3.6 (3-5) flowers per inflorescence; pistillate plants with 1-3 flowers per inflorescence. *Flower calyces* glabrous on both surfaces, the lobes 0.5 ± 0.1 (0.3-6.8) mm long and 0.3 ± 0.1 (0.2-0.4) times the length of the calyx tube. *Ovary* glabrous. *Fruits* globose, 5.8 ± 0.9 (4.2-6.8) x 5.2 ± 0.5 (4.6-6) mm.

Distribution and habitat – This species is known from montane forests at high altitudes (> 1500 m) on the Duida-Maruhaca massifs, and at a nearby site in Western Guayana Shield.

Note – This species is strongly supported as sister to all other species of the Thyrsiflora clade (Fig. 3). It is morphologically most similar to *P. thrysiflora* in having chartaceous leaves with conspicuous secondary venation (unlike most high-altitude species of the Thyrsiflora clade; see Table 4 for species comparisons). It can be distinguished from *P. thrysiflora* by having the petiole much longer in proportion to the leaf blade (ca. 20% vs.

Table 4. The Thyrsiflora clade. Characters shown have mean values that are significantly different between at least two species (Kruskall-Wallis test, P <= 0.01). Values shown are mean +/- standard deviation (min-max) averages per specimen (see Table 2 for characters).

Characters	***duidana***	***montana***	***pauciflora***	***standleyana***	***thyrsiflora***
PETIOLEN - mm	6.74 +/- 1.26 (5.06-8.07)	5.8 +/- 1.28 (3.67-10)	5.8 +/- 1.17 (3.8-8.5)	4.22 +/- 1.25 (2.17-6.96)	6.69 +/- 1.92 (3.75-12.67)
LEAFLEN - mm	33.31 +/- 3.08 (29.45-36.57)	43.17 +/- 9.75 (32.25-74.67)	31.19 +/- 4.91 (23.24-39.33)	28.44 +/- 7.71 (14.78-42.33)	58.72 +/- 13.13 (37-92)
LEAFWID - mm	11.11 +/- 2.34 (8.22-13.94)	11.05 +/- 2.2 (7.57-17)	12.03 +/- 2.58 (7.7-15.59)	9.55 +/- 1.82 (6.3-12.96)	14.62 +/- 3.5 (5-23.25)
LFSHAPE1 - ratio	0.48 +/- 0.02 (0.47-0.51)	0.5 +/- 0.05 (0.41-0.61)	0.56 +/- 0.06 (0.46-0.69)	0.53 +/- 0.05 (0.42-0.59)	0.45 +/- 0.05 (0.32-0.55)
LFSHAPE2 - ratio	0.41 +/- 0.07 (0.33-0.49)	0.3 +/- 0.04 (0.23-0.4)	0.43 +/- 0.08 (0.26-0.57)	0.41 +/- 0.07 (0.26-0.5)	0.28 +/- 0.04 (0.16-0.37)
LFSHAPE3 - ratio	0.2 +/- 0.02 (0.18-0.22)	0.14 +/- 0.03 (0.09-0.19)	0.19 +/- 0.03 (0.15-0.25)	0.15 +/- 0.02 (0.12-0.19)	0.12 +/- 0.03 (0.08-0.2)
DOMADENS - ratio	0.63 +/- 0.16 (0.49-0.87)	0.12 +/- 0.21 (0-0.72)	0 +/- 0 (0-0)	0.4 +/- 0.19 (0-0.73)	0.36 +/- 0.24 (0-0.92)
REVPROP - ratio	0.03 +/- 0.02 (0-0.06)	0.01 +/- 0.01 (0-0.05)	0.12 +/- 0.05 (0.04-0.2)	0.02 +/- 0.03 (0-0.12)	0 +/- 0.01 (0-0.05)
INFLPEDU - mm	10.72 +/- 0.54 (10.26-11.5)	17.53 +/- 7.29 (6.67-37)	11.82 +/- 4.68 (1.18-20)	7.19 +/- 3.42 (1-15)	12.23 +/- 5.44 (3.75-29)
INFLLEN - mm	11.77 +/- 1.06 (10.62-13)	21.58 +/- 8.32 (10-43.5)	13.97 +/- 5.12 (1.26-21.4)	9.29 +/- 3.58 (5.12-17.8)	31.05 +/- 9.63 (12.67-50.5)
INFLBRAN - mm	0 +/- 0 (0-0)	1.26 +/- 1.17 (0-4.03)	0.04 +/- 0.16 (0-0.6)	0.33 +/- 0.5 (0-1.35)	8.4 +/- 3.99 (0-18)
INFLNO1 - count	0.32 +/- 0.24 (0-0.5)	1.11 +/- 0.28 (0.57-1.62)	1.05 +/- 0.35 (0.2-1.5)	0.78 +/- 0.41 (0-1.33)	2.61 +/- 0.56 (1-4)
INFLNO2 - count	0 +/- 0 (0-0)	0.59 +/- 0.38 (0-1)	0.04 +/- 0.16 (0-0.6)	0.3 +/- 0.41 (0-1)	1.92 +/- 0.48 (0-3)
INFLSH1 - ratio	0.92 +/- 0.07 (0.85-1)	0.81 +/- 0.07 (0.57-0.94)	0.84 +/- 0.05 (0.77-0.95)	0.77 +/- 0.21 (0.12-1)	0.39 +/- 0.12 (0.22-0.75)
INFLSH2 - ratio	0 +/- 0 (0-0)	0.39 +/- 0.31 (0-0.92)	0.02 +/- 0.08 (0-0.31)	0.16 +/- 0.24 (0-0.69)	0.81 +/- 0.23 (0-1.44)
INFLSH4 - ratio	1 +/- 0 (1-1)	1 +/- 0.01 (0.94-1)	1 +/- 0 (1-1)	1 +/- 0 (1-1)	0.75 +/- 0.17 (0.45-1.57)
CALYXLOB - mm	0.5 +/- 0.04 (0.46-0.56)	0.75 +/- 0.22 (0.38-1.26)	0.95 +/- 0.28 (0.28-1.39)	1.04 +/- 0.35 (0.45-1.75)	0.48 +/- 0.19 (0.17-1.25)
CALYXTUB - mm	1.87 +/- 0.29 (1.54-2.24)	1.73 +/- 0.28 (1.13-2.22)	2.25 +/- 0.98 (1.25-5.31)	1.79 +/- 0.28 (1.44-2.44)	1.29 +/- 0.33 (0.9-2.75)
CALYXRAT - ratio	0.27 +/- 0.02 (0.25-0.3)	0.44 +/- 0.14 (0.24-0.72)	0.46 +/- 0.15 (0.19-0.71)	0.6 +/- 0.19 (0.24-0.95)	0.39 +/- 0.17 (0.13-1.41)
NFLOWERS - count	1.83 +/- 1.21 (1-3.57)	13.83 +/- 13.44 (2.67-54)	2.76 +/- 1.66 (1-5.33)	5.06 +/- 3.36 (1-11.83)	32.96 +/- 21.27 (1-86)
PETIPUB - score	1.66 +/- 0.79 (1.01-2.58)	3.99 +/- 1.02 (3.11-6.04)	3.47 +/- 0.15 (3.11-3.53)	3.38 +/- 0.61 (2.05-5.03)	3.87 +/- 0.95 (2.58-6.04)

ca. 10%), with the midrib densely pubescent above (*vs*. glabrous or nearly so), and by the very reduced inflorescences, which have only 1-4 flowers (*vs*. > 20 flowers). These species are sympatric at the Duida tepui, although *P. thyrsiflora* is usually found at lower elevations there (1450-1725 *vs* 650-1400).

04. ***Pagamea thyrsiflora*** Spruce ex Benth., Journ. Linn. Soc. 1:110, 1857. —TYPE: VENEZUELA, Rio Negro, San Carlos de Rio Negro, 1˚ 55' 0" N and 67˚ 4' 0" W, Apr 1853, FL-FR, *Spruce 2957* (Holotype: !K; Isotypes: !BM, !F, !NY). PLATES 2 and 8.

Shrub or tree 2.7 ± 1.5 (0.5-10) m tall. *Twigs* 1.9 ± 0.4 (1.2-2.8) mm thick. *Stipules* cylindrical, 6.8 ± 1.7 (2.4-10) mm long, caducous or only the base persistent. *Leaves*: petiole 0.7 ± 0.2 (0.3-1.5) cm long, glabrous to densely strigose; lamina elliptic, membranous to chartaceous, 5.9 ± 1.6 (2.5-10.7) x 1.5 ± 0.4 (0.5-2.5) cm, glabrous or nearly so on both sides, the margin flat; with 2.2 ± 1.6 (0-7) domatia one side of midrib below; midrib glabrous to sparsely strigose; venation eucamptodromous, veins arching, with 6 ± 1.3 (3-10) pairs of veins, these glabrous or nearly so on both sides. *Breeding system* homostylous. *Inflorescences* cymose; peduncle 1.2 ± 0.6 (0.3-3.5) cm long, sparsely to densely strigose, rarely glabrous; main axis 1.9 ± 0.7 (0.3-3.6) cm long, with 2.6 ± 0.6 (1-4) internodes; secondary axis 0.8 ± 0.4 (0-2) cm long, with 1.9 ± 0.5 (0-3) internodes; with 33.2 ± 22.4 (5-110) flowers per inflorescence. *Flower calyces* glabrous inside and outside, rarely sparsely puberulent outside, the lobes 0.5 ± 0.2 (0-6) mm long, and 0.4 ± 0.2 (0-1.6) times the length of the calyx tube. *Ovary* glabrous. *Fruits* globose, 4.8 ± 0.6 (3.8-6) x 4.1 ± 0.6 (2.6-5) mm.

Vernacular – Sakau-kêk (Arekuna).

Distribution and habitat – *Pagamea thyrsiflora* is the widespread member of the Thyrsiflora clade, having a pan-Amazonia distribution mainly on the sandstone formations of the Guayanan and Brazilian Shields and it also occurs in the Eastern Andes of Peru and Ecuador. It grows from sea-level to 1650 m (489 +/- 363 m), and prefers dense shrublands in dry, non-flooded areas, or along small streams.

Notes – *Pagamea thyrsiflora* is easy to recognize because of its small, thin leaves and lax inflorescence – a compound cyme, with well-developed branches and clearly pedicillate flowers separated along the axes. The flower calyces have short tubes and lobes. All other species of *Pagamea* (but see *P. bahiana*) have sessile flowers, usually so densely packed together that is difficult to tell them apart. Other members of the Thyrsiflora clade may have similar inflorescences, but usually much smaller and with fewer, larger flowers.

Morphological variation within *P. thyrsiflora* is highly correlated with geography (Mantel test, $r = 0.21$, $P < 0.001$) and altitude (Mantel test, $r = 0.172$, $P < 0.001$). A single axis representing this variation is highly correlated with several characters, including descriptors of size of leaves and inflorescence parts, pubescence, density of domatia, etc (Table 5). There is a decline in the size values of these characters from East Guayana Shield (circles) to Chiribiquete in Colombia and Tarapoto in Central Peru (squares in Fig. 5). The pattern is consistent with clinal variation from East to West in the northern part of the distribution of this species [see *P. capitata* (15) for a similar pattern]. The big square in East Guayana Shield (Fig. 5) represents a specimen collected at higher altitude than all other specimens in the entire Guayana Shield, and the small size of its parts may reflect phenotypic plasticity or clinal variation associated with the altitudinal gradient. Extremes of variation in this species are found in close proximity in the Western Amazon (Andes of Peru): the western-most circles in Fig. 5 around the small squares of the Tarapoto site. Observations suggest that specimens with larger parts (circles) also have more coriaceous leaves that are much darker when fresh and have conspicuous domatia, unlike the Tarapoto population. Interestingly, the specimens with larger parts grow at higher altitudes, unlike the pattern observed in the Guayana Shield. Chloroplast data further suggest that specimens from Tarapoto are more closely related to accessions from Chiribiquete in Colombia, which are also similar in parts size. The large Andean specimens are more closely related to specimens with smaller parts from Central Brazil. Although support is low and additional sampling is needed for understanding these patterns (Chapter 1), overall they suggests that *P. thyrsiflora* colonized the Andes from two sources, one from the north through the Chiribiquete, the other from the south. Whether these the two lineages arrived in the Andes at similar times, and whether they are found in fine-scale sympatry remains unclear, and similarly, whether there are reproductive barriers between them.

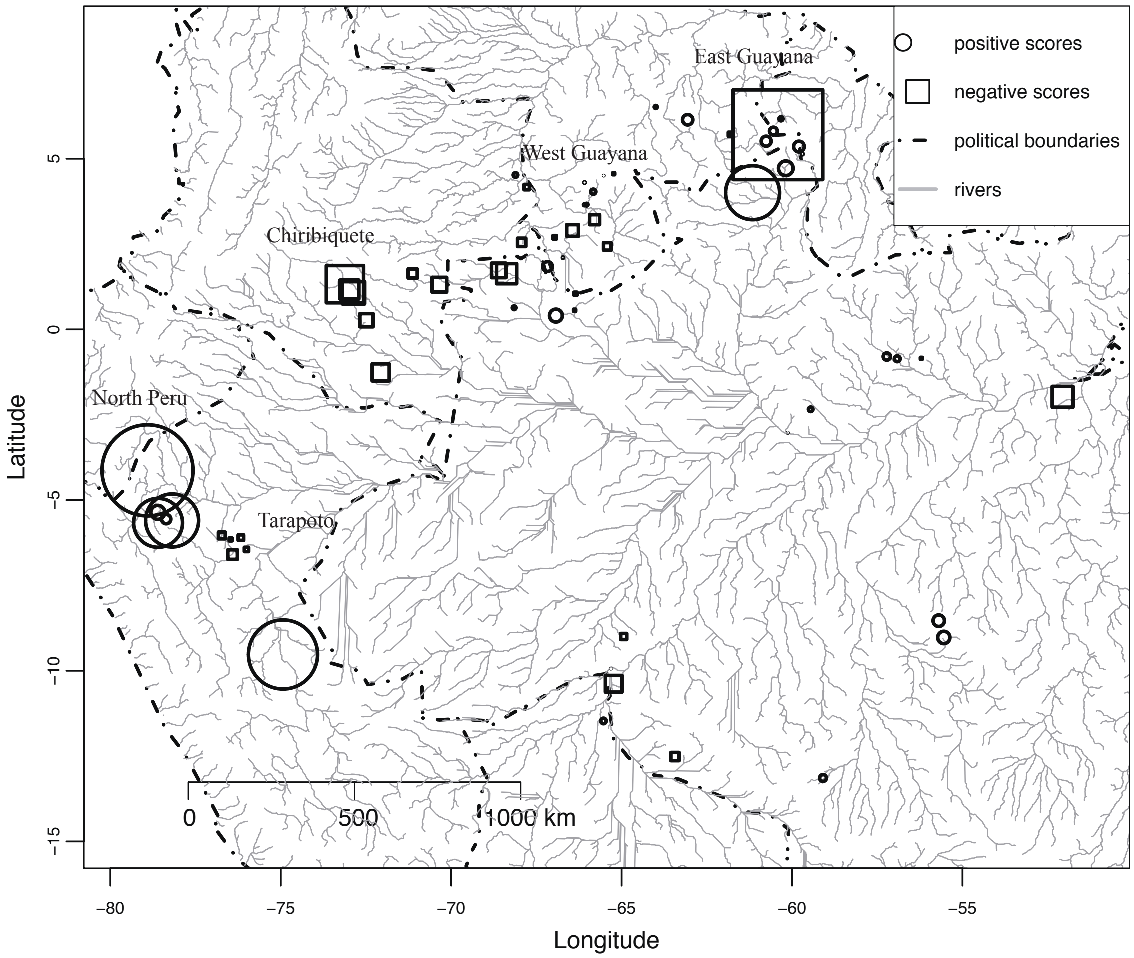

Figure 5. Geographical pattern of variation in *P. thyrsiflora*: squares correspond to negative scores on a single morphological axis obtained with non-metric multidimensional scaling, and circles to positive scores; size of symbols indicate distance from 0, with large squares and large circles corresponding to the extremes of the variation in the sample (see Table 5 for correlations with this morphological axis).

Table 5. *Pagamea thyrsiflora*. Characters significantly correlated (Spearman's rho) with the single axis representing intraspecific variation (Fig. 5; see Table 2 for characters).

Character	rho	P	Character	rho	P
INFLLEN - mm	0.82	0.000	DOMADENS - ratio	0.577	0.000
LEAFWID - mm	0.803	0.000	INFLSH2 - ratio	0.392	0.001
LEAFLEN - mm	0.799	0.000	INFLNO1 - count	0.376	0.002
INFLPEDU - mm	0.658	0.000	NFLOWERS - count	0.313	0.011
INFLBRAN 0- mm	0.655	0.000	PUBADAX - score	0.261	0.036
PETIPUB - score	0.639	0.000	INFLPUB - score	-0.479	0.000
PETIOLEN - mm	0.614	0.000	VENADENS - ratio	-0.562	0.000

05. ***Pagamea pauciflora*** Standl. & Steyerm, Fieldiana Bot. 28:588, 1953. —TYPE: VENEZUELA, Bolívar, Gran Sabana, Carrao-tepuí, 5° 24' 0" N and 62° 24' 0" W, 7 Dec 1944, FL-FR, *Steyermark 60888* (Holotype: F; Isotypes: !NY, !US). PLATE 2.

> *Pagamea magniflora* Steyerm., Mem. N. Y. Bot. Gard. 12:285, 1965. —TYPE: Ilu-Tepu, 5° 27' 16" N and 60° 57' 49" W, 15 Mar 1952, FL, *Maguire 33427* (Holotype: !NY; Isotypes: VEN). Syn. Nov.

Shrub or tree 2.3 ± 1.2 (1-5) m tall. *Twigs* 2.8 ± 0.6 (1.3-4) mm thick. *Stipules* cylindrical, 6.5 ± 1.8 (1-11) mm long, caducous or only the base persistent. *Leaves*: petiole 0.6 ± 0.2 (0.2-1.1) cm long, densely strigose; lamina obovate to elliptic, coriaceous, 3.1 ± 0.7 (1.6-5.1) x 1.1 ± 0.3 (0.5-2.1) cm, glabrous on both sides, the margin strongly revolute, lacking domatia abaxially; midrib glabrous to sparsely strigose on both sides; venation eucamptodromous, usually inconspicuous, with 3.9 ± 0.6 (3-5) pairs of veins, these glabrous on both sides. *Breeding system* homostylous. *Inflorescences* cymose; peduncle 1.1 ± 0.5 (0.1-2.7) cm long, densely or sparsely strigose to puberulent; main axis 0.2 ± 0.1 (0-0.5) cm long, with 1.1 ± 0.4 (0-2) internodes; secondary axis 0-0.5 cm long, with 0 ± 0.2 (0-0.1) internodes; 1.8 ± 1.7 (1-6) flowers per inflorescence. *Flower calyces* glabrous inside and outside, the lobes 1 ± 0.3 (0.2-1) mm long and 0.5 ± 0.2 (0.1-0.9) times the length of the calyx tube. *Ovary* glabrous (hairy). *Fruits* ellipsoid, 8 ± 1.1 (6.5-10) x 4.8 ± 0.8 (3.8-6.4) mm.

Distribution and habitat – Eastern Guayana Shield, east of the Caroni river into Guyana. At very high altitudes, (1400-) 1800-2600 m, in shrublands.

Notes – This species can be distinguished from other high-altitude species by its lamina with strongly revolute margins and absence of domatia abaxially. The only other high-altitude species with revolute margins is *P. capitata* (Capitata clade), which can be distinguished by its ovate leaves, pubescent ovary, and inflorescences with 3-36 flowers.

Variation within *Pagamea pauciflora* is correlated with space (Mantel test, r = 0.44, P<0.001), but not with altitude. However, only two characters were significantly correlated with the single axis representing morphology: inflorescence peduncle-length/total-length (Spearman's r = 0.82) and midrib pubescence on the adaxial surface (Spearman's r = 0.66). This suggests that morphological variation somewhat correlates with isolation in different tepuis. The only exception is a single specimen from the Ilú tepui, which has been described as *P. magniflora*. As the name implies, the flowers of this specimen (*Maguire 33427*) are unusually large: the calyx (and corolla) tube is much larger than those of all other specimens (3.5-7.5 vs. < 1 mm long), but the calyx and corolla lobes are similar to those of other specimens, and as a consequence the ratio between calyx lobes and tubes is unlike that of any other species of *Pagamea*. Otherwise, this specimen is identical to those of *P. pauciflora*. Because the Ilú specimen is allopatric to the others and it may represent only an unsual individual, *P. magniflora* is treated here as synonym of *P. pauciflora*.

06. ***Pagamea montana*** Gleason & Standl., Field Mus. Pub. Bot 7:421, 1931. —TYPE: VENEZUELA, Amazonas, Alto Orinoco, Cerro Duida, summit, savanna hills, 3° 36' 0” N and 65˚41' 0” W, 1928, FL-bud, *Tate 803* (Holotype: !NY). PLATE 2.

Trees 4.8 ± 2.3 (2-10) m tall. *Twigs* 2 ± 0.5 (1.1-3.4) mm thick. *Stipules* cylindrical, 6.4 ± 2 (2.3-11) mm long. *Leaves*: petiole 0.6 ± 0.2 (0.3-1.2) cm long, glabrous to densely strigose; lamina elliptic, coriaceous, 4.3 ± 1.1 (1.9-8.7) x 1.1 ± 0.3 (0.5-2.1) cm, glabrous on both surfaces, the margin flat, with 0.5 ± 0.9 (0-3) domatia abaxially; midrib glabrous to densely strigose on both surfaces; venation eucamptodromous (inconspicous), with 5.1 ± 0.8 (4-7) pairs of veins, these glabrous on both surfaces. *Breeding system* homostylous. *Inflorescences* cymose (single-flowered); peduncle 1.8 ± 0.7 (0.5-4.2) cm long, densely minutely hairy; main axis 0.4 ± 0.2 (0.6-1.7) cm long, with 1.1 ± 0.3 (0-2) internodes; secondary axis 0.1 ± 0.1 (0-0.8) cm long, with 0.6 ± 0.4 (0-2) internodes; 27.8 ± 14.4 (1-66) flowers per inflorescence. *Flower calyces* glabrous, the lobes 0.7 ± 0.3 (0.2-6.5) mm long and 0.4 ± 0.2 (0.1-1) times the length of the calyx tube. *Ovary* glabrous. *Fruits* ellipsoid, 5.7 ± 0.5 (5-6.5) x 4 ± 0.8 (3.4-6) mm.

Distribution and habitat – Western Guayana Shield at high-altitudes (1296 +/- 340 m; 650-1850 m). Found mostly in montane forest in non-flooded areas.

Notes – *Pagamea montana* includes substantial intraspecific variation that suggests it may include more than one species. At Cerros Neblina, Duida, and Yutayé, morphological variation is ample and may represent more than one species, but sampling is very low and this species is recognized here in a broad sense. In these sites, specimens differ in overall size of leaves and inflorescences, inflorescence structure and

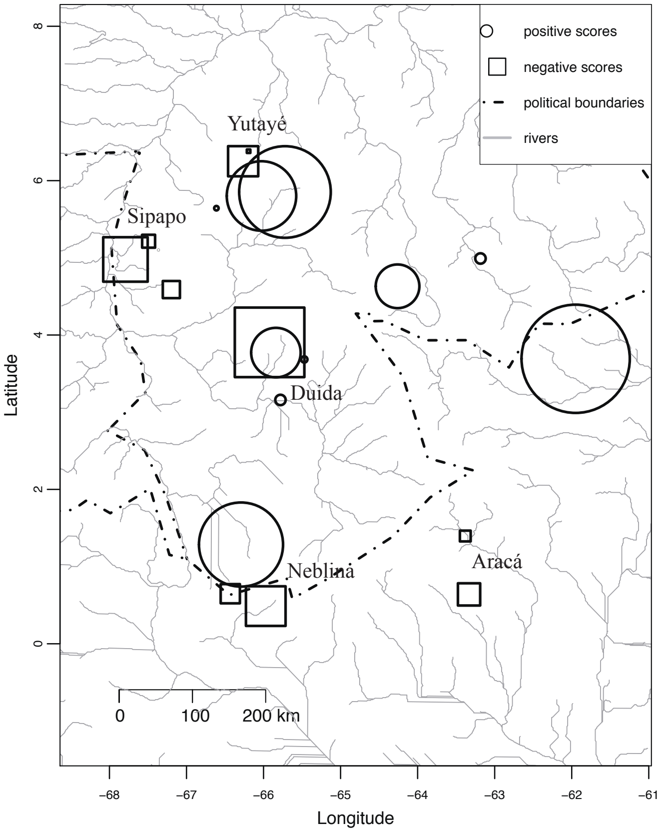

Table 6. *Pagamea montana*. Characters significantly correlated (Spearman's rho) with the single axis representing intraspecific variation. See Figure 5 for geographical distribution of morphological variation in this species (Table 2 for character descriptions).

Characters	rho	P
INFLNO2 - count	0.94	0
INFLBRAN - mm	0.922	0
INFLSH2 - ratio	0.902	0
NFLOWERS - count	0.894	0
LEAFLEN - mm	0.706	0
PUBABAX - score	0.667	0.001
LEAFWID - mm	0.665	0.001
PUBADAX - score	0.639	0.002
INFLLEN - mm	0.573	0.008
INFLPEDU - mm	0.543	0.012

Figure 6. Geographical pattern of variaton for *P. montana*. Each symbol represent a single collection: squares correspond to negative values of a single morphological axis and circles to positive values. Size of symbol indicate distance from 0, with large square and large circles corresponding to the extremes of the variation in data. See Table 6 for character correlations. Noise was added to geographical coordinates for spreading symbols.

flower number (Table 6), as indicated by circles and squares in Fig. 6. This variation correlates neither with altitude nor habitat type. Because these forms may be sympatric at these sites, the variation suggest that there are two or more species involved. Field work is needed to clarify the situation.

07. ***Pagamea standleyana*** Steyerm., Fieldiana Bot. 28:589, fig. 130,1953. —TYPE: VENEZUELA, Bolívar, Gran Sabana, Ptari-tepuí, 5° 50' 11" N and 61° 55' 38" W, 1 Nov

1944, FL-FR, *Steyermark 59634* (Holotype: F; Isotypes: !NY, !US, VEN). PLATE 2.

Pagamea reducta Steyerm. Mem. N. Y. Bot. Gard 12(3):283, 1965. —TYPE: VENEZUELA, Bolívar, Gran Sabana, Uaipán tepuí, 5° 36' 0” N and 62° 32' 0” W, 7 Feb 1948, FL-bud, *Phelps 366* (Holotype: !NY; Isotype: VEN).

Pagamea uniflora Steyerm. Mem. N. Y. Bot. Gard 12(3):284, 1965. —TYPE: VENEZUELA, Bolívar, Gran Sabana, Macizo del Chimantá, 5° 13' 0” N and 62° 15' 0” W, 13 Apr 1953, FL-FR, *Steyermark 74877* (Holotype: VEN; Isotype: !NY).

Shrub or tree 4.7 ± 3.5 (2-12) m tall. *Twigs* 1.9 ± 0.4 (1-3) mm thick. *Stipules* cylindrical, 4 ± 1.6 (1.5-9) mm long, caducous or only the base persistent. *Leaves*: petiole 0.4 ± 0.1 (0.2-0.9) cm long, densely strigose; lamina elliptic, coriaceous, 2.8 ± 0.9 (1.2-5.3) x 0.9 ± 0.2 (0.4-1.6) cm, glabrous on both surfaces, the margin flat to slightly revolute, with 1.6 ± 0.9 (0-4) domatia abaxially; midrib glabrous to sparsely strigose on both sides; venation eucamptodromous, usually inconspicuous, with 4.2 ± 0.9 (3-6) pairs of veins, these glabrous on both sides. *Breeding system* homostylous. *Inflorescences* cymose; peduncle 0.7 ± 0.4 (0.1-3) cm long, densely strigose to puberulent; main axis 0.2 ± 0.2 (0-0.7) cm long, with 0.8 ± 0.4 (0-3) internodes; secondary axis 0 ± 0 (0-0.3) cm long, with 0.3 ± 0.4 () internodes; with 5 ± 3.4 (1-19) flowers per inflorescence. *Flower calyces* glabrous inside, glabrous to sparsely puberulent outside, the lobes 1 ± 0.5 (0.1-7.5) mm long, and 0.6 ± 0.3 (0.1-1.3) times the length of the calyx tube. *Ovary* glabrous. *Fruits* ellipsoid, 6 ± 0.9 (4-7.5) x 4.4 ± 0.6 (3.2-5.3) mm.

Distribution and habitat – Eastern Guayana Shield of Venezuela and Guyana, from 1200-2200 m elevation. Usually in both riverine and non-riverine montane forests, more rarely in shrublands.

Notes – Both the relationship of this species with other high-altitude species of the Guayana Shield and its intraspecific variation need further investigation. This species is sympatric with *P. pauciflora* at Chimantá tepui, and is sister to the clade formed by *P. montana* and *P. pauciflora* (Fig. 3). From the sympatric species it can be recognized by having leaves with flat or only slightly revolute margins, and with domatia in the adaxial surface, the veins and sometimes even the midrib usually obscure, unlike the leaves of *P. pauciflora* (see above). The boundaries between *P. montana* and *P. standleyana*, and whether they are reproductively isolated remains unclear, because they are allopatric, although sympatry may occur along the Caroní river basin in the Gran Sabana region of Venezuela. These two species differ in several quantitative characters (Table 4).

Variation within *P. standleyana* is also significantly correlated with space (Mantel test, r 0.44, P = 0.002), with plants from Ayuán tepui having smaller leaves and inflorescences (squares in Fig. 6), than plants from Chimantá and other tepuis (circles in Fig. 7; see Table 7 for character correlations). Variation is not significantly correlated with altitude, and there is one specimen at Chimantá that has the morphology of Auyán (square among circles in Fig. 7). Such a pattern suggests that more than one species is involved, but additional sampling is needed to understand this pattern of variation; it does not correspond to limits of the various species recognized by Steyermark (1965) and listed above as synonyms.

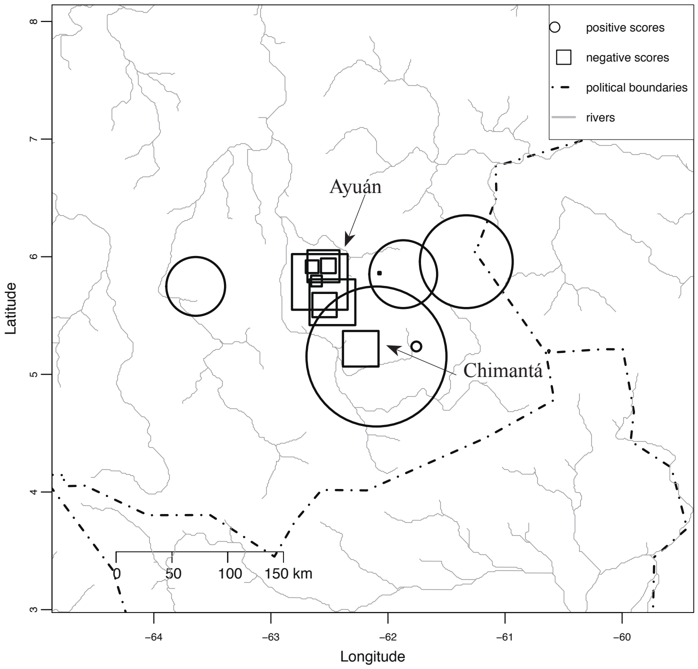

Figure 7. Geographical pattern of variation in *P. standleyana*: squares correspond to negative scores on a single morphological axis obtained with non-metric multidimensional scaling, and circles to positive scores; most squares are from Auyán tepui (see text); size of symbols indicate distance from 0, with large squares and large circles corresponding to the extremes of the variation in the sample. See Table 7 for character correlations.

Table 7. *Pagamea standleyana*. Characters significantly correlated (Spearman's rho) with the single axis representing intraspecific variation (Fig. 6; Table 2 for character descriptions).

Character	rho	P
INFLSH2 - ratio	0.864	0.000
INFLBRAN - mm	0.86	0.000
INFLNO1 - count	0.82	0.000
NFLOWERS - count	0.82	0.000
INFLLEN - mm	0.803	0.000
INFLNO2 - count	0.802	0.000
INFLSH3 - ratio	0.765	0.001
LEAFLEN - mm	0.688	0.004
LEAFWID - mm	0.656	0.007
PETIOLEN - mm	0.509	0.046
INFLSH1 - ratio	-0.712	0.003

Macrophylla clade

Members of the Macrophylla clade have conical terminal stipules that open laterally, unlike other species of *Pagamea*, and the leaves sometimes have marks parallel to the midrib resulting from the way leaves are folded in bud. The calyces of species in this clade are covered inside by appressed, usually silverish hairs, and have short lobes, or at least lobes that are shorter than the calyx tube. When fruiting, the calyces are cup-shapped and enclose about half the drupe. Other species of *Pagamea* have usually plicately-folded leaves emerging from the top of cylindrical stipules. They also lack indumentum on the inside of the calyx and the fruits either rest in a shallow calyx or the calyx lobes longer than the calyx tube.

The Macrophylla clade includes seven species, one of which, *Pagamea jauaensis*, is included because it has the putative apomorphies described above. There is one additional specimen that has the apomorphies of the Macrophylla clade, but cannot be assigned to any species. It was collected at mid elevation (426 m) in the Kaieuter National Park in Guyana, a location that makes it allopatric to all other species in the Macrophylla clade. It has the small leaves of *P. jauaensis*, *P. anisophylla* and *P. aracaensis*, but unlike these species has eucamptodromous venation. The single fruiting specimen, *Cowan 2175* (MO, NY, US) may, therefore, represent an additional species, within this clade.

Species in the Macrophylla clade are morphologically very easy to distinguish and usually have a localized distribution (see Table 8 for morphological differences).

08. ***Pagamea aracaënsis*** Boom, Brittonia 41:129, fig. 1, 1989.—TYPE: Brazil, Amazonas, Barcelos, Serra do Aracá, 3 km S da Serra Central e 8 km E do rio Javari, 0° 49' 0” S and 63° 19' 0” W, 28 Feb 1984, FR, *Amaral 1667* (Holotype: !INPA; Isotypes: !MO, !NY). PLATE 3.

Shrub or tree 3.1 ± 3.8 (0.4-15) m tall. *Twigs* 3 ± 0.6 (1.5-4) mm thick. *Stipules* conical, 32 ± 9 (19.5-49) mm long, caducous or only the base persistent. *Leaves*: petiole 1.3 ± 0.5 (0.5-2.5) cm long, glabrous or nearly so on both sides; lamina elliptic, chartaceous, 10.1 ± 3.1 (6-18.3) x 3.2 ± 0.7 (1.6-4.8) cm, glabrous or nearly so on both sides, the margin flat; with 2.6 ± 2.8 (0-8) domatia abaxially; midrib glabrous or nearly so on both sides; venation brochidodromous, with 10.9 ± 2.1 (8-17) pairs of veins, these glabrous or nearly so on both sides. *Breeding system* homostylous. *Inflorescences* thyrsoid; peduncle 2.9 ± 1.4 (0.7-6.1) cm long, glabrous to densely strigose; main axis 1.6 ± 1.3 (0-4.8) cm long, with 2.1 ± 1.5 (0-6) internodes; secondary axis 0.4 ± 0.6 (0-2.5) cm long, with 1.1 ± 1.2 (0-5) internodes; with 84 ± 20.3 (6-106) flowers per inflorescence. *Flower calyces* densely covered by appressed hairs inside, glabrous outside, the lobes 0.1 ± 0.2 (0-10) mm long, and 0.1 ± 0.1 (0-0.4) times the length of the calyx tube. *Ovary* glabrous. *Fruits* globose, 7.8 ± 1.5 (5-10) x 6.6 ± 0.6 (6-7.5) mm.

Distribution and habitat – This species is restricted to the Central Amazon and it has been collected in two major areas: the Serra do Aracá region in the middle rio Negro basin (Barcelos), and the rio Madeira basin in the vicinity of the city of Borba. Most collections are from lowland areas, but one collection, *Prance 28911* (INPA, NY), suggests it is also found at high altitudes (1200 m) in the Serra do Aracá. However, when I visited this tepui, I could not find it at high altitudes, only in the white-sand areas in the surrounding lowlands, where it is very frequent and abundant in open shrublands. In the region of Borba and on the right margin of the rio Negro (Jaú National Park) it occurs on low or tall forests and is not found in adjacent shrubland areas there (A.

Table 8. Macrophylla clade. Species are ordered by leaf size from smallest (left) to largest. Characters with a significant difference among species (Kruskall-Wallis test, P <=0.01) shown. Values are mean +/- standard deviation (min-max) averages per specimen (see Table 2)

	anisophylla	*jauaensis*	*aracaensis*	*neblinensis*	*velutina*	*hirsuta*	*glabra*	*macrophylla*
LEAFLEN - mm	83.47 +/- 12.34 (63.5-105.33)	67.81 +/- 10.68 (49.29-81.25)	91.67 +/- 13.41 (73.25-118.14)	140.38 +/- 8.19 (135-149.8)	142.58 +/- 14.41 (130.83-158.67)	173 +/- 26.77 (128-223.67)	183.5 +/- 23.33 (167-200)	206.13 +/- 31.42 (154.33-245.33)
LEAFWID - mm	31.12 +/- 5.63 (24-42.67)	22.19 +/- 3.63 (16.71-27.75)	31.03 +/- 2.7 (27.33-35.33)	43 +/- 5.17 (37.67-48)	47.86 +/- 1.75 (46.17-49.67)	51.58 +/- 9.49 (34.67-70)	48.87 +/- 6.04 (44.6-53.14)	75.39 +/- 14.04 (53.33-91)
LFSHAPE1 - ratio	0.56 +/- 0.04 (0.48-0.61)	0.6 +/- 0.04 (0.55-0.64)	0.52 +/- 0.04 (0.46-0.61)	0.58 +/- 0.02 (0.57-0.6)	0.59 +/- 0.01 (0.58-0.6)	0.61 +/- 0.05 (0.45-0.69)	0.56 +/- 0.01 (0.55-0.57)	0.55 +/- 0.03 (0.51-0.61)
LFSHAPE2 ratio	0.45 +/- 0.04 (0.39-0.52)	0.38 +/- 0.02 (0.35-0.39)	0.4 +/- 0.05 (0.32-0.46)	0.36 +/- 0.01 (0.35-0.37)	0.39 +/- 0.03 (0.35-0.42)	0.34 +/- 0.05 (0.26-0.42)	0.3 +/- 0 (0.29-0.3)	0.44 +/- 0.05 (0.37-0.52)
DOMADENS ratio	0.41 +/- 0.26 (0-0.83)	0 +/- 0 (0-0)	0.12 +/- 0.19 (0-0.46)	0.5 +/- 0.34 (0.17-0.85)	0 +/- 0 (0-0)	0 +/- 0 (0-0)	0 +/- 0 (0-0)	0 +/- 0 (0-0)
VENADENS ratio	0.08 +/- 0.01 (0.05-0.1)	0.07 +/- 0.03 (0.02-0.09)	0.14 +/- 0.02 (0.1-0.17)	0.04 +/- 0.01 (0.04-0.06)	0.05 +/- 0.01 (0.04-0.05)	0.06 +/- 0.01 (0.05-0.07)	0.11 +/- 0 (0.1-0.11)	0.05 +/- 0.02 (0.03-0.1)
INFLPEDU - mm	46.44 +/- 20.03 (15-81)	32.35 +/- 7.62 (22.12-42)	26.15 +/- 12.79 (7-56.75)	44.97 +/- 12.05 (36-58.67)	32.94 +/- 0.92 (32-33.83)	66.28 +/- 16.92 (46.5-110)	NA	26.15 +/- 7.66 (16.67-35)
INFLLEN - mm	76.64 +/- 27.23 (29.5-126)	42.6 +/- 9.44 (26.05-51)	42.08 +/- 23.67 (10-96.25)	92.14 +/- 27.89 (68-122.67)	41.47 +/- 35.95 (0-63.67)	94.3 +/- 23.52 (62.5-155)	NA	57.62 +/- 16.43 (29.33-77)
INFLBRAN - mm	12.04 +/- 5.72 (3.25-20)	1.21 +/- 1.2 (0-3.25)	5.32 +/- 9.14 (0-34)	6.62 +/- 7.65 (0-15)	7.43 +/- 1.46 (6.12-9)	5.65 +/- 3.76 (1.4-16.5)	NA	12.62 +/- 4.77 (6.5-19)
INFLNO1 - number	3.4 +/- 0.8 (2-5)	1.61 +/- 0.64 (1-2.5)	2.08 +/- 1.48 (0-4.75)	4.78 +/- 1.68 (3-6.33)	2.44 +/- 2.12 (0-3.83)	2.44 +/- 0.75 (2-5)	NA	3.28 +/- 0.99 (2-4.5)
INFLNO2 number	2.44 +/- 0.71 (1-3.67)	0.75 +/- 0.42 (0-1)	1.13 +/- 1.17 (0-3.5)	1.5 +/- 1.5 (0-3)	1.75 +/- 0.25 (1.5-2)	1.46 +/- 0.5 (1-2)	NA	2.23 +/- 0.52 (1.33-3)
INFLSH1 ratio	0.59 +/- 0.11 (0.34-0.72)	0.77 +/- 0.1 (0.61-0.85)	0.68 +/- 0.18 (0.4-1)	0.49 +/- 0.03 (0.47-0.53)	0.35 +/- 0.31 (0-0.53)	0.71 +/- 0.1 (0.48-0.89)	NA	0.46 +/- 0.09 (0.3-0.6)
INFLSH2 ratio	0.75 +/- 0.27 (0.34-1.33)	0.19 +/- 0.13 (0-0.38)	0.33 +/- 0.46 (0-1.62)	0.22 +/- 0.23 (0-0.46)	0.1 +/- 0.57 (-0.56-0.45)	0.37 +/- 0.15 (0.14-0.73)	NA	0.83 +/- 0.29 (0.3-1.27)
INFLSH4 ratio	0.59 +/- 0.15 (0.39-1)	1 +/- 0 (1-1)	0.87 +/- 0.19 (0.54-1)	0.71 +/- 0.34 (0.34-1)	0.65 +/- 0.14 (0.5-0.76)	0.86 +/- 0.16 (0.6-1)	NA	0.57 +/- 0.12 (0.46-0.87)
CALYXLOB - mm	0.14 +/- 0.12 (0-0.43)	0.35 +/- 0.12 (0.22-0.53)	0.11 +/- 0.1 (0-0.27)	0.4 +/- 0.1 (0.34-0.52)	0.65 +/- 0.37 (0.23-0.88)	0.15 +/- 0.22 (0-0.9)	NA	0.14 +/- 0.11 (0.02-0.32)
CALYXTUB - mm	1.46 +/- 0.19 (1.1-1.8)	2.29 +/- 0.35 (1.92-2.83)	1.55 +/- 0.27 (0.98-2)	1.73 +/- 0.2 (1.5-1.86)	1.38 +/- 0.32 (1.02-1.64)	2.08 +/- 0.34 (1.4-2.75)	NA	2.14 +/- 0.25 (1.67-2.5)
CALYXRAT ratio	0.09 +/- 0.08 (0-0.28)	0.15 +/- 0.05 (0.09-0.21)	0.07 +/- 0.07 (0-0.2)	0.24 +/- 0.05 (0.19-0.29)	0.54 +/- 0.37 (0.14-0.87)	0.08 +/- 0.16 (0-0.67)	NA	0.08 +/- 0.09 (0.01-0.3)
NFLOWERS - number	51.24 +/- 29.12 (13-98)	9.35 +/- 5.55 (3.5-16.25)	38.13 +/- 23.35 (7.5-84)	17.86 +/- 14.5 (7-34.33)	16.94 +/- 7.56 (10-25)	47.54 +/- 45.24 (25-224)	NA	92.03 +/- 44.45 (23.67-180)
PUBABAX - score	0.74 +/- 1.5 (0-5.52)	15.38 +/- 2.58 (11-18.04)	0.56 +/- 1.54 (0-6)	5.02 +/- 0.25 (4.87-5.31)	14.93 +/- 0 (14.93-14.93)	0.35 +/- 0.85 (0-2.08)	0 +/- 0 (0-0)	2.57 +/- 2.03 (0-6.02)
PUBADAX - score	0 +/- 0 (0-0)	12.46 +/- 3.52 (1.49-16.04)	0 +/- 0 (0-0)	0 +/- 0 (0-0)	13.84 +/- 0 (13.84-13.84)	0.08 +/- 0.2 (0-0.5)	0 +/- 0 (0-0)	0 +/- 0 (0-0)
OVARYPUB - score	5.01 +/- 0 (5.01-5.01)	3.35 +/- 1.36 (2.03-5.01)	4.88 +/- 0.52 (3.01-5.01)	2.03 +/- 0 (2.03-2.03)	2.03 +/- 0 (2.03-2.03)	4.9 +/- 0.47 (3.01-5.01)	NA	3.82 +/- 1.31 (2.03-5.01)

Vicentini, pers. obs.).

Notes – There is no support for the monophyly of *P. aracaensis*, although monophyly is rejected by neither chloroplast nor nuclear data (AU and SH tests, P > 0.06). Boom (1989) stated that *P. aracaensis* appears to be most closely related to *P. anisophylla*, although he did not mention why. These two species have similar sized leaves with brochidodromous venation. However, *P. aracaensis* has homostylous, perfect flowers, and molecular data do not indicate a relationship with the deioecious *P. anisophylla*. Furthermore, these two species can be distinguished easily by the number of secondary veins per leaf, 8-12 in *P. aracaensis* vs. 4-6 in *P. anisophylla*, and by their geographical distribution (Fig. 1).

Morphological variation within *P. aracaensis* is highly correlated with geography (Mantel test, r = 0.75, P < 0.001). Fertile specimens are known only from the Aracá region and from Borba. Specimens from Aracá, which occur in open shrubland, unlike specimens from Borba, collected in forest, have smaller leaves (< 10 cm vs. > 10 cm) that lack domatia (vs. with domatia), shorter inflorescences (< 5.5 cm vs. > 6 cm) that also have shorter branches (lateral axis < 5 mm long vs. > 8 mm long) and fewer flowers (10-55 vs. 40-85; Table 9; Fig. 8). Specimens from the Middle rio Negro region (PN Jaú), not far from the Aracá region but on the other side of the rio Negro, are sterile, but are more like the Borba specimens, with leaves having domatia and the plants were found in forest habitats. Therefore, the morphological differences appear to correlate with both habitat type and geography.

Here I consider these morphs to belong to the same species because they are allopatric, and it is unclear whether their morphological differences reflect phenotypic plasticity associated with habitat differences. Furthermore, their reciprocal monophyly is rejected by both chloroplast and ITS data (AU tests, $P < 0.0001$).

Table 9. *Pagamea aracaensis*. Characters significantly correlated (Spearman's rho) with a single axis representing morphological variation (Fig. 8; see Table 2 for character descriptions).

Characters	rho	pv
DOMADENS - ratio	-0.785	0.001
INFLPEDU - mm	-0.836	0
INFLLEN - mm	-0.942	0
INFLBRAN - mm	-0.868	0
INFLNO1 - count	-0.98	0
INFLNO2 - count	-0.904	0
INFLSH1 - ratio	0.645	0.009
INFLSH2 - ratio	-0.891	0
INFLSH4 - ratio	0.806	0
NFLOWERS - count	-0.962	0
INFLPUB - score	-0.778	0.001
CALXYPUB - score	-0.765	0.001

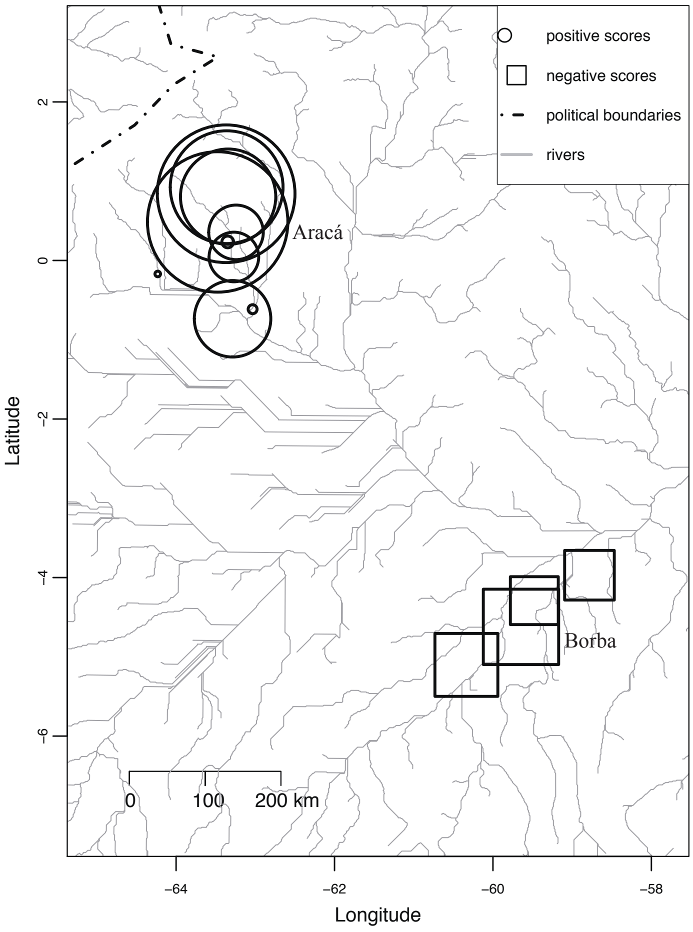

Figure 8. Geographical pattern of morphological variation in *Pagamea aracaensis*. Morphology was reduced to a single dimension using non-metric multidimensional scaling. Squares correspond to negative scores (Borba region) on this morphological axis and circles to positive scores (Serra do Aracá region); the size of symbols indicate the distance from 0, the largest squares and circles corresponding to the extremes of the variation in the sample. See Table 9 for character correlation.

09. ***Pagamea hirsuta*** Spruce ex Benth., Journ. Linn. Soc. 1:111, 1857. —TYPE: VENEZUELA, Rio Negro, San Carlos de Rio Negro, 1853, FL-FR, *Spruce 3137* (Holotype: K; Isotypes: F, P).

Shrub or tree 3 ± 1.2 (1.5-7) m tall. *Twigs* 5.8 ± 1 (4.5-7) mm thick. *Stipules* conical, 24.8 ± 10.9 (5-40) mm long, caducous or only the base persistent. *Leaves*: petiole 1.9 ± 0.5 (0.8-3.2) cm long, densely hirsute; lamina obovate to elliptic, membranous to chartaceous, 17.2 ± 3.7 (8.8-27.5) x 5.1 ± 1.2 (2.6-7.3) cm, densely hirsute on both sides, the margin flat; without domatia or these hidden by the indumentum; midrib densely hirsute on both sides; venation eucamptodromous, veins straight to arching, with 8.7 ± 1.3 (6-12) pairs of veins, these densely hirsute on both sides. *Breeding system* homostylous. *Inflorescences* thyrsoid to spicate; peduncle 6.7 ± 1.9 (3.8-11.2) cm long, densely to sparsely hirsute; main axis 2.8 ± 1.3 (1-5.6) cm long, with 2.4 ± 0.7 (2-5) internodes; secondary axis 0.6 ± 0.4 (0.1-1.7) cm long, with 1.5 ± 0.5 (1-2) internodes; with 42.3 ± 11.2 [20-58 (-240)] flowers per inflorescence. *Flower calyces* densely covered by appressed hairs inside, densely pubescent to hirsute outside, the lobes 0.2 ± 0.3 (0-10) mm long, and 0.1 ± 0.2 (0-1) times the length of the calyx tube. *Ovary* glabrous. *Fruits* ellipsoid, 7.1 ± 1.4 (5.5-10) x 4.8 ± 0.6 (3.3-5.5) mm.

Distribution and habitat – *Pagamea hirsuta* is restricted to the Upper Rio Negro, in particular to the Uaupés and Issana basins (Fig. 1). It is found only in non-flooded, Amazonian Caatinga formations, usually in the more open patches within the dense forests.

Notes – This species is very easy to recognize by its large, obovate leaf-blades that are covered by long (reddish) hairs on both surfaces. The stipule is long, conical and covered by the same indumentum. The inflorescences usually have few flowers, a very long peduncle, and short lateral branches. *Clark 6889* (VEN) is the only exception. This specimens has a multi-flowered inflorescence, and flowers with very short styles; these may in fact be staminate, unlike all other specimens that appear to have perfect flowers with relatively longer styles. This specimen is from the periphery of the range of *P. hirsuta*, yet its leaves clearly indicate it belongs with this species. Whether such variation is associated with species or populational differentiation needs further investigation.

Variation in the remaining specimens show a strong association with geography (Mantel test, $r = 0.376$, $P < 0.001$; Fig. 9, Table 10). Specimens with negative and positive scores on a single morphological dimension have distinct distributions that are largely limited by the rio Negro (Fig. 9). This morphological axis is correlated with several leaf, inflorescence and characters describing leaf indumentum (Table 10).

10. ***Pagamea glabra*** Vicentini, sp. nov. —TYPE: Brazil, Amazonas, São Gabriel da Cachoeira, rio Içana, vila Baniwa de Juivitera, 1° 16' 15" N and 68° 33' 24" W, 22 Jun 2004, STERILE, *Vicentini 2231* (Holotype: INPA; Isotype: MO).

Pagamea glabra is monophyletic according to both chloroplast and nuclear (ITS)

Table 10. *Pagamea hirsuta*. Characters significantly correlated (Spearman's rho) with a single axis representing morphological variation (Fig. 9; see Table 2 for character descriptions).

Characters	rho	P
PETIOLEN - mm	-0.805	0
REVPROP - ratio	0.567	0.018
INFLLEN - mm	-0.483	0.049
INFLBRAN - mm	-0.679	0.003
INFLNO2 - count	-0.792	0
INFLSH2 - ratio	-0.658	0.004
INFLSH4 - ratio	0.748	0.001
PETIPUB - score	0.684	0.002
PUBABAX - score	0.67	0.003
PUBADAX - score	0.698	0.002
INFLPUB - score	-0.758	0
CALXYPUB - score	-0.504	0.039

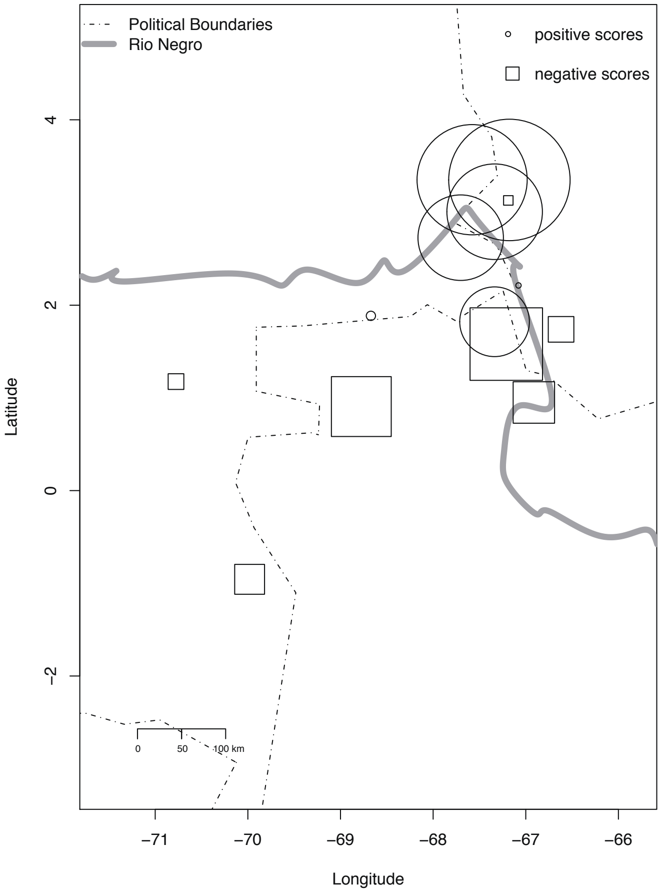

Figure 9. Geographical pattern of morphological variation in *Pagamea hirsuta*. Morphology was reduced to a single dimension using non-metric multidimensional scaling. Squares correspond to negative scores on this morphological axis and circles to positive scores; the size of symbols indicate the distance from 0, the largest squares and circles corresponding to the extremes of the variation in the sample. See Table 10 for character correlation. Noise was added to coordinates to better spread the symbols.

molecular markers, which suggest relationship with *P. hirsuta*. Contrary to *P. hirsuta*, *P. glabra* has glabrous leaves (vs. hirsute on both surfaces), with brochidodromous venation (vs. eucamptodromous) and a greater number of pairs of secondary veins (15-20 vs. 6-12). These two species grow side-by-side.

Shrub or tree 4 ± 1.4 (3-5) m tall. *Stipules* conical, 27.5 ± 3.5 (25-30) mm long, caducous. *Leaves*: petiole 1.8 ± 0.3 (1.2-2.2) cm long, glabrous; lamina oblancelate to elliptic, chartaceous, 18.6 ± 2.2 (13.9-21.2) x 5 ± 0.6 (3.9-5.9) cm, glabrous, the margin flat; without domatia; midrib glabrous on both sides; venation brochidodromous, veins straight, with 17.9 ± 1.4 (15-20) pairs of veins, these glabrous on both sides. *Inflorescences,* flowers and fruits unknown.

Notes – This species is known from a single population in the Issana river in the Upper Rio Negro region, where it occurs in tall caatinga forests. Although flowers and fruits remain unknown, molecular data from both chloroplast and nucleus (ITS) support its monophyly and suggest it is sister to *Pagamea hirsuta,* with which it is sympatric and morphologically very distinct (Chapter 1). The leaves of *P. hirsuta* have the lamina covered by long hirsute hairs on both sides, fewer vein pairs (6-12 vs. 15-20), and eucamptodromous venation. *Pagamea glabra* has the conical stipule that splits lateraly and the lamina has brochidodromous venation as in several other species of the Macrophylla clade. In terms of lamina shape and size it is more similar to *P. aracaensis* (the Borba morph, see under *P. aracaensis*), but the lamina of *P. glabra* have a higher number of secondary veins (15-20 vs. ~ 10), and these are straight and parallel to each other unlike those of *P. aracaensis*.

11. ***Pagamea macrophylla*** Spruce ex Benth., Journ. Linn. Soc. 1:110, 1857. —TYPE: Brazil, Amazonas, São Gabriel da Cachoeira, Panuré, ad rio Uapés, Sep 1852, 0° 30' N and 68° 00' W, FL, *Spruce 2578* (Holotype: !K; Isotypes: !BM, F (fragment), !NY, P).

Shrub or tree 7.8 ± 3.5 (3-15) m tall. *Twigs* 5-7 mm thick. *Stipules* conical, 28 (15-45) mm long, caducous. *Leaves*: petiole 2.9 ± 1 (1.2-4.7) cm long, glabrous; lamina elliptic, membranous to chartaceous, 20.2 ± 4.5 (8.3-28) x 7.4 ± 1.8 (3.2-10.7) cm, glabrous on both sides, the margin flat; without domatia; midrib glabrous to densely strigose abaxially, glabrous adaxially; venation eucamptodromous or brochidodromous, veins arching, with 7.4 ± 1.2 (5-10) pairs of veins, these glabrous to densely strigose abaxially, glabrous adaxially. *Breeding system* dioecious or homostylou. *Inflorescences* thyrsoid; peduncle 2.6 ± 0.8 (1.5-4.2) cm long, densely or sparsely strigose; main axis 3.1 ± 1.1 (1-5.2) cm long, with 3.3 ± 1 (1-5) internodes; secondary axis 1.3 ± 0.5 (0.6-2.5) cm long, with 2.2 ± 0.5 (1-3) internodes; with 92 ± 44.5 (20-180) flowers per inflorescence. *Flower calyces* densely covered by appressed hairs inside, glabrous to densely strigose outside, the lobes 0.1 ± 0.1 (0-1.3) mm long, and 0.1 ± 0.2 (0-1.1) times the length of the calyx tube. *Ovary* glabrous or sparsely hairy. *Fruits* ellipsoid, 11.1 ± 1.6 (9-13.7) x 8 ± 1.1 (6.6-11.1) mm.

Distribution and habitat – Known from three sites: forests around Manaus, at São Paulo de Olivença in the Upper Solimões river, and in the Uaupés river in the Upper Rio Negro region. Collections suggest it prefers tall non-flooded forests, and in the Manaus region, at least, is a rare plant.

Notes – *Pagamea macrophylla* can be easily recognized by its large, broad lamina with sparsely distributed veins, and large flowers, in particular when compared to other (glabrous) species of the Macrophylla clade (Table 8). In terms of leaf size and shape it is more similar to *P. velutina*, a high-altitude species in the Guayana Shield. These two may also be sister species according to molecular data (Fig. 3), although there is strong support for the relationship. *Pagamea velutina* has smaller leaves, less branched and fewer flowered inflorescences (Table 8).

Within *Pagamea macrophylla* there is a significant correlation between pairwise morphological distance and geographical distance (Mantel test, r + 0.68, P ; 0.001; Fig. 10), and this quantitative variation is also correlated with a difference in breeding

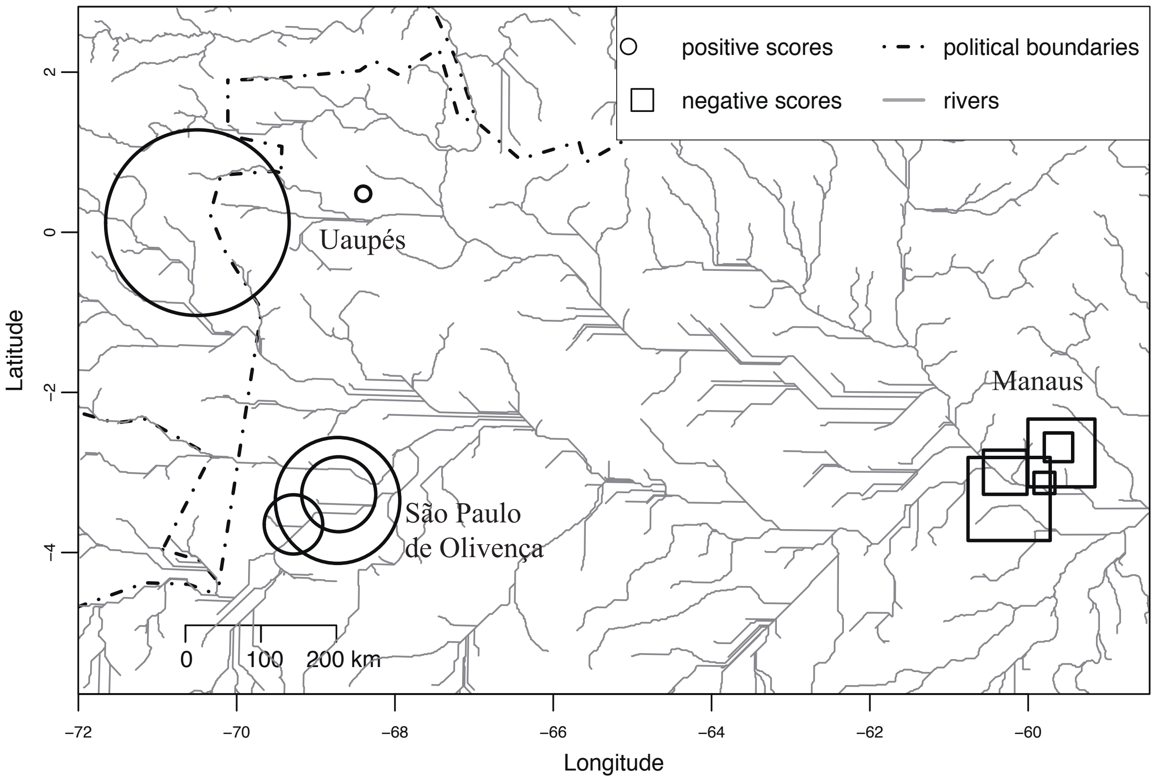

Figure 10. Geographical pattern of morphological variation in *Pagamea macrophylla*. Squares correspond to negative scores on single morphological axis and circles (Manaus) to positive scores; the size of symbols indicate the distance from 0, the largest squares and circles corresponding to the extremes of the variation in the sample. See Table 11 for character correlation.

system. The Manaus population (squares in Fig. 10), has strongly dimorphic flowers, probably unisexual, like *P. anisophylla* (a sister relationship that is not rejected by molecular data; AU test, P>0.05) and *P. jauaensis*; the western populations from São Paulo de Olivença and Uaupés, despite poor sampling, appear to have perfect, homostylous flowers (circles in Fig. 10). Only the dioecious population was sampled for molecular data. Because they are allopatric and very similar they are recognized as a single-species, but further sampling is need to understand this variation and whether there are two reproductively isolated lineages here (Table 11 for character variation between homostylous and dioecious populations).

Table 11. *Pagamea macrophylla*. Characters significantly correlated (Spearman's rho) with a single axis representing morphological variation (Fig. 10; see Table 2 for character descriptions).

Characters	rho	P	Characters	rho	P
INFLPEDU - mm	-0.945	0.000	CALYXLOB - mm	-0.733	0.021
OVARYPUB - scores	-0.855	0.002	INFLSH2 - ratio	0.661	0.042
INFLNO1 - count	-0.774	0.009	INFLPUB - scores	0.75	0.012
CALYXRAT - ratio	-0.758	0.016	PETIOLEN - mm	0.842	0.004
INFLLEN - mm	-0.745	0.018			

12. ***Pagamea velutina*** Steyerm. Mem. N. Y. Bot. Gard. 12(3):275, 1965. —TYPE: VENEZUELA. **Amazonas**. Autana: San Pedro, Cerro Sipapo (Paráque), altitude 1500 m, 4° 51' 26" N and 67° 24' 0" W, 21 Jan 1949, FR, *Maguire 28538* (Holotype: !NY; Isotypes: !K, !US, VEN). PLATE 4.

Tree 3-12 m tall. *Twigs* 4.3 ± 0.9 (3-6) mm thick. *Stipules* conical, 47.8 ± 17.2 (25-

69) mm long, caducous or only the base persistent. *Leaves*: petiole 1.9 ± 0.5 (1.1-2.8) cm long, densely pubescent or glabrous; lamina obovate to elliptic, membranous to chartaceous, 14 ± 2.9 (8.4-18.8) x 4.6 ± 1 (2.9-6.4) cm, densely pubescent on both sides (*velutina*) or completely glabrous (*neblinensis*), the margin flat; with 1.5 ± 2.2 (0-6) domatia along one side of midrib abaxially; midrib densely pubescent on both sides; venation eucamptodromous, with 6 ± o.8 (4-7) pairs of veins, these densely pubescent on both sides. *Breeding system* homostylous. *Inflorescences* thyrsoid, somewhat spicate; peduncle 3.9 ± 1.1 (2.4-6.7) cm long, densely pubescent or glabrous; main axis 2.8 ± 3.3 (-3.3-6.5) cm long, with 4.3 ± 1.3 (3-7) internodes; secondary axis 0.7 ± 0.5 (0-1.8) cm long, with 1.6 ± 1 (0-3) internodes; with 15.8 ± 3.7 (7-46) flower per inflorescence. *Flower calyces* densely covered by appressed hairs inside, densely pubescent or glabrous outside, the lobes .5 ± .4 (0-13) mm long, and 0.4 ± 0.3 (0-1) times the length of the calyx tube. *Ovary* densely hairy. *Fruits* globose, 9.3 ± 2.5 (6.6-13) x 8.4 ± 1.9 (5.7-13) mm.

Distribution and Habitat – High elevations at two sites on the western Guayana Shield (800-1500 m): Serrania Paru (Sipapo) and Neblina tepui. At Sipapo plants are found in shrubland at 1500 m, and at Neblina from 800-1500 m in montane or sub-montane forests.

Notes – The Sipapo and Neblina populations differ in the indumentum of their leaves, inflorescences and flowers (calyx), but these are the only characters that differ significantly between the two. The Neblina plants are completely glabrous and those from Cerro Sipapo (type locality) have a dense soft indumentum. They may also differ habitat type; both occur at high altitudes (see above). Although only the pubescent population has been sampled for molecular data, the Neblina population is morphologically identical despite being glabrous. Unlike other species of *Pagamea* from high elevations in the Guayana Shield, *P. velutina* has much larger leaves that makes it easy to reconize.

13. ***Pagamea anisophylla*** Standl. & Steyermark, Fieldiana Bot. 28:584, fig. 128, 1953. —TYPE: VENZUELA, Amazonas, Autana, río Samariapo, 5° 14' 11” N and 67° 46' 54” W, 8 Sep 1944, FL, *Steyermark 58461* (Holotype: !F; Isotypes: !NY, !VEN). PLATE 4

Shrub or tree 3 ± 2.5 (1.2-13) m tall. *Twigs* 3.3 ± 0.5 (2.4-4.5) mm thick. *Stipules* conical, 19.3 ± 6.5 (13-34) mm long, caducous. *Leaves*: petiole 1.5 ± 0.4 (0.8-2.4) cm long, glabrous (sparsely strigose abaxially); lamina obovate to elliptic, chartaceous to coriaceous, 8.3 ± 1.9 (4-14) x 3.1 ± 0.8 (1.6-5.4) cm, glabrous or nearly so on both sides, the margin flat; with 1.9 ± 1.4 (0-5) domatia; midrib glabrous or nearly so on both sides; venation brochidodromous (inconspicous), with 5 ± 0.8 (3-7) pairs of veins, these glabrous or nearly so on both sides. *Breeding system* dioecious. *Inflorescences* thyrsoid; peduncle 4.6 ± 2 (1.2-8.4) cm long, glabrous to sparsely strigose; main axis 3 ± 1 (1-5.5) cm long, with 3.4 ± 0.8 (2-5) internodes; secondary axis 1.2 ± 0.6 (0.2-2.9) cm long, with 2.4 ± 0.7 (1-4) internodes; staminate plants with 92.3 ± 5.9 (56-130) flowers per inflorescence; pistillate plants with 35.7 ± 17.8 (11-162) flowers per inflorescence.

Flower calyces densely covered by appressed hairs inside, glabrous outside, the lobes 0.2 ± 0.2 (0-7) mm long, and 0.1 ± 0.1 (0-0.4) times the length of the calyx tube. *Ovary* glabrous. *Fruits* globose, 5.9 ± 0.8 (4.4-7) x 5.4 ± 0.7 (4.5-7) mm.

Distribution and habitat – Restricted to the lowlands (up to 500 m) of the Middle Orinoco river basin, from Autana to La Esmeralda, in particular in the Ventuari river basin. Plants have been collected in both shrublands and low forests, in both dry and periodically flooded areas.

Notes – Unlike most members of the Macrophylla clade, the flowers of *P. anisophylla* are highly dimorphic, with some specimens having flowers with a very reduced styles and well-developed anthers, and other specimens having a well-developed style and shrunken, pollen-free anthers, suggesting this species may be dioecious. This character and overall morphology (Chapter 1) suggest a relationship with *P. jauaensis*, which also occurs in the same general area but at higher altitudes (above 1500 m), and is the only other dioecious member of the Macrophylla clade.

Pagamea anisophylla and *P. jauaensis* can be distinguished by the flower calyx. Flowers of *anisophylla* have calyx tubes smaller than 1.7 mm long (vs. 2-3 mm), and the calyx lobes up to 0.2 mm (vs. 0.2-0.6 mm) long. The inflorescences of *P. anisophylla* are also usually longer (up to 13 cm long vs. < 5 cm long), with more flowering nodes along the main axis (2-5 vs. 1-2), and longer lateral branches (4-20 mm vs. 0-4 mm).

Although I was not was not able to include *Pagamea jauaensis* in my molecular analyses, I keep it separate from *P. anisophylla.* The morphological differences measured allow the two to be separated but they correlate with altitude. Specimens so far collected do not overlap in altitudinal distribution (Table 12, Fig. 11), so whether these are distinct species and/or reproductively isolated remains unclear.

14. ***Pagamea jauaensis*** Steyerm., Mem. N. Y. Bot. Gard. 23:883, fig. 15, 1972. —TYPE: VENEZUELA, Bolívar, Sucre, Meseta del Jaua, Cerro Jáua, cumbre de la porción Central-Occidental de la Meseta, 4° 45' 0” N and 64° 26' 0” W, 25 Mar 1967, FL, *Steyermark 97928* (Holotype: VEN; Isotypes: !MO, !NY). PLATE 4.

Shrub or tree 4.3 ± 3.3 (1.5-9) m tall. *Twigs* 3.6 ± 1.3 (2.1-6) mm thick. *Stipules* conical, 18.1 ± 8.1 (9.5-35) mm long, caducous. *Leaves*: petiole 0.8 ± 0.2 (0.5-1.4) cm long, glabrous; lamina obovate to elliptic, chartaceous to coriaceous, 6.6 ± 1.6 (3.7-10.5) x 2.2 ± 0.5 (1.2-3.4) cm, glabrous on both sides, the margin flat; without domatia; midrib glabrous on both sides; venation brochidodromous, with 5.5 ± 0.8 (4-7) pairs of veins, these glabrous on both sides. *Breeding system* dioecious. *Inflorescences* thyrsoid; peduncle 3.1 ± 0.9 (1.7-4.9) cm long, glabrous or nearly so; main axis 1 ± 0.5 (0.2-1.8) cm long, with 1.6 ± 0.6 (1-3) internodes; secondary axis 0.1 ± 0.1 (0-0.4) cm long, with 0.8 ± 0.4 (0-1) internodes; staminate plants with 14.3 ± 1.8 (12-18) flowers per inflorescence; pistillate plants with 4.9 ± ? (3-7) flowers per inflorescence. *Flower calyces* densely covered by appressed hairs inside, glabrous to sparsely puberulent outside, the lobes 0.3 ± 0.2 (0-0.7) mm long, and 0.2 ± 0.1 (0-0.3) times the length of the

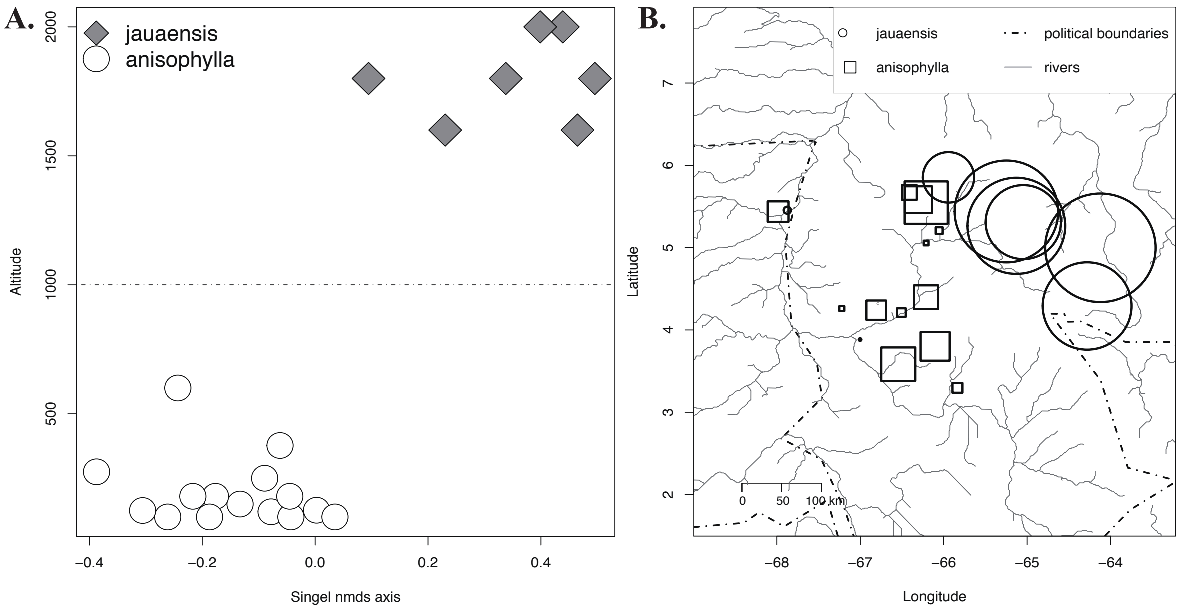

Figure 11. Comparison between *Pagamea anisophylla* and *P. jauaensis.* **A.** Morphology vs. altitude; **B**. Geographical pattern of morphological variation. Morphology was reduced to a single dimension using non-metric multidimensional scaling. Squares in B correspond to negative scores on this morphological axis and circles to positive scores; the size of symbols indicate the distance from 0, the largest squares and circles corresponding to the extremes of the variation in the sample. See Table 12 for character correlation.

Table 12. *Pagamea anisophylla* and *P. jauaensis*. Characters significantly correlated (Spearman's rho) with a single axis representing morphological variation (Fig. 11; see Table 2 for characters descriptions).

character	rho	P	character	rho	P
PETIOLEN - mm	-0.64	0.001	INFLSH2 - ratio	-0.834	0
LEAFLEN - mm	-0.632	0.001	INFLSH3 - ratio	0.681	0
LEAFWID - mm	-0.716	0	INFLSH4 - ratio	0.823	0
LFSHAPE2 - ratio	-0.599	0.003	CALYXLOB - - mm	0.602	0.002
INFLPEDU - mm	-0.744	0	CALYXTUB - - mm	0.714	0
INFLLEN - mm	-0.898	0	NFLOWERS - count	-0.858	0
INFLBRAN - mm	-0.961	0	CALXYPUB - score	-0.539	0.008
INFLNO1 - count	-0.878	0	OVARYPUB - score	-0.617	0.002
INFLNO2 - count	-0.91	0			

calyx tube. *Ovary* glabrous to densely hairy. *Fruits* globose, 6.1 ± 0.6 (5.5-7) x 5.3 ± 0.8 (4.5-6.2) mm.

Vernacular – Wajöna Tajededato.

Distribution and habitat – Endemic to high altitudes (1600-2000 m) in Western Guayana Shield (Meseta del Jaua and Sierras Maigualida and Yutayé). Apparently in shrublands.

Notes – This species is inferred to be a member of the Macrophylla clade (Fig. 3) because of the its conical stipules and calyx densely covered inside by appressed silverish hairs. The flowers are unisexual, which suggest it may be related to *P. anisophylla,* a morphologically similar species that occurs in the lowlands of the same region (see note under *P. anisophylla* for differences between the two).

Capitata clade

The placement of this clade in the molecular phylogeny remains unclear due to lack of support (see Fig. 3). Its monophyly, on the other hand, is strongly supported for three accessions, from Central Amazon, Suriname and the Gran Sabana region of the Venezuela (Chapter 1). It includes just one species.

15. ***Pagamea capitata*** Bentham, J. Linn. Soc. Bot. 1:109, 1857. —TYPE: British Guyana, Roraima (BM), 1842, FL, *Robert Schomburgk 578* (Holotype: !K; Isotypes: !BM); same as *Richard Schomburgk 870* (as annotated on the BM specimen; see van Dam 2002), likely collected in the surroundings of the Roraima tepui. PLATES 5-6.

Pagamea brevipedunculata Steyerm., Mem. New York Bot. Gard. 12(3):283, 1963. —TYPE: VENZUELA, Cerro Guaiquinima, 5° 44' 30" N and 63° 40' 20" W, 11 Jan 1952, FR, *Maguire 33070* (Holotype: !NY; Isotypes: !US, VEN).

Pagamea caudata Huber, Bull. Soc. Bot. Genève (sér. 2) 6: 211, 1915. *Pagamea capitata* Benth. subsp. *caudata* (Huber) Steyerm., Mem. N. Y. Bot. Gard. 12(3): 280, 1965. —TYPE: Brazil, Oriximiná, rio Trombetas, Alto Ariramba, rio Jaramacarú, 1° 17' 29" S and 55° 56' 54" W, 2 Dec 1910, FL-old, *Ducke 11269* (Holotype: MG; Isotypes: !F (fragment), !K, !US).

Pagamea capitata Benth. subsp. *thibaudiaefolia* (Wernham) Steyerm., Mem. N. Y. Bot. Gard. 12(3):280, 1965. —TYPE: SURINAME, FL, *Hostmann 801* (Lectoype: !K; Isolectotypes: !BM, !F (fragment), !MO, P). Basionym: *Cephaelis thibaudiaefolia* Wernham.

Pagamea conferta Standl., Field Mus. Pub. Bot 7:419, 1931. *Pagamea capitata* Benth. subsp. *conferta* (Standl.) Steyerm., Mem. N. Y. Bot. Gard 12(3):281, 1965. —TYPE: VENEZUELA, Duida tepui, 3° 25' 30" N and 65° 40' 0" W, 1928, FL, *Tate 794* (Holotype: !NY; Isotype: !F)

Pagamea capitata Benth. subsp. *conferta* (Standl.) Steyerm. forma *breviloba* Steyerm., Mem. New York Bot. Gard. 12(3):281, 1965. —TYPE: VENEZUELA, Duida tepui, plateau above Culebra, 3° 13' 0" N and 65° 58' 0" W, 20 Nov 1950, FR, *Maguire 29573* (Holotype: !NY; Isotypes: !US, VEN).

Shrub or tree 2.4 ± 1.1 (0.8-8) m tall. *Twigs* 2.5 ± 0.6 (1.5-5) mm thick. *Stipules* cylindrical, 3.5 ± 0.8 (1.5-6.7) mm long, persistent on nodes with leaves. *Leaves*: petiole 0.7 ± 0.3 (0.2-1.9) cm long, densely strigose to densely pubescent, rarely glabrous; lamina ovate to elliptic, coriaceous, 6.3 ± 1.8 (2.4-10.8) x 1.6 ± 0.5 (0.5-3.2) cm, glabrous on both sides or sparsely puberulent abaxially, the margin slightly to strongly revolute, rarely flat; with 2.1 ± 2.2 (0-6) pairs of domatia; midrib sparsely or densely strigose to pubescent on both sides, rarely glabrous; venation eucamptodromous, veins arching or straight, with 6.1 ± 1.1 (4-10) pairs of veins, these glabrous or sparsely strigose abaxially. *Breeding system* distylous or homostylous. *Inflorescences* capitate; peduncle 1.7 ± 1.1 (0.2-5) cm long, densely pubescent or strigose; main axis 0.3 ± 0.3 (0.1-1) cm long, with 0.7 ± 0.3 (0-2) internodes; secondary axis 0.1 ± 0.1 (0-0.4) cm long, with 0.5 ± 0.4 (0-1) internodes; with 20 ± 5.9 (3-36) flowers per inflorescence. *Flower calyces* sparsely to densely pubescent outside, glabrous inside, the lobes 1.5 ± 0.5 (0.4-7) mm long, and 1.2 ± 0.4 (0.4-2.6) times the length of the calyx tube. *Ovary* densely hairy (glabrous). *Fruits* globose, 4.5 ± 0.7 (3-7) x 5.2 ± 0.8 (2.3-7) mm.

Vernacular – Tabiru-yek (Camarata), Trombó-yek (Pemón).

Distribution and habitat – Most specimens are from the Guayana Shield region, were it occurs from sea-level to up to 1850 m. A few specimens have been collected south of the Amazon river, in the lowlands of Central Amazon, and in the Serra do Cachimbo, in the border between the Amazon and the Cerrado biomes at an elevation of up to 600 m. This species has been collected only in shrublands, usually in areas with periodic flooding, or along river banks.

Notes – *Pagamea capitata* is easy to recognize by its capitate inflorescences, ovate leaf blades with an acute apex, strongly revolute margins, densely pubescent ovary, and usually persistent stipules. It may be confounded with the unrelated *P. spruceana* (Guianensis clade), which also has capitate inflorescences, leaves with strongly revolute margins and a pubescent ovary. From this species *P. capitata* can be distinguished by its ovate leaf blades, persistent stipules, and both petiole and inflorescence peduncle densely pubescent (vs. glabrous or with minute hairs). Both species occur in the Issana river basin in the Upper Rio Negro of Brazil. There, *P. capitata* is restricted to dry shrublands on standstone formations, while *P. spruceana* is found on highly-flooded igapó forests (pers. obs.).

Morphological variation within *Pagamea capitata* is highly correlated with both geography (Mantel test, r = 0.54, P < 0.001) and altitude (Mantel test, r = 0.38, P < 0.001). Both these correlations are shown by collections from the Guayana Shield region, which have strong differences between eastern (Guiana and Suriname) and western (Venezuela) specimens (see *P. thyrsiflora* for a similar pattern), and along the altitudinal gradient within the Guayana shield (from 1000 to 1850 m altitude; Fig. 12, Table 13). I had previously (Vicentini and Steyermark 2004) recognized two subspecies corresponding to the eastern and western specimens: subsp. *capitata* (eastern) and subsp. *conferta* (western), which appear to be correlated with the presence (eastern) or absence (western) of leaf-like bracts subtending the clusters of flowers, and with the number of domatia on the leaf blade, 2-6 vs. 0-2, respectively. Other characters are in general overlapping. There is no geographical overlap between eastern and western morphs; they have a parapatric distribution (Fig. 12B). Hence, reproductive isolation

Table 13. *Pagamea capitata*. Characters significantly correlated (Spearman's rho) with a single axis representing morphological variation (Fig. 12; see Table 2 for character descriptions.

Character	rho	P	Character	rho	P
PETIOLEN - mm	-0.773	0	INFLNO2 - count	-0.917	0
LEAFLEN - mm	-0.561	0	INFLSH2 - ratio	-0.819	0
LEAFWID - mm	-0.488	0	CALYXLOB - mm	-0.46	0
LFSHAPE3 - ratio	-0.565	0	CALYXRAT - ratio	-0.549	0
DOMADENS - ratio	-0.674	0	NFLOWERS - count	-0.378	0.002
VENADENS - ratio	0.479	0	PETIPUB - score	0.435	0
INFLPEDU - mm	-0.758	0	PUBABAX - score	0.561	0
INFLLEN - mm	-0.825	0	PUBADAX - score	0.441	0
INFLBRAN - mm	-0.91	0	INFLPUB - score	-0.626	0
INFLNO1 - count	-0.577	0	OVARYPUB - score	0.669	0

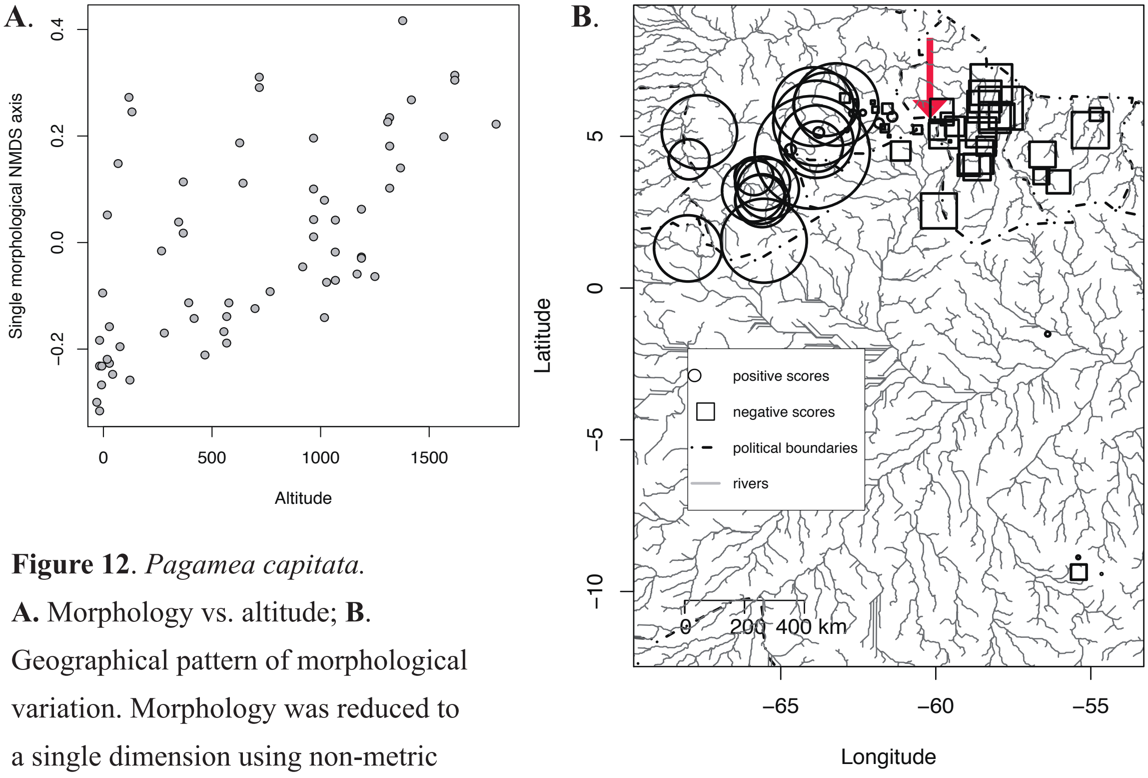

Figure 12. *Pagamea capitata*. **A.** Morphology vs. altitude; **B.** Geographical pattern of morphological variation. Morphology was reduced to a single dimension using non-metric multidimensional scaling (NMDS). Squares in B correspond to negative scores on this morphological axis and circles to positive scores; the size of symbols indicate the distance from 0, the largest squares and circles corresponding to the extremes of the variation in the sample. Arrow indicates intermediate morphological values (small symbols) at the zone of contact between squares and circles. See Table 13 for character correlation with this morphological axis.

between them cannot be inferred, and a subspecies status seemed to be the appropriate choice. However, after examining additional specimens, leaf-like bracts are not always preserved and specimens from the region of putative contact between the two morphs are more or less indermediate (arrow in Fig. 12B).

Variation correlating with altitude follows a general trend of a decrease in the size of leaves and inflorescences with increasing altitude (Fig. 12A, Table 13), and very high-altitude (> 1500 m) specimens have been described as *Pagamea brevipedunculata*. Steyermark (1965) stated that *P. brevipedunculata* differed from *P. capitata* in having a “glabrous ovary, smaller nearly glabrate leaves, and shorter petioles”. However, these characters, in particular a glabrous ovary, are also found in low-altitude specimens from different parts of the range of *P. capitata*. Furthermore, such a trend of a decrease in size with increasing altitude may only reflect phenotypic plasticity or clinal variation, rather than species differences; note that there is also no altitudinal overlap between morphs. Given these observations, I prefer to circumscribe *P. capitata* broadly.

Duckei clade

Placement and monophyly of the single species in this clade are well-supported (Chapter 1, Fig. 3), although only one of two disjunct populations has been sampled for molecular data (see below). This clade is in an isolated part of morphological space (Chapter 1).

16. ***Pagamea duckei*** Standl., Field Mus. Publ. Bot. 17:278, 1937. —TYPE: Brazil, **Amazonas**, Manaus, igarapé Tarumã-mirin, 22 Dec 1912, FL, *Ducke 12415* (Holotype: MG; Isotypes: !F - fragment).

Shrub or tree 3.5 ± 1.3 (1-6.5) m tall. *Twigs* 6 ± 1 (4.8-8.5) mm thick. *Stipules* cylindrical, 11.5 ± 6.4 (7-16) mm long, caducous or only the base persistent. *Leaves*: petiole 1.3 ± 0.2 (0.7-1.7) cm long, densely pubescent; lamina elliptic, membranous, 15 ± 3.1 (10.2-24) x 6 ± 1.5 (2.8-9.2) cm, densely pubescent abaxially, glabrous adaxially, the margin flat or slightly revolute; midrib with 1.1 ± 3.1 (0-11) barbate tufts of hairs along one side of midrib below, densely pubescent on both sides; venation eucamptodromous, veins usually straight, with 9.6 ± 1 (7-11) pairs of veins, these densely pubescent abaxially, sparsely pubescent adaxially. *Breeding system* dioecious. *Inflorescences* thyrsoid to capitate; peduncle 1.6 ± 0.7 (0.7-3.4) cm long, densely pubescent; main axis 0.4 ± 0.4 (0-1.4) cm long, with 0.6 ± 0.5 (0-2) internodes; secondary axis 0.1 ± 0.1 (0-0.5) cm long, with 0.6 ± 0.5 (0-2) internodes; staminate plants with 40.6 ± 11.2 (18-70) flowers per inflorescence; pistillate plants with 20.9 (15-40) flowers per inflorescence. *Flower calyces* densely pubescent inside and outside, hairs erect, the lobes 2.4 ± 0.6 (1-3) mm long, and 1.7 ± 0.6 (0.6-3) times the length of the calyx tube. *Ovary* densely hairy. *Fruits* ellipsoid, 8.1 ± 0.8 (6.9-10) x 6.3 ± 0.6 (5.4-7.6) mm.

Distribution and habitat – This species is known from two disjunct areas (Fig. 1): the surroudings of Manaus, where it occurs in non-flooded low white-sand forests, usually at the border of more open areas; and in the region of Benjamin Constant, at the border between Colombia and Brazil.

Notes – *Pagamea duckei* is easy to recognize by its membranous, large and broad, and densely pubescent leaves, with secondary veins impressed and pubescent (also adaxially), bullate or plicate leaf blades. Other species with pubescent and plicate leaf blades, have either strongly coriaceous (*P. plicata*) or narrower (*P. plicatiformis*) leaf blades, and lobes of the flower clayx are also much longer in *P. duckei* (2-2.5 mm vs. 0.8-1.6 mm).

Photographs only of the specimens from Benjamin Constant region were seen (see Appendix A). They have the distinctic leaves and inflorescence and fruit size of *P. duckei*, although details of the flower could not be seen. These specimens considerably extend the geographical range of this species.

Plicata clade

The Plicata clade includes two well-supported reciprocally monophyletic species, *P. plicata* and *P. glabrescens* (Fig. 3). These are sympatric and clearly morphologically distinct in Central Amazon (see below).

17. ***Pagamea glabrescens*** (Benth.) Vicentini, comb. nov. Basionym: *P. plicata* var.

glabrescens Benth., Journ. Linn. Soc. Lond. Bot 1:110, 1857. —TYPE: Brazil, Pernambuco, banks of rio Preto, Sep 1839, FL, *Gardner 2891* (Holotype: !BM).

Pagamea glabrescens is sister to *P. plicata,* and both species are monophyletic according to nuclear molecular markers (ITS). These species are morphologically different in the region of range overlap (Table 14). In contrast to *P. plicata*, the inflorescences of *P. glabrescens* have in general a longer basal lateral branch [(1-)2-4 cm long with 2-4 internodes *vs*. 0-1(-2) cm long with 0-2 internodes], calyces with shorter lobes (0.3-0.9 vs. 1.2-1.8 mm long), and the ovary and the veins and midrib on the adaxial surface of the lamina are glabrous (vs. pubescent).

Shrub or tree 6.8 ± 4.8 (1-20) m tall. *Twigs* 6 ± 1 (4.6-8.4) mm thick. *Stipules* cylindrical, 23 ± 8 (6-30) mm long, caducous or only the base persistent. *Leaves*: petiole 2.4 ± 0.9 (0.9-5.6) cm long, glabrous, rarely sparsely puberulent; lamina elliptic, coriaceous, 16.2 ± 5.9 (7.3-33) x 4.8 ± 1.6 (2-9.5) cm, glabrous to densely pubescent abaxially, glabrous adaxially, the margin flat to slightly revolute; with 0.8 ± 2.2 (0-9) paris of domatia; midrib densely or sparsely pubescent abaxially, usually glabrous adaxially; venation eucamptodromous, veins straight, with 8.2 ± 2 (5-14) pairs of veins, these densely or sparsely pubescent abaxially, glabrous adaxially. *Breeding system* dioecious. *Inflorescences* paniculate; peduncle 5.7 ± 2.5 (1.5-13.2) cm long, glabrous to densely puberulent or strigose; main axis 5.6 ± 2.1 (1.9-9.8) cm long, with 4.9 ± 1.6 (1-8)

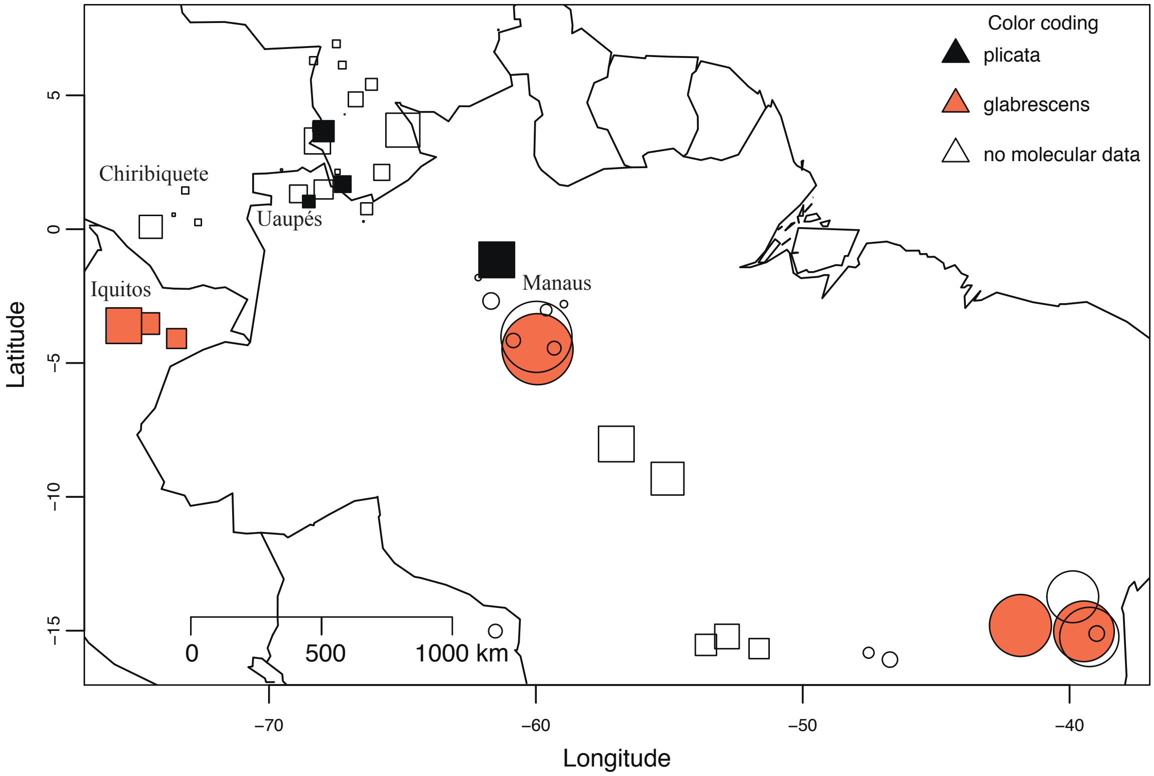

Figure 13. The geographical pattern of morphological variation of *Pagamea plicata* and *P. glabrescens*. Morphology was reduced to a single dimension using non-metric multidimensional scaling. Squares correspond to negative scores (mostly *plicata*) and circles to positive scores (*glabrescens*); the size of symbols indicate the distance from 0, the largest squares and circles corresponding to the extremes of variation in the sample. See Table 14 for character correlation with this morphological axis. Noise was added to collection coordinates to spread the symbols.

Table 14. Plicata clade. Characters significantly correlated (Spearman's rho) with a single axis representing morphological variation (Fig. 13; see Table 2 for character descriptions).

Characters	**rho**	**P**	**Characters**	**rho**	**P**
DOMADENS - ratio	-0.419	0.002	CALYXTUB - mm	0.58	0
INFLLEN - mm	-0.38	0.006	CALYXRAT - ratio	0.606	0
INFLBRAN - mm	-0.707	0	NFLOWERS - count	-0.668	0
INFLNO1 - count	-0.613	0	PETIPUB - score	-0.507	0
INFLNO2 - count	-0.664	0	PUBABAX - score	-0.479	0
INFLSH1 - ratio	0.423	0.002	PUBADAX - score	-0.752	0
INFLSH2 - ratio	-0.692	0	INFLPUB - score	0.695	0
INFLSH4 - ratio	0.7	0	OVARYPUB - score	-0.426	0.002
CALYXLOB - mm	0.799	0			

internodes; secondary axis 1.9 ± 1.3 (0-4.2) cm long, with 2.8 ± 1.4 (0-5) internodes; staminate plants with 230.7 ± 134.5 (108-544) flowers per inflorescence; pistillate plants with 87.7 ± 40.1 (22-279) flowers per inflorescence. *Flower calyces* glabrous inside, glabrous or sparsely puberulent outside, the lobes 0.6 ± 0.3 (0.2-9.5) mm long, and 0.6 ± 0.2 (0.2-1.3) times the length of the calyx tube. *Ovary* usually glabrous, or sparsely to densely hairy. *Fruits* ellipsoid, 7.6 ± 1.1 (5.5-9.5) x 6.1 ± 0.8 (4.8-8) mm.

Vernacular – Maogua (Miraña), Jiguha (Huitoto), Jigiro (Witoto), Uicaidonuai (Huitoto), Cariganoó (Muiname).

Distribution and habitat – Widespread extending from the Western Amazon of Colombia and Peru to the high-lands of Central Brazil. In the Brazilian Amazon it occurs mostly south of the Amazon river, although some collections are from Manaus. Mostly lowlands, but from 400-1200 in Central Brazil. It usually grows in in tall forests, both in highly-flooded and non-flooded systems; high altitude plants are shrubs or treelets on sand patches along streams.

Notes – *Pagamea glabrescens* is sister and morphologically very similar to *P. plicata*. Both are supported as monophyletic groups, and their ranges overlap in southern Central Amazon, although they have yet to be found growing together. In the region of range overlap they are morphologically, different (Fig. 13), in inflorescence structure, calyx lobe length, and indumentum of leaves and ovary (Table 14). The inflorescences of *P. glabrescens* have in general a long basal lateral branch (1-)2-4 cm long with 2-4 internodes, very short calyx lobes (0.3-0.9 mm long), and the ovary and the adaxial surface of the lamina are glabrous. In contrast, the inflorescences of *P. plicata* have an at most very short basal branch [0-1(-2) cm long with 0-2 internodes] of flowers, the calyx lobes are longer (1.2-1.8 mm long), the ovary and the veins and midrib on the adaxial surface are usually pubescent. Specimens of *P. glabrescens* from Western Amazon (squares from Iquitos in Fig. 13) are more similar to *P. plicata* in terms of inflorescence structure.

It may be difficult to distinguish between the two species in the Chiribiquete-Uaupés region (Fig. 13), which is where they might be sympatric in addition to Central Amazon (Manaus). However, although variation is overlapping in Western Amazon, dried specimens can readily be distinguished. The leaf blades of *P. glabrescens* dry with a brownish-reddish color abaxially and both tertiary and higher order veins are clearly visible; leaf blades are obovate with an attenuate base and a short distinct acumen. The leaf blades of *P. plicata*, however, dry greyish-yellow color and the fine venation is inconspicuous, sometimes the tertiary veins only being slightly visible; the leaf blades are elliptic, the base acute, and the apex acute or obtuse, lacking a distinct accumen. *Pagamea glabrescens* from this regions also has somewhat shorter inflorescences and smaller flowers (both calyx tubes and lobes are smaller), but the variation is overlapping. Molecular data strongly support the plants from Iquitos as being in the *P. glabrescens* clade. At Iquitos, *P. glabrescens* may also be confused with *P. peruviana* (23), which also occurs in Western Amazon of Peru and Colombia (see discussion under

P. peruviana).

18. ***Pagamea plicata*** Spruce ex Benth., Journ. Linn. Soc. 1:109, 1857. —TYPE: Brazil, São Gabriel da Cachoeira, rio Negro, 0° 7' 45" S and 67° 5' 30" W, 1852, FR, *Spruce 2342* (Holotype: !BM). PLATES 7-8.

> *Pagamea plicata* var. *multinervia* Steyerm., Mem. N. Y. Bot. Gard 12(3):274, 1965. —TYPE: VENEZUELA, Bolívar, Gran Sabana: rio Arequi, region Urimãn, 5° 21' 0" N and 62° 29' 0" W, 5 Sep 1954, FR, *Bernardi 1690* (Holotype: VEN; Isotypes: !NY, P).

Shrub or tree 8.3 ± 6.3 (2-21) m tall. *Twigs* 6.1 ± 1 (4.8-8.5) mm thick. *Stipules* cylindrical, 25.2 ± 15.4 (3.5-51) mm long, caducous or only the base persistent. *Leaves*: petiole 3.3 ± 0.9 (1-5.3) cm long, glabrous or sparsely strigose; lamina elliptic, coriaceous, 21.5 ± 6.8 (7.2-36.3) x 6.8 ± 2 (2.7-11) cm, sparsely to densely pubescent abaxially, glabrous adaxially, the margin flat to slightly revolute; with 0.2 ± 1.1 (0-7) pairs of domatia; midrib sparsely to densely pubescent abaxially, glabrous adaxially; venation eucamptodromous, veins straight, with 10 ± 2.3 (5-16) pairs of veins, these sparsely to densely pubescent abaxially, glabrous or sparsely strigose adaxially. *Breeding system* dioecious. *Inflorescences* thyrsoid to subspicate; peduncle 5.9 ± 1.6 (2.5-10.1) cm long, sparsely to densely strigose; main axis 4.3 ± 1.4 (0.5-7.1) cm long, with 4.2 ± 3.9 (1-40) internodes; secondary axis 0.6 ± 0.5 (0-2.2) cm long, with 1.3 ± 0.5 (0-2) internodes; staminate plants with 139.9 ± 10.9 (106-174) flowers per inflorescence; pistillate plants with 88.6 ± 36.7 (38-140) flowers per inflorescence. *Flower calyces* glabrous inside, sparsely to densely puberulent or pubescent outside, the lobes 1 ± 0.3 (0.3-8.7) mm long, and 0.7 ± 0.3 (0.2-1.8) times the length of the calyx tube. *Ovary* glabrous to densely hairy. *Fruits* globose, 7.3 ± 0.9 (4.8-8.7) x 6.6 ± 1 (4.8-8.5).

Vernacular – Werrãma, durro (Baniwa), Cachira-huaro (Baniwa), Ají-de-paloma (spanish)

Distribution and habitat – Widespread from the Orinoco and Upper Rio Negro river, south to the Serra do Cachimbo in South Central Amazon region, mostly lowlands, and usually in tall forests.

Note – The leaf blades of *P. plicata* are large, strongly coriaceous and with straight secondary veins raised on the abaxial surface, impressed and usually covered by hairs adaxially; the petiole is thick, cylindrical or flattened. This species it easy to recognize. It is usually a tree in tall non-flooded forests.

Populations of *P. plicata* north of the Amazon river only were sampled for molecular data, while southern populations, which largely overlap in range with its sister-species, *P. glabrescens* (squares south of Manaus in Fig. 13), have not been sampled for molecular data and their placement in the phylogeny is unclear. However, these southern specimens have the inflorescence with short lateral branches of *P. plicata*, and the leaf blades are also densely pubescent in both respects, unlike the specimens of *P. glabrescens* from this region (see also discussion for *P. glabrescens*).

Coriacea clade

Included in the Coriacea clade are three morphologically distinct species (Table 15), two of which are apparently monophyletic, and one, *P. coriacea*, paraphyletic (Chapter 1, Fig. 3). These three species are sympatric in the Upper Rio Negro region, and the morphological and molecular differences in sympatry indicate they are reproductively isolated species (Chapter 1).

19. ***Pagamea coriacea*** Spruce ex Benth., J. Linn. Soc. Bot. 1:110, 1857. —TYPE: BRAZIL, Amazonas, São Gabriel da Cachoeira, Uanauáca, Jan 1852, FR, *Spruce 2026* (Holotype: !K; Isotypes: !BM, !F (fragment), !NY, P). PLATES 7-8.

> *Pagamea coriacea* var. *pubescens* Steyerm., Mem. New York Bot. Gard. 12(3):273, 1965. —TYPE: BRAZIL, Amazonas, rio Negro infer., Acajutuba, 22 Mar 1941, FL, *Ducke 683* (Holotype: !US; Isotypes: !F, !MO, !NY).
>
> *Pagamea coriacea* var. *acuta* Steyerm., Mem. N. Y. Bot. Gard. 12(3):273, 1965. —TYPE: COLOMBIA, río Vaupés, between Mitú and Javareté, 1° 15' 0" N and 70° 13' 0" W, 15 May 1953, FL-old, *Schultes 19367* (Holotype: !US; Isotypes: !F, !US).

Shrub or tree 4.2 ± 2.9 (0.5-18) m tall. *Twigs* 7 ± 1.3 (4.8-9) mm thick. *Stipules* cylindrical, 19.2 ± 8.1 (7.8-36) mm long, caducous or only the base persistent. *Leaves*: petiole 3.4 ± 1 (1.1-7.4) cm long, glabrous or nearly so; lamina elliptic, coriaceous, 15.5 ± 4.5 (6.2-33.8) x 4.6 ± 1.2 (1.7-8.3) cm, glabrous or nearly so, the margin flat; with 1.3 ± 2.1 (0-8) pairs of domatia; midrib glabrous or nearly so; venation brochidodromous or eucamptodromous, veins arching, with 6.1 ± 1.4 (4-14) pairs of veins, these glabrous or nearly so. *Breeding system* distylous, homostylous or dioecious. *Inflorescences* paniculate to subspicate; peduncle 7.7 ± 2.3 (2.4-14.9) cm long, glabrous to densely strigose; main axis 7.7 ± 2.4 (0.1-15.2) cm long, with 6.3 ± 1.4 (1-10) internodes; secondary axis 3.3 ± 2 (0-10.2) cm long, with 4.3 ± 1.6 (0-12) internodes; with 192 ± 130 (20-650) flowers per inflorescence. *Flower calyces* glabrous or nearly so inside, glabrous to sparsely puberulent outside, the lobes 0.4 ± 0.2 (0-10) mm long, and 0.3 ±

Table 15. Coriacea clade. Characters showing a significant difference in mean values (Kruskall-Wallis test, P <=0.01), are listed. Values are mean +/- standard deviation (min-max) averages per specimen (see Table 2 for character descriptions).

Characters	***coriacea***	***igapoana***	***acrensis***
PETIOLEN - mm	33.54 +/- 7.92 (19.75-65.25)	25.65 +/- 2.9 (22-31.4)	8.9 +/- 3.14 (5-18.25)
LEAFLEN - mm	146.22 +/- 29.83 (86.83-249.25)	136.1 +/- 13.16 (121.67-156.75)	57.18 +/- 10.09 (40.4-78.67)
LEAFWID - mm	46.18 +/- 9.83 (19.75-74)	19.03 +/- 1.87 (15.5-21.75)	19.31 +/- 2.46 (14.86-25.33)
LFSHAPE1 - ratio	0.52 +/- 0.04 (0.4-0.62)	0.47 +/- 0.04 (0.42-0.55)	0.51 +/- 0.02 (0.46-0.56)
LFSHAPE2 - ratio	0.42 +/- 0.07 (0.16-0.57)	0.17 +/- 0.02 (0.15-0.2)	0.41 +/- 0.06 (0.28-0.49)
LFSHAPE3 - ratio	0.23 +/- 0.04 (0.12-0.33)	0.19 +/- 0.02 (0.16-0.23)	0.15 +/- 0.03 (0.11-0.23)
DOMADENS - ratio	0.17 +/- 0.26 (0-1)	0 +/- 0 (0-0)	0.5 +/- 0.23 (0-0.78)
VENADENS - ratio	0.04 +/- 0.01 (0.01-0.1)	0.1 +/- 0.02 (0.07-0.12)	0.1 +/- 0.03 (0.04-0.15)
INFLPEDU - mm	77.37 +/- 22.55 (26.5-139.67)	63.19 +/- 14.3 (30.5-74.5)	22.82 +/- 7.65 (12-53)
INFLLEN - mm	155.06 +/- 38.88 (85.33-254)	115.63 +/- 28.51 (59-146)	35.47 +/- 10.21 (16-71)
INFLBRAN - mm	33.05 +/- 20.31 (0.5-92)	15.76 +/- 8.25 (1.75-28.67)	0.85 +/- 0.85 (0-3)
INFLNO1 - - count	6.27 +/- 1.39 (2.5-9.5)	4.5 +/- 0.8 (3-5.5)	2.27 +/- 0.78 (1-4)
INFLNO2 - - count	4.31 +/- 1.6 (0.5-8.33)	2.69 +/- 0.86 (1-3.5)	0.61 +/- 0.58 (0-2)
INFLSH1 - ratio	0.5 +/- 0.09 (0.23-0.73)	0.55 +/- 0.03 (0.51-0.61)	0.65 +/- 0.09 (0.48-0.78)
INFLSH2 - ratio	0.8 +/- 0.4 (0.02-2.14)	0.56 +/- 0.24 (0.12-0.87)	0.13 +/- 0.13 (0-0.45)
INFLSH3 - ratio	0.39 +/- 0.51 (0.18-5.83)	0.42 +/- 0.02 (0.39-0.45)	0.42 +/- 0.14 (0.17-0.83)
INFLSH4 - ratio	0.31 +/- 0.13 (0.07-1)	0.51 +/- 0.22 (0.29-1)	0.95 +/- 0.11 (0.5-1)
CALYXLOB - mm	0.42 +/- 0.18 (0.1-0.94)	0.52 +/- 0.15 (0.25-0.73)	0.57 +/- 0.16 (0.32-0.94)
CALYXTUB - mm	1.39 +/- 0.2 (1.01-1.93)	1.76 +/- 0.16 (1.58-2.1)	1.03 +/- 0.14 (0.68-1.32)
CALYXRAT	0.31 +/- 0.13 (0.08-0.67)	0.3 +/- 0.08 (0.14-0.41)	0.56 +/- 0.12 (0.32-0.82)
NFLOWERS - count	194.23 +/- 131.6 (20-647.33)	41.67 +/- 19.89 (17.5-76.67)	33.33 +/- 14.39 (12-70.67)

0.2 (0-1.4) times the length of the calyx tube. *Ovary* glabrous to densely hairy. *Fruits* ellipsoid, 5.9 ± 1 (3.6-10) x 4.9 ± 0.7 (3.2-7) mm.

Vernacular – Wa-kö-gö (Desaro), Ochatíbae (Miraña), Duidotimai (Huitoto),Ticidotia (Huitoto), Chaorini-e (Miraña).

Distribution and habitat – This species is restricted to the Amazon lowlands, in the basins of the Negro, Orinoco, Madeira and Urubú rivers (Fig. 1). It occurs in shrublands or tall forests, usually in areas associated with periodic flooding, although it is not found in highly-flooded igapó forests.

Notes – *Pagamea coriacea* can be easily recognized by its large, strongly coriaceous, glabrous leaf blades with a rounded or obtuse apex and with flat or only slightly raised secondary veins, and also a long multi-flowered inflorescence. There are no other species of *Pagamea* with which it may be confused.

Molecular data support the monophyly of *P. coriacea* (specimens collected throughout its range; Chapter 1), but this species is paraphyletic in relation to *P. igapoana* (Chapter 1, Fig. 3), which is morphologically and ecologically distinct (see under *P. igapoana*).

Some observations suggest that *P. coriacea*, as here circumscribed, may include two species. In some localities this species appears to be polymorphic in inflorescence structure, some plants having inflorescences with long, well-developed, lateral axes (*laxa* morph), and other plants having inflorescences with very short lateral axes, the flowers thus being densely clustered along the main axis (*congesta* morph) . Inflorescence lateral branch length is the character with highest load in morphological space when variation is reduced to a single dimension (r = 0.88, P < 0.0001; Table 16), and the plot of such variation in geographical space indicates that both morphs are sympatric (Fig. 14). The *congesta* morph is the only one found south of the Amazon river, while both the *laxa* and *congesta* morphs are found together at several sites along the rio Negro basin. Because of the overlapping distribution of these two morphs, the correlation between morphological distance and geographical distance for *P. coriacea* is weak (Mantel test, r = 0.06, P = 0.042) when compared to all other widespread species, and it increases when the morphs are treated as separate groups (arbitrarily defined by a cutoff value of 3 cm of inflorescence branch length), *congesta* (Mantel test, r 0.142, P = 0.003) and *laxa* (Mantel test, r = 0.1233, P = 0.019). The two morphs do not correlate with features suggesting either dioecy or distyly (Chi-sqr test, P = 0.43) . These patterns may well be suggestive of species differences, because there is morphological difference in sympatry. However, whether these morphs are reproductively isolated remains unclear. Additional information is needed to test the hypothesis that these morphs are two species.

20. ***Pagamea igapoana*** Vicentini, sp. nov. —TYPE: Brazil, São Gabriel da Cachoeira, rio Içana, vila de Jauacanã, na margem do lago atrás da vila, 0° 33' 47” N and 67° 24' 9” W, 27 Jun 2004, FR, *Vicentini 2277* (Holotype: INPA; Isotype: MO).

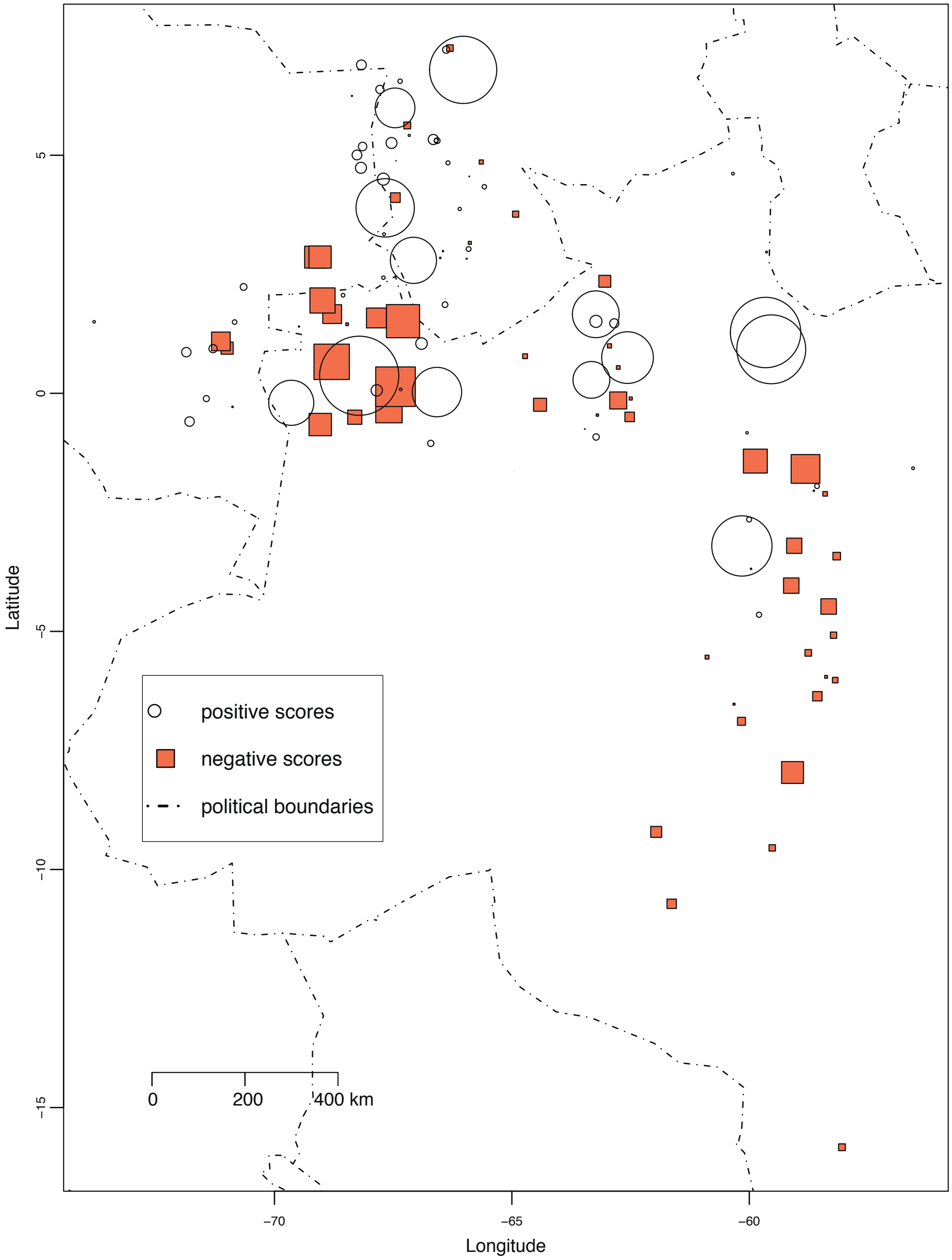

Figure 14. Geographical pattern of morphological variation in *P. coriacea*. Morphology was reduced to a single dimension using non-metric multidimensional scaling. Squares correspond to negative scores (*congesta* morph) and circles to positive scores (*laxa* morph); size of symbols indicate the distance from 0, the largest squares and circles corresponding to the extremes of the variation in the sample. See Table 16 for character correlation with morphological axis. Noise was added to collection coordinates to spread the symbols.

Table 16. *Pagamea coriacea*. Characters significantly correlated (Spearman's rho) with a single axis summarizing morphological variation (Fig. 14; see Table 2 for character descriptions).

Character	**rho**	**P**	**Character**	**rho**	**P**
PETIOLEN - mm	0.385	0	INFLSH1 - ratio	-0.444	0
LFSHAPE2 - ratio	0.349	0	INFLSH2 - ratio	0.74	0
LFSHAPE3 - ratio	0.527	0	CALYXLOB - mm	-0.379	0
DOMADENS - ratio	-0.351	0	CALYXTUB - mm	-0.241	0.009
INFLLEN - mm	0.513	0	CALYXRAT - ratio	-0.273	0.003
INFLBRAN - mm	0.887	0	NFLOWERS - count	0.771	0
INFLNO1 - count	0.652	0	OVARYPUB - score	0.332	0
INFLNO2 - count	0.779	0			

Pagamea igapoana is closely related to *P. coriacea* according nuclear and chloroplast molecular markers. Sympatric populations of these two species are independent clades according to these markers and are morphologically distinct. *P. igapoana* has narrower leaf-blades (lamina-width/height ratio <0.2 *vs*. >0.4), a different venation pattern (brochidodromous with veins straight and perpendicular to the midrib *vs*. eucampdodromous with arching and ascending veins), lacks domatia (vs. with domatia on vein axis), and the inflorescences are shorter, with fewer nodes along the main and secondary axes, and with fewer flowers than those of *P. coriacea*.

Tree 6.9 ± 1.1 (5-8) m tall. *Twigs* 4-5 mm thick. *Stipules* cylindrical, 18-24 mm long, caducous or only the base persistent. *Leaves*: petiole 2.6 ± 0.4 (1.5-3.5) cm long, glabrous; lamina elliptic, coriaceous, 13.6 ± 2.2 (8.3-17.5) x 1.9 ± 0.3 (1-2.5) cm, glabrous on both sides, the margin flat; lacking domatia barbate; midrib glabrous on both surfaces; venation brochidrodromous, with 12 ± 1.9 (7-15) pairs of veins, these glabrous on both sides. *Breeding system* homostylous. *Inflorescences* thyrsoid; peduncle

6.5 ± 1.4 (2.4-8.5) cm long, glabrous; main axis 5.2 ± 1.5 (2.1-8.3) cm long, with 4.5 ± 0.8 (3-6) internodes; secondary axis 1.6 ± 0.8 (0.2-3.3) cm long, with 2.7 ± 0.9 (1-4) internodes; with 34 ± 15.1 (17-83) flowers per inflorescence. *Flower calyces* densely to sparsely puberulent inside and outside, the lobes 0.5 ± 0.3 (0.1-6.2) mm long, and 0.3 ± 0.1 (0.1-0.8) times the length of the calyx tube. *Ovary* glabrous. *Fruits* globose, 5.6 ± 0.4 (4.8-6.2) x 5.4 ± 0.7 (4-6.3) mm.

Distribution and habitat – Known from a single population in the lower Issana river in the Upper Negro river basin. Plants were found in flooded forest, at the border of a lake, at the boundary with non-flooded caatinga forests.

Notes – Recognition of this population as a species makes *Pagamea coriacea* paraphyletic; both species are sympatric at the site where *P. igapoana* was found.
The most strinking difference between the two is leaf shape and venation. *Pagamea igapoana* has narrower leaf-blades than *P. coriacea* (lamina-width/height ratio below 0.2 *vs*. > 0.4). The venation in *P. igapoana* is clearly brochidodromous, with secondary veins straight and almost perpendicular to the midrib, and the venation density is higher than the leaves of *P. coriacea*, which are only rarely completely brochidromous, and have arching and ascending veins (see Table 15 for character differences).

Pagamea igapoana is clearly morphologically and ecologically different to the sympatric population of *P. coriacea*; *P. igapoana* in flooded forest, and *P. coriacea* in non-flooded tall caatinga and in open caatinga. Furthermore, molecular analyses of accessions of *P. igapoana* indicate that it is more closely related to *P. coriacea* from Central Amazon than to the sympatric representatives of *P. coriacea*. Note that two further species may be in *P. coriacea,* and habitat variation may also be correlated with these species (see note under *P. coriacea*; also Chapter 1).

21. ***Pagamea acrensis*** Steyermark*,* Brittonia 33:385, 1981. — TYPE: Brazil. Acre, Cruzeiro do Sul, 10 Feb 1976, *Rosa 706* (Holotype: VEN; Isotype: IAN).

> *Pagamea guianensis* var. *parviflora* Spruce in Mart. ex Progel, Fl. Bras. 6(1):285, 1868. TYPE: Brazil, Amazonas, São Gabriel da Cachoeira, 1852, FL, *Spruce 2260* (!BM, !NY, P).

Shrub or tree 6.3 ± 3.6 (0.6-15) m tall. *Twigs* 2.3 ± 0.2 (2-2.5) mm thick. *Stipules* cylindrical, 7.4 ± 2.3 (4-10) mm long, caducous or only the base persistent. *Leaves*: petiole 0.9 ± 0.3 (0.2-2.2) cm long, densely puberulent or densely strigose, rarely glabrous; lamina elliptic, chartaceous, 5.9 ± 1.3 (2.5-9.2) x 2 ± 0.4 (1-3.1) cm, glabrous on both sides, the margin flat; with 2.7 ± 1.6 (0-6) pairs of domatia; midrib densely or sparsely strigose to puberulent adaxially, usually glabrous abaxially; venation eucamptodromous, veins arching, with 5.8 ± 1.1 (4-9) pairs of veins, these glabrous or nearly so on both sides. *Breeding system* dioecious. *Inflorescences* thyrsoid; peduncle 2.3 ± 0.7 (0.9-5.5) cm long, densely or sparsely strigose to puberulent, rarely glabrous; main axis 1.3 ± 0.5 (0.4-2.6) cm long, with 2.3 ± 0.8 (1-4) internodes; secondary axis 0.1 ± 0.1 (0-0.4) cm long, with 0.6 ± 0.6 (0-2) internodes; staminate plants with 45.5 ± 13.1 (20-84) flowers per inflorescence; pistillate plants with 29.6 ± 10.3 (10-60) flowers per inflorescence. *Flower calyces* glabrous inside and outside, the lobes 0.6 ± 0.2 (0.1-6.8) mm long, and 0.6 ± 0.2 (0.1-1.1) times the length of the calyx tube. *Ovary* glabrous. *Fruits* ellipsoid, 6 ± 0.6 (4.6-6.8) x 4.5 ± 0.4 (3.7-5.3) mm.

Vernacular – Café-bravo (Portuguese), Jigiro (Witoto).

Distribution and habitat – This species is known from two disjunct areas in Western Amazon (Fig. 1): a southern area, corresponding basically to the white-sand savannas and forest in the region of Cruzeiro do Sul, Acre, Brazil; and a northern area, corresponding to the Vaupés and Issana river basins, from Araracuara in Colombia to São Gabriel da Cachoeira in the Upper Rio Negro of Brazil. Plants from the northern area have been collected only in forest habitats that do not flood (Campinarana, Amazon caatinga); those in the southern area have been collected in both forests and open shrublands, these usually associated with periodic flooding.

Notes – This species has been considered to be related to *P. guianensis* because of the venation pattern and distinctive inflorescence, with short (sessile) lateral branches with flowers densely clustered together, the inflorescence appearing interrupted (Steyermark 1981). Plants from the northern area have been considered a variety of *P. guianensis* and usually identified as such. However, molecular data (ITS) indicate that *P. acrensis* is not immediately related to *P. guianensis*, rather suggesting that *P. acrensis* is sister to a paraphyletic *P. coriacea* (Chapter 1, 2; see also under *P. coriacea*). Although this relationship is not strongly supported, it is bounded by two well supported nodes (Fig.

3). Morphologically, *P. acrensis* and *P. coriacea*, which are sympatric in the northern area, cannot be confounded. *P. coriacea* has much larger leaves (9-26 cm vs. 2.5-9 cm long) and larger inflorescences (9-26 cm vs. 0.9-5.5 (-7) cm long) that *P. acrensis* (see also Table 15).

This species has been confounded with *P. guianensis* and *P. sessiliflora,* which have similar sized leaves, and it may be sympatric with these species in the Upper Rio Negro region, but fine-scale co-occurence is unclear. *P. acrensis* can be distinguished from *P. guianensis* by its glabrous ovary (vs. densely hairy) and leaves with inconspicous tertiary venation (vs. highly conspicous). From *P. sessiliflora* it can be distinguished by its much longer pedunculate inflorescences (16-71 vs. 0-1.5 mm long), and much shorter calyx lobes (0.32-0.94 *vs*. 1.7-2.66 mm long).

Morphological distance and geographical distance are highly correlated for this species (Mantel test, $r = 0.35$, $P<0.0001$), the two disjunct areas having substantial morphological differences (Fig. 15, Table 17). Plants from the north have larger leaves than those from the southern (5-8 cm vs. 4-5.5 cm long); the inflorescences are similar in length, but northern plants have fewer internodes along the main axis [1-2(-3) vs 2-4], and shorter lateral axes (0-1.5 mm vs. 1-3 mm) that are usually so reduced that flowers appear clustered on the main axis. Southern plants have more coriaceous leaves than northern plants.

Table 17. *Pagamea acrensis*. Characters significantly correlated (Spearman's rho) with single axis summarizing morphological variation (Fig. 15; see Table 2 for character descriptions).

Character	rho	P
PETIOLEN - mm	-0.521	0.003
LEAFLEN - - mm	-0.798	0
LFSHAPE2 - ratio	0.542	0.002
INFLBRAN - - mm	0.702	0
INFLNO1 - count	0.677	0
INFLNO2 - count	0.613	0
INFLSH1 - ratio	-0.748	0
INFLSH2 - ratio	0.567	0.001

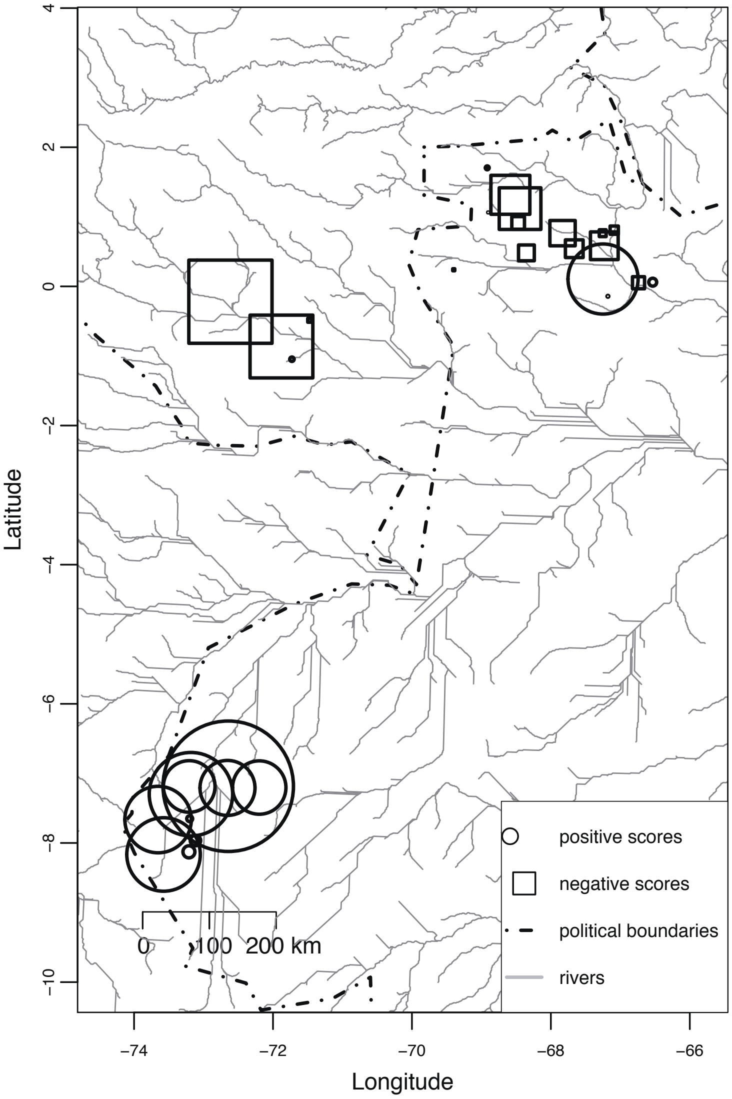

Figure 15. Geographical pattern of morphological variation in *P. acrensis*. Morphology was reduced to a single dimension using non-metric multidimensional scaling. Squares correspond to negative scores and circles to positive scores on this morphological axis; size of symbols indicate the distance from 0, the largest squares and circles corresponding to the extremes of the variation in the sample. See Table 17 for character correlation with this morphological dimension.

Guianensis clade

This clade is the most diverse and widespread, encompassing the range of the genus as a whole and including nine species. All species are dioecious, the flowers are sessile and usually densely clustered, and the calyces have long lobes. The Guianensis clade can be divided into two groups. One including species from Western Amazon (Andes and lowlands of Peru and Colombia), *P. resinosa, P. dudleyi*, *P. macrocarpa*, *P. peruviana,* and *P. sessiliflora* from the upper rio Negro (see Fig. 3). These species form a grade but relationships have no support (Fig. 3), and most species are narrow endemics. The other group corresponds to the Guianensis complex and includes *P. guianensis* itself, *P. occulta*, *P. spruceana* and *P. plicatiformis*. These species are widespread and have a more easterly distribution (Fig. 1).

In the Western Amazon group, the sister species *P. macrocarpa* (25) and *P. dudleyi* (24) are morphologically overlapping, yet they are genetically, ecologically and morphologically distinct where sympatric. A similar pattern of difference in sympatry but overlap when all specimens are considered is found within the Guianensis complex between *P. guianensis* (30) and *P. occulta* (28). Other species in the Guianensis clade are easy to recognize. *Pagamea sessiliflora* (22) is unlike any other species in the genus in having sessile inflorescences that may appear terminal rather than axillary, very small leaves and flowers with long calyces lobes. *Pagamea peruviana* (23) and *P. plicatiformis* (29) have large plicate leaf blades and are morphologically more similar to species in the Plicata clade (17, 18) (see also notes under these species).

22. ***Pagamea sessiliflora*** Spruce ex Benth., Journ. Linn. Soc. 1:110, 1857. —TYPE: VENEZEULA, Amazonas, Rio Negro, Prope San Carlos del Rio Negro, 1° 55' 0” N and 67° 4' 0” W, Mar 1853, FR, *Spruce 3045* (Holotype: !K; Isotypes: !BM, !NY). PLATE 9.

Shrub or tree 3.4 ± 1.6 (1.3-5) m tall. *Twigs* 1.6 ± 0.2 (1.2-1.9) mm thick. *Stipules* cylindrical, 3.1 ± 0.5 (2.2-4) mm long, caducous or only the base persistent. *Leaves*: petiole 0.4 ± 0.1 (0.2-0.7) cm long, sparsely to densely strigose; lamina elliptic, membranaecous, 4.3 ± 1.2 (2-7.3) x 1.3 ± 0.3 (0.7-2.2) cm, glabrous on both sides, rarely sparsely pubescent, the margin flat; with 0.6 ± 1.3 (0-4) pairs of domatia; midrib glabrous or sparsely strigose on both sides; venation eucamptodromous, with 5.3 ± 0.9 (4-7) pairs of veins, these glabrous on both sides, rarely sparsely strigose abaxially. *Breeding system* dioecious. *Inflorescences* forming a many-flowered pseudoterminal head; peduncle 0-0.2 cm long, glabrous or sparsely puberulus; staminate plants with 13.6 ± 10 (3-30) flowers per inflorescence; pistillate plants with 3.1 ± 0 (1-6) flowers per inflorescence. *Flower calyces* glabrous inside and outside, the lobes 2.2 ± 0.4 (1.5-10) mm long, and 1.5 ± 0.4 (0.9-2.5) times the length of the calyx tube. *Ovary* glabrous to sparsely hairy. *Fruits* ellipsoid, 8.7 ± 0.6 (7.5-10) x 6.3 ± 0.8 (5-8) mm.

Distribution and habitat – Endemic to lowlands of the Casiquiare region at the Orinoco and Negro confluence. Known from tall forests, on moist or riverine soils.

Notes – This is one of the easiest species of *Pagamea* to recognize because of its sessile, pseudo-terminal inflorescences, small leaves and flowers with long calyx lobes. No other species of *Pagamea* has this combination of characters. *P. sessiliflora* is sister to *P. peruviana* (see note under *P. peruviana*).

23. ***Pagamea peruviana*** Vicentini, sp. nov. —TYPE: PERU, Loreto, Iquitos, Carretera Iquitos-Nauta, km 31.5, 4° 00' 09” S and 73° 26' 02” W, 29 Feb 2004, FR, *Vicentini 2182* (Holotype: AMAZ; Isotypes: HUT, INPA, MO, USM).

Pagamea peruviana form with *P. sessiliflora* a well-supported clade according to nuclear (ITS) molecular data. *P. peruviana* has much larger leaves (19-32 x 65-130 cm *vs*. 34-68 x 9-17 cm) than those of *P. sessiliflora*, and the inflorescences are longer (4-16 cm *vs*. 0-2 cm), clearly pedunculate and with a well-developed main axis (vs. sessile, or nearly so, without an obvious main axis).

Tree 9.6 ± 4 (2.6-16) m tall. *Twigs* 6-7 mm thick. *Stipules* cylindrical, 20-25 mm long, caducous or only the base persistent. *Leaves*: petiole 3.7 ± 0.8 (1.2-5.4) cm long, glabrous or nearly so; lamina oblancelate to elliptic, chartaceous, 25.5 ± 5.2 (13.8-35.8) x 9.2 ± 2.4 (3.6-13.3) cm, glabrous on both sides to densely strigose abaxially, the margin flat; with 7.6 ± 2.9 (0-12) pairs of domatia, densely strigose to puberulent abaxially, glabrous adaxially; venation eucamptodromous, veins straight, with 10.3 ± 1.3 (7-13) pairs of veins, these densely strigose to puberulent abaxially, glabrous adaxially. *Breeding system* dioecious. *Inflorescences* thyrsoid to subspicate; peduncle 4.5 ± 2.2 (1.8-12.4) cm long, densely strigose; main axis 4.7 ± 1.5 (1.7-11.8) cm long, with 3.2 ± 0.7 (1-5) internodes; secondary axis 1.1 ± 0.5 (0-2.8) cm long, with 1.6 ± 0.6 (0-2) internodes; staminate plants with 99 ± 62 (24-170) flowers per inflorescence; pistillate plants with 69.4 ± 28.5 (26-135) flowers per inflorescence. *Flower calyces* glabrous inside, sparsely to densely puberulent outside, the lobes 1.8 ± 0.7 (0.5-13.5) mm long, and 1.1 ± 0.4 (0.6-2.8) times the length of the calyx tube. *Ovary* sparsely to densely hairy. *Fruits* ellipsoid, 10.7 ± 1 (9-13.5) x 8.3 ± 1 (6-11) mm.

Vernacular – Mishango-caspi (Peru), Namuu-caatío or náamom-cáatiho (Muiname), Pintura de zorra (Spanish), Katio (Muiname), Caimitillo (Huitoto).

Distribution and habitat – Known from the lowlands [90-300 (-500) m] of the Amazon in Peru and Colombia, always in tall forests on white-sand soils.

Notes – *Pagamea peruviana* is sister to *P. sessiliflora* according to molecular data (Chapter 1, Fig. 3). These two species are allopatric but morphologically very different – non-overlapping in several characters (Table 18). On the other hand, *P. peruviana* is similar to the sympatric *P. glabrescens* (17), yet both chloroplast and nuclear markers indicate these are not closely related. Because these species are phylogenetically independent and sympatric, reproductive isolation between them can be inferred. At Iquitos, where individuals of these two species were collected side-by-side, they are indeed difficult to tell apart and have in the past been considered to be the same species.

Pagamea peruviana is distinct from *P. glabrescens* from Central Amazon and Central Brazil, in particular because the inflorescences of the latter have long basal branches. At Iquitos the two species have similar inflorescence structure, with short, almost sessile basal branches, but the calyx lobes of *P. glabrescens* are much smaller than those of *P. peruviana* (Table 18), and the leaves are smaller, narrower, yet with more secondary veins. In the field the two species can be easily recognized by the color of the inner bark, which is reddish in *P. glabrescens* and white in *P. peruviana*. The leaf blades of *P. glabrescens* when dry have conspicuous tertiary venation, while those of *P. peruviana* usually have the tertiary venation inconspicuous. The midrib and veins of *P. peruviana* are densely covered, at least near the apex, by a short strigose indumentum.

Table 18. *Pagamea peruviana*, its sister species *P. sessiliflora* and the morphologically similar *P. glabrescens*. Characters significantly different in mean values (Kruskall-Wallis test, P <=0.01) are shown. Values are mean +/- standard deviation (min-max) averages per specimen (see Table 2 for character descriptions).

Characters	***peruviana***	***glabrescens***	***sessiliflora***
PETIOLEN - mm	35.94 +/- 5.1 (27.33-45)	22.21 +/- 6.01 (10.5-33)	3.88 +/- 1.2 (2.8-6.67)
LEAFLEN - mm	248.39 +/- 40.29 (195.67-314)	148.15 +/- 31.71 (96-220.5)	44.85 +/- 10.34 (34.5-68)
LEAFWID - mm	91.46 +/- 22.04 (65.25-130)	47.25 +/- 11.94 (29.75-76)	12.97 +/- 2.28 (9.48-16.25)
LFSHAPE2 - ratio	0.43 +/- 0.06 (0.32-0.52)	0.37 +/- 0.05 (0.27-0.45)	0.32 +/- 0.03 (0.26-0.36)
LFSHAPE3 - ratio	0.15 +/- 0.02 (0.12-0.18)	0.15 +/- 0.02 (0.11-0.19)	0.09 +/- 0.01 (0.07-0.1)
DOMADENS - ratio	0.76 +/- 0.2 (0.26-0.93)	0.14 +/- 0.3 (0-1)	0.1 +/- 0.11 (0-0.31)
VENADENS - ratio	0.05 +/- 0.01 (0.03-0.06)	0.06 +/- 0.01 (0.03-0.07)	0.13 +/- 0.02 (0.1-0.16)
INFLPEDU - mm	45.06 +/- 19.67 (20-90.5)	58.28 +/- 23.85 (15.5-121)	0.25 +/- 0.5 (0-1.35)
INFLLEN - mm	92.53 +/- 31.35 (44-162)	114.47 +/- 40.13 (49.5-211.5)	0.25 +/- 0.5 (0-1.35)
INFLBRAN - mm	10.81 +/- 5.35 (0.5-21.5)	18.88 +/- 13.15 (0.33-39)	0 +/- 0 (0-0)
INFLNO1 - count	3.24 +/- 0.68 (2-4)	4.88 +/- 1.62 (2.25-7.5)	0 +/- 0 (0-0)
INFLNO2 - count	1.58 +/- 0.61 (0-2)	2.75 +/- 1.35 (0.33-5)	0 +/- 0 (0-0)
INFLSH2 - ratio	0.44 +/- 0.18 (0.05-0.71)	0.6 +/- 0.35 (0.03-1.41)	0 +/- 0 (0-0)
INFLSH3 - ratio	0.45 +/- 0.09 (0.32-0.58)	0.4 +/- 0.1 (0.26-0.59)	0 +/- 0 (0-0)
INFLSH4 - ratio	0.68 +/- 0.23 (0.12-1)	0.59 +/- 0.24 (0.34-1)	1 +/- 0 (1-1)
CALYXLOB - mm	1.8 +/- 0.5 (0.99-2.5)	0.67 +/- 0.23 (0.3-1.12)	2.15 +/- 0.35 (1.7-2.66)
CALYXTUB - mm	1.64 +/- 0.35 (0.98-2.07)	1.14 +/- 0.18 (0.87-1.51)	1.38 +/- 0.26 (0.8-1.62)
CALYXRAT - ratio	1.12 +/- 0.22 (0.67-1.62)	0.59 +/- 0.18 (0.28-0.93)	1.62 +/- 0.36 (1.25-2.17)
NFLOWERS - count	75.54 +/- 35.66 (41.33-165)	166.96 +/- 122.29 (30.33-544)	7.26 +/- 7.56 (2-25)
PETIPUB - score	5.89 +/- 0.54 (4.09-6.04)	5.43 +/- 1.01 (2.56-6.04)	3.38 +/- 0.33 (3.11-4.02)
PUBABAX - score	12.2 +/- 3.32 (3.1-14.41)	9.19 +/- 4.89 (3.1-18.24)	14.76 +/- 2.59 (10.88-18.24)
PUBADAX - score	16.12 +/- 0.33 (15.03-16.21)	15.05 +/- 2.42 (8.87-16.21)	14.71 +/- 0.87 (13.75-15.7)
INFLPUB - score	4.97 +/- 1.41 (3.52-8.47)	4.15 +/- 2.17 (1.05-8.86)	1.34 +/- 0.96 (0-2.19)
OVARYPUB - score	2.02 +/- 1 (0-3.01)	4.32 +/- 1.39 (1.01-5.01)	4.14 +/- 1.24 (2.03-5.01)

24. ***Pagamea dudleyi*** Steyerm., Phytologia 31:226, 1975. —TYPE: PERU, Huánuco, Pucallpa, SW slope of rio Llulla Pichas watershed, Cerros del Sira, 9° 25' 0” S and 74° 42' 0” W, 31 Jul 1969, FL, *Dudley 13543* (Holotype: !NA).

> *Psychotria macbridei* Standl., Field Columbianus, Bot. Ser. 8:68, 1930. —TYPE: PERU, **Junin**,La Merced, hacienda Schunke,1 Sep 1923, FL, *Macbride 5785* (Holotype: !BM).

Shrub or tree 4.4 ± 3.8 (1-14) m tall. *Twigs* 3-4 mm thick. *Stipules* cylindrical, 16.8 ± 0.4 (6-24) mm long, caducous or only the base persistent. *Leaves*: petiole 1.6 ± 0.5 (0.5-2.7) cm long, usually glabrous, rarely sparsely pubescent; lamina elliptic, chartaceous to coriaceous, 11.4 ± 2.4 (6.5-16) x 3.1 ± 0.8 (0.5-5.3) cm, usually glabrous on both sides, or sparsely puberulent to pubescent abaxially, the margin flat; with 5.4 ± 1.9 (0-9) pairs of domatia; midrib usually glabrous on both surfaces, rarely sparsely pubescent abaxially; venation eucamptodromous, veins arching, with 6.7 ± 1.5 (4-10) pairs of veins, these usually glabrous on both sides, rarely sparsely pubescent abaxially. *Breeding system* dioecious. *Inflorescences* thyrsoid to subspicate; peduncle 2.4 ± 0.9 (0.8-4.5) cm long, sparsely to densely pubescent or puberulent; main axis 1.1 ± 0.4 (0.3-2.4) cm long, with 1.4 ± 0.3 (0-2) internodes; secondary axis 0.1 ± 0.2 (0-0.9) cm long, with 0.6 ± 0.4 (0-2) internodes; staminate plants with 37.4 ± 22.1 (15-92) flowers per inflorescence; pistillate plants with 20.6 ± 7 (8-108) flowers per inflorescence. *Flower calyces* glabrous or with erect hairs inside, glabrous to sparsely strigose outside, the lobes 0.8 ± 0.3 (0-1.2) mm long, and 0.7 ± 0.3 (0-1.3) times the length of the calyx tube. *Ovary* sparsely to densely hairy, rarely glabrous. *Fruits* ellipsoid, 8.1 ± 1.4 (5.3-10.2) x

6.5 ± 1 (4.9-8.8) mm.

Vernacular – Tinchi (Shuar)**.**

Distribution and habitat – This species is known from the Andes (from 600-2000 m) and the lowlands of the Chocó region of Colombia. In the Andes, it occurs in both shrublands and montane forests, and in the Chocó region it appears to be associated with riverine systems.

Notes – Molecular data indicate that this species (Andean specimens only; those from the Chocó were not sampled) is sister to *P. macrocarpa* also from the Western Amazon. Although their sister relationship is poorly supported (Fig. 3), the monophyly of each of these species is strongly supported (Chapter 1), and they are sympatric, growing side by side, in northern Peru. These two species are morphologically very similar, but fertile specimens of *P. macrocarpa* are few, and in fruit only, which makes comparison between the two difficult (see Table 19). Both species were found at Cerro Tayu-Muhaji nearby Imacita in northern Peru. At this site *P. macrocarpa* grows in the forest and *P. dudleyi* in the summit shrubland, and *P. macrocarpa* is also found in tall forests in the surrounding lowlands. At Cerro Tayu-Muhaji these species are also different in leaf size and shape (Table 20). *Pagamea dudleyi* is known only from above 1000 m elevation in the Andes, although it is found at low elevations in the Chocó.

25. ***Pagamea macrocarpa*** (Steyerm.) Vicentini, stat. nov. Basionym: *Pagamea* *guianensis* var. *macrocarpa* Steyerm., Mem. N. Y. Bot. Gard 12(3):278, 1965. —TYPE: COLOMBIA, Caquetá, Araracuara, 8 km SE of Tres Esquinas, río Caquetá below río Orteguaza, 0° 43' 0" N and 75° 16' 0" W, 4 Mar 1945, FR, *Little 9533* (Holotype: !NY; Isotypes: !COL, !K, P, !US).

Pagamea macrocarpa is reciprocally monophyletic with *P. dudleyi* according to nuclear (ITS) molecular data. Morphologically, these species can be clearly distinguished only in the region where they are sympatric, in part, because of poor sampling. In region of sympatry, *P. macrocarpa* has much larger leaves (13-20 x 4-6 cm vs. 9-11.5 x 2.2-3.5 cm), with more chartaceous (vs. strongly coriaceous) leaf-blades.

Shrub or tree 8.1 ± 4.7 (4-18) m tall. *Twigs* 3-4 mm thick. *Stipules* cylindrical, 17.5 (10-22) mm long, caducous. *Leaves*: petiole 2.4 ± 0.6 (0.7-3.6) cm long, glabrous; lamina elliptic, membranous to chartaceous, 17.1 ± 3.1 (10-23) x 5.1 ± 0.9 (3.4-7.2) cm, glabrous on both sides, the margin flat; with 4.9 ± 3.1 (0-9) pairs of domatia; midrib densely or sparsely strigose abaxially, glabrous adaxially; venation eucamptodromous, veins arching, with 9.4 ± 1 (7-12) pairs of veins, these densely to sparsely strigose abaxially, glabrous adaxially. *Breeding system* unknown, plants known only in fruit. *Inflorescences* thyrsoid to subspicate; peduncle 1.9 ± 0.3 (1.5-2.6) cm long, sparsely strigose; main axis 0.6 ± 0.1 (0-1) cm long, with 0.7 ± 0.6 (0-1) internodes; secondary axis absent; with 5.2 ± 3.1 (-16) flowers (calyces) per inflorescence. *Flower calyces* glabrous inside and outside, the lobes 0.7 ± 0.3 (0.4-1.2) mm long, and 0.5 ± 0.2 (0.2-

1) times the length of the calyx tube. *Ovary* densely hairy. *Fruits* ellipsoid, 11.1 ± 0.5 (10.3-12) x 8.7 ± 1.1 (7.4-10.5) mm.

Distribution and habitat – Known from the Western Slopes of the Andes in Peru and Colombia; not yet found in Ecuador, but likely there. From lowlands to up to 800 m altitude, always in tall, non-flooded forests.

Notes – This species is sister to *P. dudleyi*; for morphological differences between the two, see Tables 19-20. There are few collections of *P. macrocarpa,* which is known only in fruit. Sympatric *P. dudleyi* is morphologically, molecularly and ecologically distinct (Chapter 1; see note under *P. dudleyi*).

26. ***Pagamea resinosa*** Vicentini, sp. nov. —TYPE: PERU, Loreto, Iquitos, Carretera Iquitos-Nauta, km 22, 3° 54' 52” S and 73° 24' 15” W, 5 Mar 2004, FR, *Vicentini 2192* (Holotype: AMAZ; Isotypes: HUT, INPA, MO, USM).

Pagamea resinosa is monophyletic according to chloroplast markers, and it is more closely related to other species of the Guianensis clade that are also from Western Amazon: *P. peruviana*, *P. macrocarpa*, *P. dudleyi* and *P. occulta*. The leaf-blades of *P. resinosa* are narrower (lamina length/width ratio < 0.24 *vs*. > 0.26) than those of any of its immediate relatives, and have resinous marks when dried (vs. no resinous marks), and also a highly conspicuous tertiary venation that is perpendicular to the midrib and veins (vs. tertiary venation is inconspicuous or reticulate).

Tree 5.8 ± 2.4 (4-10) m tall. *Twigs* 3-5 mm thick. *Stipules* cylindrical, 8-12 mm long, caducous or only the base persistent. *Leaves*: petiole 1.3 ± 0.3 (0.9-2.2) cm long, glabrous; lamina elliptic, membranous, 15.5 ± 2 (11.5-19.3) x 3.1 ± 0.4 (2.1-3.8) cm, glabrous on both sides to sparsely pubescent abaxially, the margin flat; with 2.8 ± 2.8 (0-8) pairs of domatia; midrib glabrous on both surfaces to sparsely pubescent abaxially; venation eucamptodromous, veins arching, with 9.1 ± 1 (7-11) pairs of veins, these glabrous on both sides to sparsely pubescent abaxially. *Breeding system* dioecious. *Inflorescences* thyrsoid; peduncle 2.5 ± 0.8 (0.6-3.9) cm long, densely strigose or puberulent; main axis 1.2 ± 0.9 (-0.5-2.7) cm long, with 1 ± 0 (1-1) internodes; secondary axis 0.2 ± 0.2 (0-0.6) cm long, with 0.6 ± 0.3 (0-1) internodes; staminate plants with 75 (66-84) flowers per inflorescence; pistillate plants with 20.2 (12-35) flowers per inflorescence. *Flower calyces* glabrous inside and outside, the lobes 1.1 ± 0.3 (0.5-8.7) mm long, and 1 ± 0.3 (0.4-1.8) times the length of the calyx tube. *Ovary* glabrous to densely hairy. *Fruits* ellipsoid, 7.8 ± 0.6 (6.6-8.7) x 6 ± 0.5 (4.9-6.9) mm.

Distribution – Known only from white-sand forests along the Iquitos-Nauta road, Peru. Found in tall (25-30) to low (7-8) forests, apparently in secondary and/or more open forests (“monte abierto varillal”).

Notes – *Pagamea resinosa* is a small endemic clade (N=2, 100% bootstrap, chloroplast data only; not shown, see Chapter 1), a member to the Guianensis clade (Fig. 3). *P. resinosa* is morphologically distinct from all other members of the Guianensis clade (Table 21), both sympatric (*P. peruviana*) and growing nearby (*P. occulta* at

Table 19. *Pagamea dudleyi* and *P. macrocarpa.* Characters shown have mean value different at P<0.05 (Wilcox test). Mean +/- standard deviation (min-max) values indicated (see Table 2 for character descriptions).

character	***macrocarpa***	***dudleyi***
LEAFLEN - mm	129 +/- 7.09 (121.33-135.33)	109.08 +/- 16.94 (85.75-142)
LEAFWID - mm	40.11 +/- 2.12 (37.67-41.33)	30.79 +/- 6.02 (20.4-45.33)
INFLLEN - mm	24.36 +/- 1.25 (23.33-25.75)	35.45 +/- 9.85 (23.67-63)
INFLBRAN - - mm	0 +/- 0 (0-0)	1.39 +/- 1.65 (0-6.17)
INFLNO1 - count	0.67 +/- 0.58 (0-1)	1.4 +/- 0.35 (1-2)
INFLNO2 - count	0 +/- 0 (0-0)	0.58 +/- 0.4 (0-1.33)
INFLSH1 - ratio	0.79 +/- 0.01 (0.77-0.8)	0.68 +/- 0.08 (0.51-0.81)
INFLSH2 - ratio	0 +/- 0 (0-0)	0.21 +/- 0.24 (0-0.96)
INFLSH3 - ratio	0.77 +/- 0.09 (0.66-0.83)	0.47 +/- 0.14 (0.22-0.82)
NFLOWERS - count (pistillate plants only)	10.33 +/- 3.06 (7-13)	20.6 +/- 7 (8-108)
INFLPUB - score	2.6 +/- 0.49 (2.12-3.11)	4.16 +/- 0.93 (2.58-5.87)

Table 20. Specimens of *Pagamea dudleyi* and *P. macrocarpa* from the Tayu-Muhaji site (area of sympatry). Vegetative characters having mean values different at P<0.05 (Wilcox test). Mean +/- standard deviation (min-max) values indicated (see Table 2 for character descriptions).

Character	***dudleyi***	***macrocarpa***
LEAFLEN - mm	99.49 +/- 11.04 (89.4-112.8)	170.01 +/- 22.54 (130.33-196.6)
LEAFWID - mm	29.15 +/- 5.4 (22.6-35)	50.93 +/- 5.97 (41.33-59.2)
LFSHAPE3 - ratio	0.17 +/- 0.03 (0.14-0.21)	0.14 +/- 0.02 (0.11-0.16)
RIBTYPAB - score	1.25 +/- 0.5 (1-2)	1.85 +/- 0.24 (1.5-2)
VENTYPAB - score	1.62 +/- 0.48 (1-2)	2 +/- 0 (2-2)

Genaro Herrera and Pacaya-Samiria; and *P. dudleyi* and *P. macrocarpa* in the Andes). Herbarium specimens of *P. resinosa* have leaves with shiny patches of a resinous appearance (hence the epithet). These marks are also present in living plants, in which the stipules are covered by a sticky exudate and the leaves emerge glued to each other. Its leaves are large and narrow and do not overlap in size or shape with the leaves of any of its immediate relatives (Table 21). They also have conspicuous tertiary venation perpendicular to the midrib and veins, while in the other species the tertiary venation

Table 21. *Pagamea resinosa* and close relatives. Character differences between resinosa and each species are shown when the mean value is different at P<0.05 (t-test). Mean +/- standard deviation (min-max) values indicated (see Table 2 for character descriptions).

Character	***resinosa***	***dudleyi***	***macrocarpa***	***occulta***	***peruviana***
PETIOLEN mm	13.228 +/- 2.655 (10-17.2)	–	22.656 +/- 5.501 (14-28)	–	35.937 +/- 5.096 (27.333-45)
LEAFLEN mm	155.203 +/- 9.49 (140.167-165.8)	107.509 +/- 17.956 (85.75-142)	–	92.783 +/- 11.107 (79.3-108.833)	248.391 +/- 40.29 (195.667-314)LEAFLEN
LEAFWID mm	30.678 +/- 2.223 (27.833-34.4)	–	49.728 +/- 6.93 (37.667-59.2)	24.404 +/- 3.57 (20.6-30.33)	91.463 +/- 22.041 (65.25-130)
LFSHAPE1 ratio	0.479 +/- 0.039 (0.43-0.523)	–	–	–	0.564 +/- 0.03 (0.517-0.604)
LFSHAPE2 ratio	0.217 +/- 0.016 (0.197-0.236)	0.336 +/- 0.049 (0.26-0.462)	0.349 +/- 0.016 (0.323-0.38)	0.306 +/- 0.021 (0.27-0.335)	0.427 +/- 0.056 (0.324-0.521)
LFSHAPE3 ratio	0.085 +/- 0.012 (0.069-0.103)	0.141 +/- 0.034 (0.091-0.208)	0.135 +/- 0.017 (0.107-0.157)	0.14 +/- 0.02 (0.106-0.18)	0.145 +/- 0.018 (0.117-0.18)
DOMADENS ratio	0.289 +/- 0.288 (0-0.69)	0.833 +/- 0.197 (0.256-1)	–	–	0.762 +/- 0.197 (0.263-0.926)
VENADENS ratio	0.059 +/- 0.012 (0.04-0.073)	–	–	0.075 +/- 0.018 (0.031-0.09)	–
INFLPEDU cm	25.028 +/- 5.602 (16-31)	–	–	–	45.064 +/- 19.672 (20-90.5)
INFLLEN cm	37.292 +/- 9.462 (23.25-48.5)	–	–	–	92.526 +/- 31.353 (44-162)
INFLBRAN cm	1.882 +/- 1.939 (0.125-4.667)	–	–	–	10.814 +/- 5.353 (0.5-21.5)
INFLNO1 count	1 +/- 0 (1-1)	1.388 +/- 0.337 (1-2)	–	–	3.244 +/- 0.679 (2-4)
INFLNO2 count	0.597 +/- 0.343 (0.25-1)	–	–	–	1.577 +/- 0.607 (0-2)
INFLSH1 ratio	0.685 +/- 0.169 (0.502-0.929)	–	–	–	0.485 +/- 0.092 (0.335-0.604)
INFLSH2 ratio	0.218 +/- 0.148 (0.028-0.405)	–	–	–	0.436 +/- 0.177 (0.048-0.709)
CALYXLOB mm	1.122 +/- 0.268 (0.725-1.429)	0.854 +/- 0.22 (0.545-1.175)	–	0.681 +/- 0.09 (0.58-0.886)	1.798 +/- 0.499 (0.988-2.5)
CALYXTUB mm	1.185 +/- 0.145 (1.025-1.4)	–	–	–	1.635 +/- 0.347 (0.975-2.067)
CALYXRAT ratio	0.961 +/- 0.184 (0.705-1.127)	0.668 +/- 0.124 (0.431-0.844)	–	0.71 +/- 0.113 (0.543-0.864)	–
NFLOWERS count	30.097 +/- 22.428 (17.25-75)	–	–	–	75.538 +/- 35.661 (41.333-165)
PETIPUB pcoA score	6.035 +/- 0 (6.035-6.035)	–	4.778 +/- 0.355 (4.527-5.029)	2.181 +/- 1.351 (1.008-5.029)	–
PUBABAX pcoA score	6.31 +/- 1.866 (3.856-9.485)	–	1.434 +/- 0.907 (0-3.072)	–	–

is usually inconspicuous (but see *P. guianensis*), at least in dried specimens, and there are no resinous marks. Inflorescence and fruit characters distinguish *P. resinosa* from all species but *P. macrocarpa* (Table 21), although variation in these characters are poorly understood in either: *P. resinosa* is known from six fruiting specimens and *P. macrocarpa* from three fruiting collections. However, the fruits of *P. macrocarpa* are larger, ca. 10-12 x 7-10 mm vs. 7-8 x 5-6 mm in *P. resinosa*.

27. ***Pagamea spruceana*** Vicentini, sp. nov. —TYPE: Brazil, Amazonas, São Gabriel da Cachoeira, rio Içana, Jauacanã, 0° 23' N and 67° 33' W, 2 Nov 1987, FL, *Farney 1859* (Holotype: INPA; Isotype: MO).

Pagamea spruceana is closely related to *P. occulta* according to molecular data. *Pagamea spruceana* has capitate inflorescences (vs. thyrsoid), leaf-blades with strongly revolute margins (vs. flat or nearly so) and a densely pubescent ovary (vs. glabrous or sparsely pubescent), unlike *P. occulta* (Table 22), in particular *P. occulta* collected nearby.

Tree 4 ± 1.7 (3-6) m tall. *Twigs* 4 ± 0.4 (3.8-4.5) mm thick. *Stipules* cylindrical, 9.2 ± 3.1 (5-13) mm long, caducous or only the base persistent. *Leaves*: petiole 1.3 ± 0.4 (0.6-2) cm long, glabrous to densely strigose; lamina elliptic, chartaceous, 8.4 ± 2 (5-12.7) x 2.3 ± 0.6 (1.1-3.7) cm, glabrous on both sides, the margin strongly revolute; with 0.8 ± 1.6 (0-6) pairs of domatia; midrib densely strigose abaxially, glabrous adaxially; venation eucamptodromous, veins arching, with 5.3 ± 0.9 (4-7) pairs of veins, these densely puberulent abaxially, glabrous adaxially. *Breeding system* dioecious. *Inflorescences* capitate; peduncle 3.8 ± 0.8 (2-5.1) cm long, densely minutely puberulent; main axis 0.5 ± 0.3 (0.2-1) cm long, with 0.9 ± 0.2 (0-1) internodes; secondary axis absent; staminate plants with 34.6 (30-40) flowers per inflorescence; pistillate plants with 26.6 (15-50) flowers per inflorescence. *Flower calyces* glabrous or nearly so inside and outside, the lobes 0.9 ± 0.4 (0.3-8.7) mm long, and 0.8 ± 0.3 (0.3-1.5) times the length of the calyx tube. *Ovary* densely hairy. *Fruits* ellipsoid, 7.1 ± 1.5 (5.2-8.7) x 5 ± 0.7 (4.2-5.6) mm.

Distribution and habitat – This species is known from the Issana river in the Upper Rio Negro region. It occurs in open vegetation that is deeply flooded ("lake habitat"; see Ferreira 1997, 2000).

Notes – *Pagamea spruceana* makes *P. occulta* paraphyletic (Fig. 3), although resolution and support for relationships within the Guianensis complex (see note in *P. guianensis*) are low and alternative relationships are not rejected (Chapter 1). *Pagamea spruceana* is sympatric with *P. occulta*, but molecular data suggest that it is more closely related to an accession of *P. occulta* from the southern part of the Amazon region ca. 1000 km away (an island in the Madeira river near Porto Velho) than to accessions collected at nearby locations. *Pagamea spruceana* is still poorly known, but it has capitate inflorescences, strongly revolute leaf margins and a densely pubescent ovary, unlike *P. occulta*, in particular *P. occulta* collected nearby (Table 22). *Pagamea occulta* from the Upper Rio Negro region also prefers highly flooded habitats, but usually grows in tall forests, while

P. spruceana occurs in open lake or low igapó forest.

Specimens of *P. spruceana* have been identified as *P. capitata*, which is phylogenetically distantly placed but morphologically similar. The two species differ significantly in mean values of vegetative, inflorescence and flower characters (Table 22). *Pagamea capitata* has ovate (vs. elliptic) leaf blades, shorter inflorescences and longer calyces lobes than those of *P. spruceana*. Although both species are found in the Issana basin,

Table 22. *Pagamea spruceana* comparisons. Character differences between *spruceana* and *occulta,* the latter paraphyletic in relation to the former (see Fig. 3), and the morphologically similar but distantly related *P. capitata.* Values shown only when the mean was different at P<0.05 (two-tailed t-test). Mean +/- standard deviation (min-max) values indicated. See Table 2 for character descriptions.

Characters	***spruceana***	***occulta***	***Capitata***
PETIOLEN - mm	11.07 +/- 3.30 (7.2-15.25)	16.13 +/- 3.26 (10.6-26)	n.s.
LEAFWID - mm	22.61 +/- 6.99 (16.8-31.75)	30.91 +/- 6.2 (19.6-46.5)	n.s.
LFSHAPE1 - ratio	0.47 +/- 0.05 (0.41-0.52)	n.s.	0.36 +/- 0.05 (0.22-0.53)
LFSHAPE2 - ratio	0.312 +/- 0.05 (0.24-0.34)	0.37 +/- 0.05 (0.27-0.50)	n.s.
LFSHAPE3 - ratio	0.135 +/- 0.01 (0.12-0.15)	0.163 +/- 0.027 (0.11-0.23)	n.s.
VENADENS - ratio	0.067 +/- 0.01 (0.05-0.07)	n.s.	0.11 +/- 0.02 (0.07-0.17)
REVPROP - ratio	0.034 +/- 0.068 (0-0.137)	0 +/- 0.001 (0-0.00)	n.s.
INFLPEDU - mm	37.317 +/- 6.996 (30-43.5)	n.s.	18.84 +/- 10.13 (4.07-41)
INFLLEN - mm	42.8 +/- 8.543 (33.667-53)	n.s.	21.78 +/- 11.69 (4.6-48.5)
INFLBRAN - mm	0 +/- 0 (0-0)	2.08 +/- 2.21 (0-10.5)	0.79 +/- 0.84 (0-3.75)
INFLNO1 - count	0.917 +/- 0.167 (0.667-1)	2.03 +/- 0.73 (0-3.67)	n.s.
INFLNO2 - count	0 +/- 0 (0-0)	0.84 +/- 0.54 (0-2)	0.51 +/- 0.43 (0-1)
INFLSH1 - ratio	0.87 +/- 0.05 (0.82-0.93)	0.69 +/- 0.10 (0.4-0.86)	n.s.
INFLSH2 - ratio	0 +/- 0 (0-0)	0.18 +/- 0.16 (0-0.59)	0.35 +/- 0.43 (0-2.5)
INFLSH3 - ratio	0.562 +/- 0.272 (0.28-0.81)	n.s.	0.345 +/- 0.34 (0-2.5)
CALYXLOB - mm	1.01 +/- 0.26 (0.76-1.3)	n.s.	1.50 +/- 0.41 (0.65-2.47)
CALYXRAT - ratio	0.82 +/- 0.17 (0.67-1.07)	n.s.	1.27 +/- 0.34 (0.59-1.97)
NFLOWERS - count	29.19 +/- 11.86 (15.33-42.5)	n.s.	12.85 +/- 5.49 (3-33)
PETIPUB - score	3.7 +/- 0.91 (3.113-5.029)	n.s.	1.77 +/- 0.85 (1.01-4.53)
PUBADAX - score	14.97 +/- 1.18 (13.75-16.21)	15.70 +/- 1.41 (8.31-16.2)	n.s.
INFLPUB - score	4.36 +/- 1.743 (3.11-6.93)	n.s.	8.26 +/- 1.46 (3.11-9.611)
OVARYPUB - score	2.01 +/- 2.00 (1.01-5.01)	3.82 +/- 1.50 (0-5.01)	n.s.

P. capitata occurs in much drier habitats, being found in the shrublands of the Serra do Tunuhy.

28. ***Pagamea occulta*** Vicentini, sp. nov. —TYPE: Brazil, Amazonas, São Gabriel da Cachoeira, rio Negro, 1 hour upstream by motorboat from mouth of rio Xié, behind Indian village fo Campina, 0° 57' N and 67° 11' W, 25 Oct 1987, FL, *Maas 6861* (Holotype: INPA (2 specimens); Isotypes: MO). PLATES 5-6.

Pagamea occulta is morphologically overlapping with, and closely related to *P. guianensis*. These species can be clearly distinguished only where their ranges overlap, in Central Amazon: the leaf-blades of *P. occulta* are larger [9 (7-15) x (2-) 2.8-4.5 cm *vs*. 8 (-10) x 2.5 (-2.8) cm]; the petiole is much shorter [1.5-2.5 cm *vs*. 0.5-1(-1.5) cm] and glabrous or nearly so (*vs*. densely strigose); higher-order venation is inconspicuous (*vs*. highly conspicuous); secondary veins and midrib are glabrous or nearly so (*vs*. densely strigose); the ovary is glabrous (*vs*. densely pubescent); and, *Pagamea occulta* is found in flooded forests, while *P. guianensis* occurs in non-flooded forests.

Shrub or tree 5.3 ± 3.1 (1.2-14) m tall. *Twigs* 4 ± 1 (2.6-6.5) mm thick. *Stipules* cylindrical, 8.1 ± 4.6 (2-17) mm long, caducous or only the base persistent. *Leaves*: petiole 1.6 ± 0.5 (0.6-3.8) cm long, glabrous to densely strigose or pubescent; lamina elliptic, usually membranous, 10 ± 2.2 (4.8-18) x 3.1 ± 0.8 (1-6) cm, usually glabrous on both sides, to sparsely pubescent abaxially, the margin flat; with 3 ± 2.2 (0-8) pairs of domatia; midrib glabrous adaxially, glabrous to densely pubescent abaxially; venation eucamptodromous, veins arching, with 6.1 ± 1.1 (3-10) pairs of veins, these glabrous adaxially, glabrous to densely strigose or pubescent abaxially. *Breeding system* dioecious. *Inflorescences* thyrsoid; peduncle 4.1 ± 1.7 (0.6-11.6) cm long, sparsely to densely strigose or pubescent, rarely glabrous; main axis 1.8 ± 0.8 (0.1-4.4) cm long, with 2 ± 0.7 (0-5) internodes; secondary axis 0.2 ± 0.2 (0-1.1) cm long, with 0.9 ± 0.5 (0-2) internodes; staminate plants with 72.4 ± 39.6 (15-240) flowers per inflorescence; pistillate plants with 31.5 ± 23.6 (9-105) flowers per inflorescence. *Flower calyces* glabrous inside, glabrous to sparsely puberulent outside, the lobes 0.9 ± 0.3 (0.2-8.5) mm long, and 0.9 ± 0.3 (0.1-2.7) times the length of the calyx tube. *Ovary* glabrous to densely hairy. *Fruits* ellipsoid, 6.8 ± 1.2 (4.4-8.5) x 5.2 ± 1 (4-7.2) mm.

Vernacular – Ají-de-paloma (Spanish), Caatêe (Miraña), Caimo-de-monte (Spanish), Bajimisesee (Muiname), Amu-i-yu-ai, Maogua (Miraña), Jipicona (Witoto).

Distribution and habitat – Western and Central Amazon basin, and along the middle to upper Orinoco basin, with an eastern limit in Central Amazon along the Madeira and Negro rivers, always in the lowlands. In the Negro, Orinoco and Madeira rivers in flooded habitats or gallery forests, in Peru in the understory of tall non-flooded *varillal* and in flooded habitats.

Notes – *Pagamea occulta* is paraphyletic in relation to *P. spruceana*, but these species are largely sympatric, and they differ in morphology, ecology and genetically (see under *P. spruceana*). Within *P. occulta* there is a strong relationship between pairwise morphological and geographical distances (Mantel test, r 0.386, P < 0.001), with a major morphological difference between the northern and southern margins of the Amazon river (Fig. 16 and 17).

Table 23. *Pagamea occulta*. Characters significantly correlated (Spearman's rho) with a single axis summarizing morphological variation (Fig. 16; see Table 2 for character descriptions).

Character	**rho**	**P**
INFLLEN - mm	0.79	0
INFLNO2 - count	0.695	0
INFLBRAN - mm	0.663	0
INFLPEDU - mm	0.656	0
PETIPUB - score	0.6	0
INFLNO1 - count	0.57	0
INFLSH2 - ratio	0.565	0
INFLSH4 - ratio	-0.554	0
NFLOWERS - count	0.547	0
PETIOLEN - mm	0.539	0
LEAFLEN - mm	0.473	0
LEAFWID - mm	0.454	0
OVARYPUB - score	0.435	0
INFLPUB - score	-0.429	0
INFLSH3 - ratio	0.421	0
PUBABAX - score	0.406	0

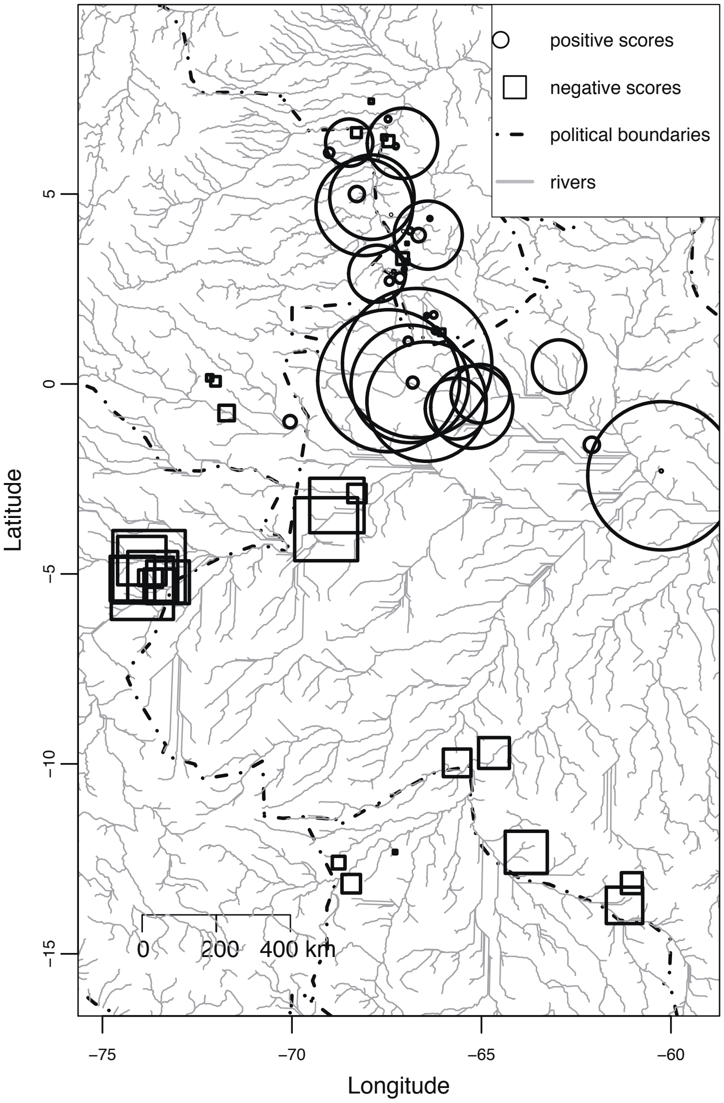

Figure 16. Geographical pattern of morphological variation in *P. occulta*. Morphology was reduced to a single dimension using non-metric multidimensional scaling. Squares correspond to negative scores and circles to positive scores; size of symbols indicate the distance from 0, the largest squares and circles corresponding to the extremes of the variation in the sample. See Table 23 for character correlation with morphological axis.

Pagamea occulta is sister to *P. guianensis*+*P. plicatiformis* (Fig. 3), and it is sympatric to and morphologically distinct from both these species in Central Amazon (Chapter 1). *P. occulta* overlaps in morphological space with *P. guianensis*, from which it can be distinguished easily only in Central Amazon where their ranges overlap (Fig. 17). In the Rio Negro basin, sympatric accessions of *P. occulta* and *P. guianensis*, are genetically, ecologically and morphologically distinct. On the other hand, accessions of

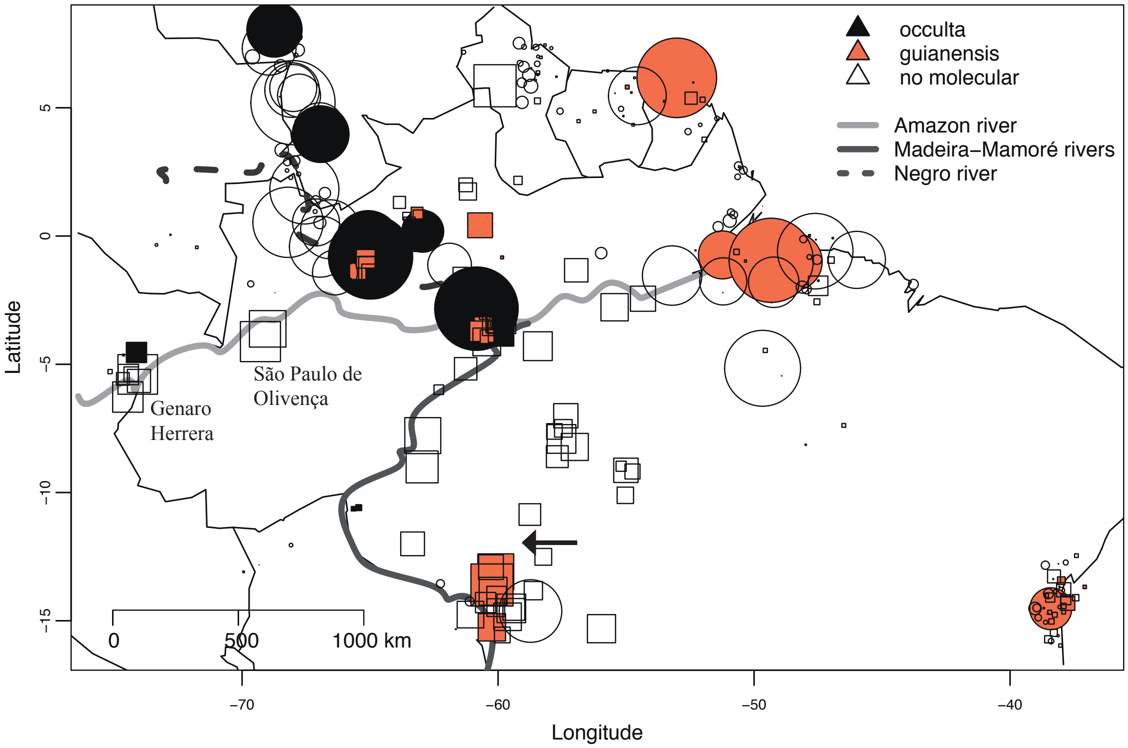

Figure 17. Morphological variation of *P. occulta* and *P. guianensis.* Morphology was reduced to a single dimension using non-metric multidimensional scaling. Squares correspond to negative scores and circles to positive scores; size of symbols indicate the distance from 0, the largest squares and circles corresponding to the extremes of the variation in the sample. Color of symbols indicate sampling for molecular data (summarized in Fig. 3). Note that in Central Amazon, along the Rio Negro, the two clades (colors) are morphologically distinct (circles *vs*. squares), while samples of *P. guianensis* from the Atlantic coast are morphogically more similar to *P. occulta* from Central Amazon (circles). Arrow indicates accessions falling in the *occulta* clade. Noise was added to geographical coordinates for spreading symbols. See Table 24 for character correlations.

the *P. occulta* clade from Western Amazon (Genaro Herrera) are morphologically more similar to *P. guianensis* from Central Amazon (squares in Fig. 17), while specimens of *P. occulta* from the Rio Negro basin are morphologically more similar to *P. guianensis* from the Atlantic coast region (circles in Fig. 17). Although plants of both clades have been sampled along the Madeira-Mamoré rivers, the morphological distinction between the two species are less clear in this southern region (Fig. 17). There, it is still unclear whether the two species co-occur, or whether the Madeira-Mamoré is a geographical barrier separating the two. Additional sampling along both sides of these rivers is needed for understanding the level of reproductive isolation, or lack thereof, between the southern populations of these species.

Table 24. *Pagamea occulta* and *Pagamea guianensis*. Characters significantly correlated (Spearman's rho) with a single axis summarizing morphological variation for these two species combined (Fig. 17; see Table 2 for character descriptions).

Character	rho	P	Character	rho	P
INFLLEN - mm	0.73	0.000	INFLSH2 - ratio	0.41	0.000
PETIPUB - score	0.68	0.000	VENADENS - ratio	-0.39	0.000
INFLPEDU - mm	0.66	0.000	INFLPUB - score	-0.38	0.000
PUBADAX - score	0.61	0.000	LFSHAPE3 - ratio	0.37	0.000
PUBABAX - score	0.61	0.000	NFLOWERS - count	0.34	0.000
INFLNO1 - count	0.55	0.000	LFSHAPE2 - ratio	0.3	0.000
PETIOLEN - mm	0.54	0.000	LFSHAPE1 - ratio	0.3	0.000
OVARYPUB - score	0.54	0.000	CALXYPUB - score	0.24	0.000
LEAFWID - mm	0.53	0.000	CALYXRAT - ratio	0.23	0.000
LEAFLEN - mm	0.49	0.000	CALYXLOB - mm	0.22	0.000
INFLBRAN - mm	0.49	0.000	INFLSH1 - ratio	-0.16	0.011
INFLNO2 - count	0.47	0.000	INFLSH3 - ratio	0.15	0.016
INFLSH4 - ratio	-0.43	0.000			

In the Rio Negro basin, *P. guianensis* and *P. occulta* can be distinguished as follows: the leaf blades of *P. guianensis* are smaller (8 (-10) x 2.5 (-2.8) cm vs. 9 (7-15) x (2-) 2.8-4.5 cm in *P. occulta*); the petiole in *P. guianensis* is much shorter [0.5-1(-1.5) vs. 1.5-2.5 cm] and densely strigose (vs. glabrous or sparsely pubescent); higher-order venation is highly conspicuous in the thin, dried leaves of *P. guianensis*, while in *P. occulta* higher-order venation is inconspicuous and the leaves are thicker; the secondary veins and midrib are densely strigose in *P. guianensis*, in particular towards the leaf apex, and glabrous or nearly so in *P. occulta*; the ovary is also densely pubescent in *P. guianensis* and usually glabrous in *P. occulta*. In the middle and lower Rio Negro basin, at least, *P. occulta* is also found in flooded forests (igapó, chavascal), while *P. guianensis* occurs in non-flooded forests (campina, campinarana; see Chapter 2). *Pagamea occulta* from Western Amazon (Genero Herrera, São Paulo de Olivença) is more similar in leaf characters to *P. guianensis* from Central Amazon (squares in Fig. 17), but it may still be distinguished by its short (sub-) capitate inflorescences that are never found in *P. guianensis*.

Pagamea occulta and *P. guianensis*, as here circumscribed, form two separate clades which are morphologically distinct, particularly where their ranges overlap. This pattern indicates some level of reproductive isolation between them. The boundaries between these species are still unclear. Both these species are polyphyletic according to chloroplast data, which is consistent with a pattern of retention of ancestral polymorphisms in each of these species at different geographical localities (Chapter

1 and 2). Although both species may be monophyletic according to ITS data (Chapter 1), support and molecular variation is still low. Because these species are also morphologically overlapping, a population level sampling is need to help clarify the history of this complex and the extend of reproductive isolation within the Guianensis complex as a whole. The fact that *P. guianensis* and *P. occulta* are morphologically and ecologically distinct in the region of sympatry, but allopatric specimens are overlapping, further suggests character displacement with secondary contact (Central Amazon) following divergence in allopatry. Therefore, the Guianensis complex represents an interesting case for studying speciation because its species are in the early stages of divergence.

29. ***Pagamea plicatiformis*** Steyerm., Mem. N. Y. Bot. Gard. 12(3):274, 1965. —TYPE: VENEZUELA, Amazonas, Maroa, 2° 44' 11" N and 67° 33' 45" W, 9 Feb 1942, *Williams 14190* (Holotype: !F; Isotypes: !US, !VEN).

Shrub or tree 3.1 ± 2.3 (0.3-7.5) m tall. *Twigs* 2.7 ± 1.2 (0.3-4.2) mm thick. *Stipules* cylindrical, 13.8 ± 5.4 (4-24) mm long, caducous or only the base persistent. *Leaves*: petiole 1.4 ± 0.6 (0.6-2.5) cm long, densely strigose to pubescent; lamina elliptic, chartaceous to coriaceous, 11.3 ± 3.6 (4.6-19) x 3 ± 0.9 (1.5-4.7) cm, sparsely to densely pubescent abaxially, usually glabrous adaxially, the margin flat to slightly revolute; lacking domatia; midrib sparsely to densely pubescent on both sides; venation eucamptodromous, veins arching, with 7.7 ± 1.6 (4-11) pairs of veins, these sparsely to densely pubescent on both sides. *Breeding system* dioecious. *Inflorescences* thyrsoid; peduncle 2.6 ± 1.2 (0.4-5.1) cm long, densely puberulent or pubescent; main axis 1.4 ± 0.5 (0-2.3) cm long, with 1.6 ± 0.6 (0-3) internodes; secondary axis 0.1 ± 0.1 (0-0.4) cm long, with 0.6 ± 0.6 (0-2) internodes; staminate plants with 84.1 ± 27.2 (48-120) flowers per inflorescence; pistillate plants with 44 ± 15.2 (9-110) flowers per inflorescence. *Flower calyces* glabrous inside, sparsely pubescent outside, the lobes 1.2 ± 0.3 (0.5-9) mm long, and 1 ± 0.3 (0.3-2.3) times the length of the calyx tube. *Ovary* densely hairy. *Fruits* ellipsoid, 6.6 ± 1.5 (4.2-9) x 5 ± 0.9 (3.7-7) mm.

Distribution and habitat –Known from two disjunct areas (Fig. 1), one in the lower rio Negro basin, close to Manaus, the other in the upper Orinoco river around the Casiquiare channel. Lowlands, in low caating forests and riverine forests, dry or flooded habitats.

Notes – This species can be easly distinguished from other members of the Guianensis clade by its pubescent leaves, with veins on the adaxial surface covered by hairs. The leaves are plicate- or bullate-like, and have a similar texture and appearance to *P. duckei* (see note under *P. duckei*).

Morphological variation in *P. plicatiformis* is only weakly correlated with geography (Mantel test, r = 0.23, P = 0.02; Fig. 18), with the northern collections having longer inflorescences with longer peduncles and longer lateral branches, and flower calyxes with longer lobes than southern collections (Fig. 18 and Table 25).

Table 25. *Pagamea plicatiformis*. Characters significantly correlated (Spearman's rho) with a single axis summarizing morphological variation (Fig. 18; see Table 2 for character descriptions).

Character	rho	P
INFLBRAN - mm	-0.856	0
INFLNO2 - count	-0.812	0
INFLNO1 - count	-0.8	0.001
INFLSH2 - ratio	-0.784	0.001
LFSHAPE2 - ratio	-0.609	0.024
PUBADAX - score	-0.59	0.026

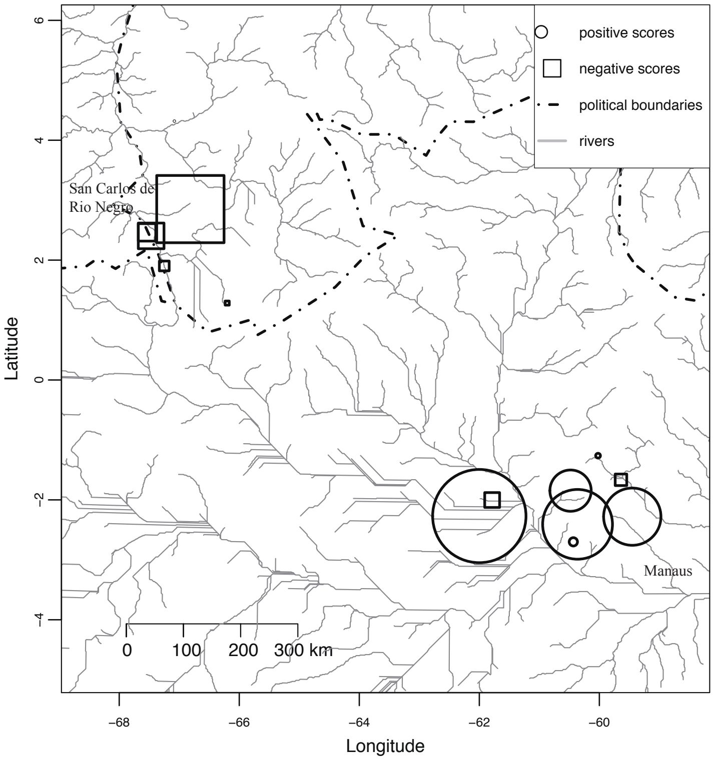

Figure 18. Geographical pattern of morphological variation in *P. plicatiformis*. Morphology was reduced to a single dimension using non-metric multidimensional scaling. Squares correspond to negative scores and circles to positive scores; size of symbols indicate the distance from 0, the largest squares and circles corresponding to the extremes of the variation in the sample. See Table 25 for character correlation with this morphological axis.

30. ***Pagamea guianensis*** Aubl., Hist. Pl. Guiane 113, pl. 44, 1775. —TYPE: GUYANE FRANÇAISE, sommet de la montagne Serpent, à l'habitation appellée Gallion, FL-old, *Aublet* (Holotype: !BM).

Shrub or tree 2.7 ± 1.7 (0.6-12) m tall. *Twigs* 2.2 ± 0.5 (1.5-4) mm thick. *Stipules* cylindrical, 8.2 ± 4.7 (2.9-28.2) mm long, caducous or only the base persistent. *Leaves*: petiole 1.1 ± 0.4 (0.3-2.5) cm long, glabrous to densely strigose or pubescent; lamina elliptic, membranous to chartaceous, 8 ± 1.8 (3.5-17.4) x 2.2 ± 0.6 (0.7-8) cm, glabrous or nearly so on both sides, the margin flat; with 3.7 ± 1.8 (0-8) pairs of domatia; midrib usually glabrous, to densely strigose on both surfaces; venation eucamptodromous, veins arching, with 6.4 ± 1.3 (4-11) pairs of veins, these usually glabrous on both sides, to densely strigose abaxially. *Breeding system* dioecious. *Inflorescences* thyrsoid; peduncle 3 ± 1 (0.5-7.5) cm long, densely to sparsely strigose, puberulent or pubescent, rarely glabrous; main axis 1.7 ± 0.8 (0.3-5.7) cm long, with 2.1 ± 0.8 (0-6) internodes; secondary axis 0.2 ± 0.3 (0-3) cm long, with 0.8 ± 0.7 (0-4) internodes; staminate plants with 77.3 ± 32.3 (12-192) flowers per inflorescence; pistillate plants with 26.5 ± 17.4 (5-108) flowers per inflorescence. *Flower calyces* usually glabrous, or sparsely hairy outside, the lobes 0.7 ± 0.3 (0-7.2) mm long, and 0.7 ± 0.3 (0-2) times the length of the calyx tube. *Ovary* glabrous to densely hairy. *Fruits* globose, 5.6 ± 0.7 (4.3-7.2) x 5 ± 1 (3-6.8) mm.

Vernacular – Canela-de-véu (Portuguese), Olho-de-pomba (Portuguese).

Distribution – Throughout the Atlantic Coast of tropical South America, from Guiana to Espírito Santo in Brazil, although absent in the drier areas of the horn of Brazil, and inland to the Central Amazon up to the rio Maderia and rio Negro . Lowlands, but up to 600 m elevation in the southern part of the Amazon basin (Chapada dos Parecis and Serra do Cachimbo).

Notes – The name *P. guianensis* has been broadly applied to specimens that are treated here as different species: *P. guianensis*, *P. occulta*, *P. resinosa*, *P. dudleyi*, *P. macrocarpa*, *P. puberula*, *P. acrensis* and even the distantly related *P. bahiana* (see also notes for these species). *Pagamea guianensis* forms with three additional species the Guianensis complex, a moderately supported clade (Fig. 3). *Pagamea guianensis* is sympatric to, and morphologically and/geneticalically distinct from the three other species in the Guianensis complex. *Pagamea guianensis* is more similar to *P. occulta*, and there is indeed great overlap in morphological space between the two, but only when geography is ignored (Fig. 17; see discussion under *P. occulta*). Within *P. guianensis* there is a significant relationship between pairwise morphological and geographical distances (Mantel test, r 0.16, P < 0.001), with a major morphological difference between populations from the Atlantic coast (which are also monophyletic according to ITS data; see Chapter 1), and those of Central Amazon (Fig. 19; Table 26).

Table 26. *Pagamea guianensis*. Characters significantly correlated (Spearman's rho) with a single axis summarizing morphological variation (Fig. 19; see Table 2 for character descriptions).

Character	rho	P			
INFLLEN - mm	0.702	0	PETIOLEN - mm	0.447	0
INFLNO1 - count	0.676	0	NFLOWERS - count	0.436	0
PUBABAX -score	0.659	0	LEAFWID - mm	0.417	0
INFLSH4 - ratio	-0.653	0	INFLPUB -score	-0.412	0
PUBADAX -score	0.652	0	INFLSH1 - ratio	-0.403	0
INFLBRAN - mm	0.592	0	VENADENS - ratio	-0.39	0
OVARYPUB -score	0.58	0	LEAFLEN - mm	0.37	0
PETIPUB -score	0.577	0	LFSHAPE1 - ratio	0.298	0
INFLPEDU - mm	0.571	0	LFSHAPE3 - ratio	0.27	0
INFLNO2 - count	0.528	0	LFSHAPE2 - ratio	0.196	0.007
INFLSH2 - ratio	0.528	0			

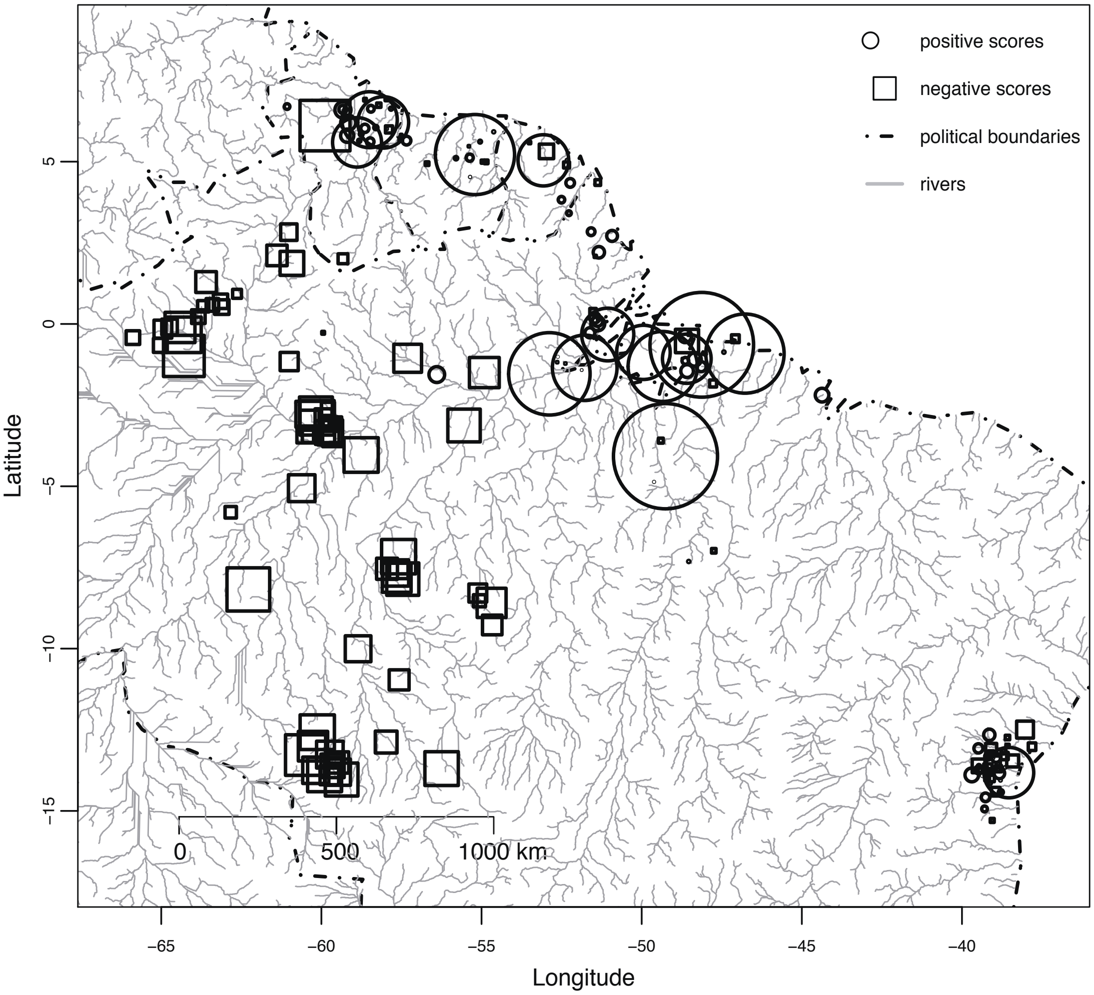

Figure 19. Geographical pattern of morphological variation in *P. guianensis*. Morphology was reduced to a single dimension using non-metric multidimensional scaling. Squares correspond to negative scores and circles to positive scores; size of symbols indicate the distance from 0, the largest squares and circles corresponding to the extremes of the variation in the sample. See Table 26 for character correlation with morphological axis.

Unplaced

31. ***Pagamea diceras*** Steyerm., Mem. N. Y. Bot. Gard 12(3):281, 1965. —TYPE: VENEZUELA, Amazonas, Manapiare, Serrania Parú, río Parú, Caño Asisa, 4° 30' 32" N and 65˚48' 0" W, 4 Feb 1951, FL-bud, *Cowan 31241* (Holotype: !NY; Isotypes: !K, !US, !VEN). PLATE 2.

Shrub or tree 3 ± 1.4 (2-4) m tall. *Twigs* 3 ± 1 (1.6-4.8) mm thick. *Stipules* , 8.8 ± 3.6 (5.2-18) mm long, caducous or only the base persistent. *Leaves*: petiole 0.4 ± 0.1 (0.3-0.6) cm long, glabrous; lamina elliptic, coriaceous, 4 ± 0.9 (2.5-5.2) x 1.5 ± 0.3 (1-2) cm, glabrous, the margin slightly revolute; lacking domatia; midrib glabrous; venation eucamptodromous, veins arching, with 5.7 ± 1.7 (3-9) pairs of veins, these glabrous. *Breeding system* dioecious. *Inflorescences* spicate; peduncle 2.4 ± 0.8 (1.4-3.8) cm long, glabrous; main axis 0.9 ± 0.2 (0.7-1.2) cm long, with 2.4 ± 0.6 (1-4) internodes; secondary axis 0-0.2 cm long, with 0-1 internodes; staminate plants with 16.7 (11-20) flowers per inflorescence; pistillate plants with 7.3 (-16) flowers per inflorescence. *Flower calyces* glabrous inside and outside, the lobes 0.5 ± 0.3 (0.1) mm long, and 0.3 ± 0.2 (0.1-0.7) times the length of the calyx tube. *Ovary* glabrous. *Fruits* unknown.

Notes – This species is known from only two specimens, both collected by R.S. Cowan in the Serrania Parú in Western Guayana Shield, at 2000 m elevation, and could not be sampled for molecular data. Morphology does not suggest a relationship to any other species of the genus. Morphologically, *P. diceras* is unique in having short inflorescences with the main axis broader towards the apex (a trait sometimes found in *P. coriacea*), the rather few flowers being arranged along the sides of the main axis, the nodes and internodes indistinguishable.

32. ***Pagamea puberula*** Steyerm., Mem. N. Y. Bot. Gard 12(3):276, 1965. —TYPE: Brazil, Pará, in sabulosis Campos do chicodacá frequens, Campos a E de Faro, 2° 8' 0” S and 56° 43' 59” W, 21 Aug 1907, FL-old, *Ducke 8462* (Holotype: RB; Isotypes: !F, !US).

Shrub or tree 5.1 ± 4.2 (0.4-10) m tall. *Twigs* 2.8 ± 0.8 (2-3.5) mm thick. *Stipules* cylindrical, 6.7 ± 1.6 (5-9) mm long, caducous or only the base persistent. *Leaves*: petiole 1.1 ± 0.3 (0.6-1.8) cm long, densely pubescent; lamina elliptic, chartaceous, 8.2 ± 2.1 (4.9-13.1) x 2.5 ± 0.6 (1.5-3.9) cm, densely pubescent abaxially, usually glabrous adaxially, the margin flat; with 3.9 ± 2 (0-7) pairs of domatia; midrib densely pubescent on both surfaces; venation eucamptodromous, veins arching, with 6.8 ± 1 (5-9) pairs of veins, these densely pubescent abaxially, usually glabrous adaxially. *Breeding system* dioecious. *Inflorescences* thyrsoid; peduncle 2.1 ± 0.7 (0.8-3.8) cm long, densely pubescent; main axis 1.3 ± 0.6 (0-3.3) cm long, with 1.5 ± 0.7 (0-3) internodes; secondary axis 0.2 ± 0.2 (0-0.9) cm long, with 0.7 ± 0.6 (0-2) internodes; staminate plants with 90.4 ± 24.1 (25-150) flowers per inflorescence; pistillate plants with 10.5 ± (-36) flowers per inflorescence. *Flower calyces* glabrous inside, sparsely pubescent outside, the lobes 0.7 ± 0.4 (0.1-10) mm long, and 0.6 ± 0.3 (0.1-1.6) times the length of the calyx tube. *Ovary* densely hairy. *Fruits* ellipsoid, 9.4 ± 0.7 (8.1-10) x 7.9 ± 1 (6.5-9) mm.

Distribution and habitat – Central Amazon, North of the Amazon river and East of the Negro river. Campos do Ariramba region and North of Manaus.

Notes – DNA was extracted from herbarium material of two collections, one from Manaus the other from Campos do Ariramba, but the ITS could not be amplified. The chloroplast data place this species in the Macrophylla clade. However, *P. puberula* does not have the apomorphies present in all other species of the Macrophylla clade. Overall morphology suggests it may be related to the Guianensis clade, although it is distinct from the other species of this clade. I cannot rule out the possibility of contamination for these chloroplast accessions and prefer to treat this species as unplaced.

Pagamea puberula may be sympatric with, and is morphologically similar to three species of the Guianensis complex, *P. guianensis*, *P. occulta* and *P. plicatiformis*. From the first two it can be distinguished by its densely pubescent chartaceous leaf blades, and from *P. plicatiformis* by having flat, not bullate leaf blades that lack pubescence along the veins adaxially. The calyx lobes of *P. puberula* are also much sorter than those of *P. plicatiformis*.

Some specimens from the region of Manaus, listed as paratypes for this species (Steyermark 1965) are here considered as *P. guianensis*.

Species uncertain

Three specimens from Guyana could not be assigned to any other species, and may represent additional, undescribed, species. *Cowan 2175* is clearly a member of the

Macrophylla clade, and has small leaves, a few-flowered inflorescences like *P. jauaensis* and *P. aracaensis*, but the venation pattern is eucampdodromous. *Maguire 32410* is similar to the glabrous form of *P. velutina* from the Neblina tepui, and it also occurs at high elevations, but it is not clear to me that this fruiting specimens has the apomorphies of the Macrophylla clade. *Clark 9895* is similar to *P. spruceana*, but has fruit calyces with long lobes and is from a very different geographical location.

Excluded names

Pagamea auyantepuiensis Steyerm., Fieldiana Bot. 28: 584, fig. 129. 1953 = *Coryphothammus auyantepuiensis* (Steyerm.) Steyerm.

Pagamea garryoides Standl., Field Mus. Publ. Bot 7: 420, 1931 = *Pagameopsis garryoides* Standl. (Steyermark)

Pagamea spadicea Pittier, Bol. Soc. Venez. Cienc. Nat 9: 123, 1944 = *Psychotria spadicea* (Pittier) Standl. & Steyerm.

Pagamea steyermarkii Standl., Fieldiana Bot. 28: 589, fig. 131, 1953 = *Aphanocarpus steyermarkii* (Standl.) Steyerm.

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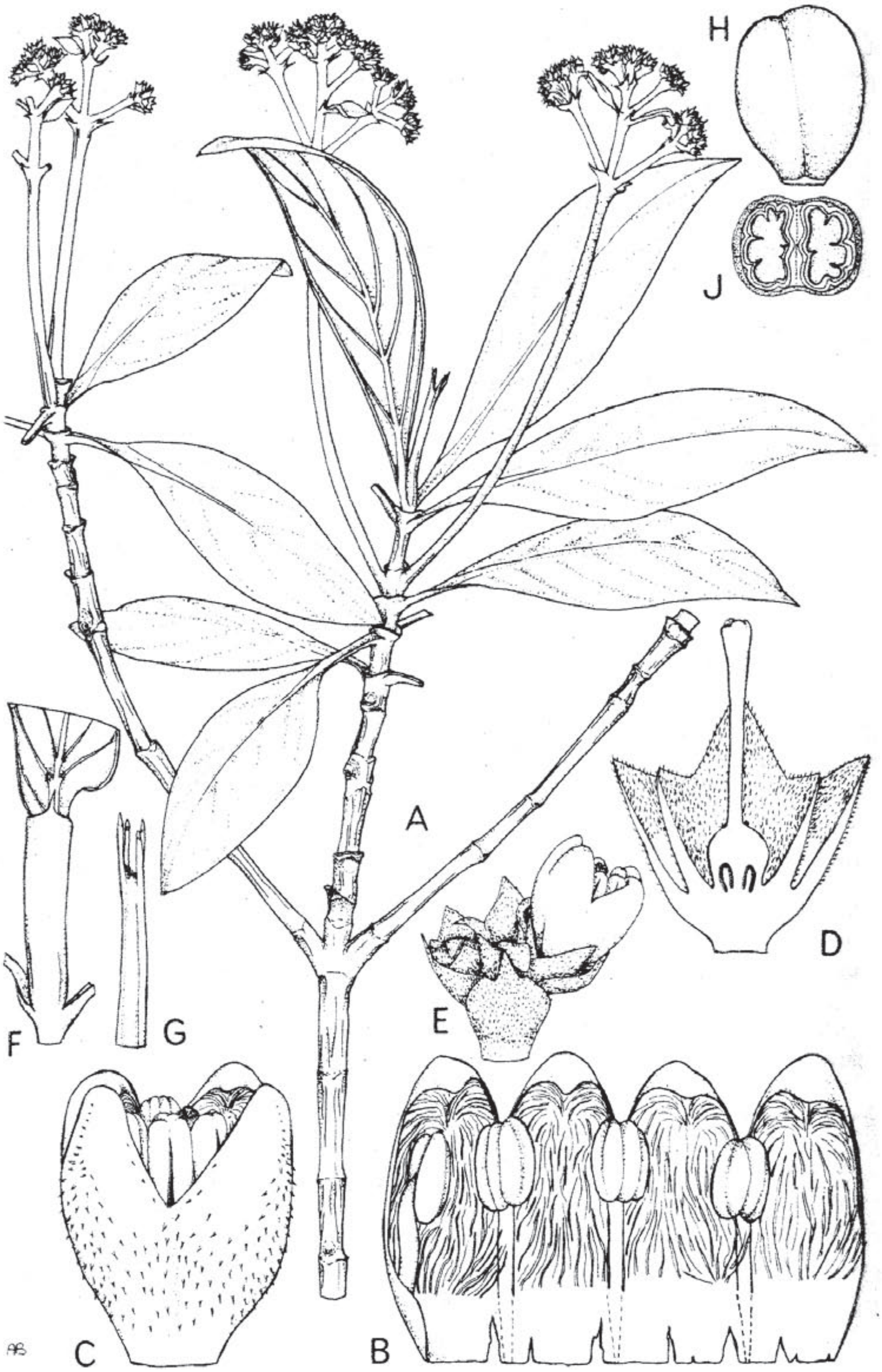

PLATE 1. *Pagamea harleyi Steyermark*. A. Habit. B. Corolla inner surface; C. Corolla; D. dissected flowers; E. flower cluster at node; F. leaf growing from stipular sheath; G. younge stipule; H. drupe side view; J drupe TS. Reproduced from Steyermark 1983, Kew Bulletin 38(2) pg. 318. Drawn by Anne Berkeley.

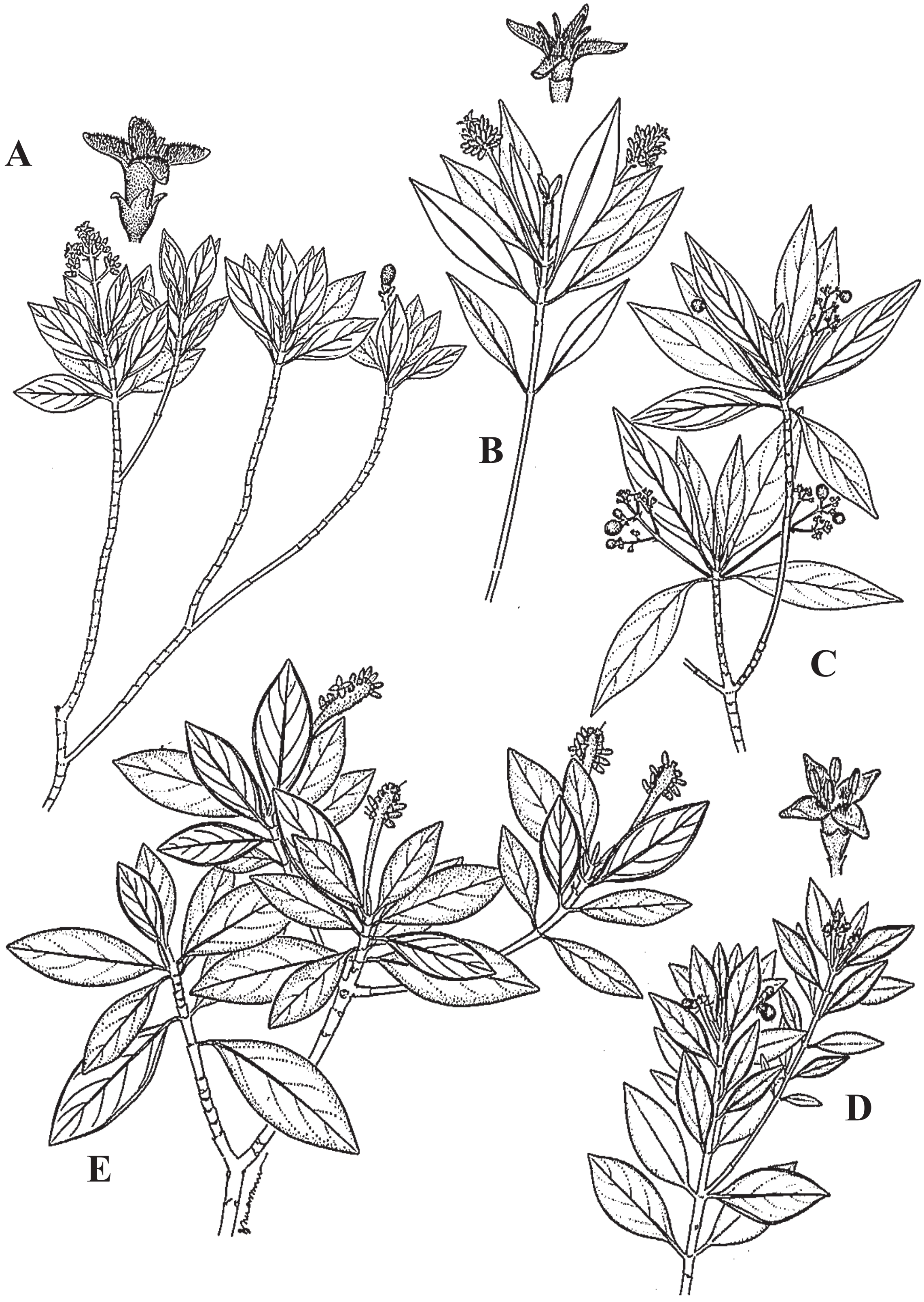

PLATE 2. A. *Pagamea pauciflora*. B. *Pagamea montana*. C. *Pagamea thyrsiflora*. D. *Pagamea standleyana*. E. *Pagamea diceras.* Reproduced from Vicentini and Steyermark 2004.

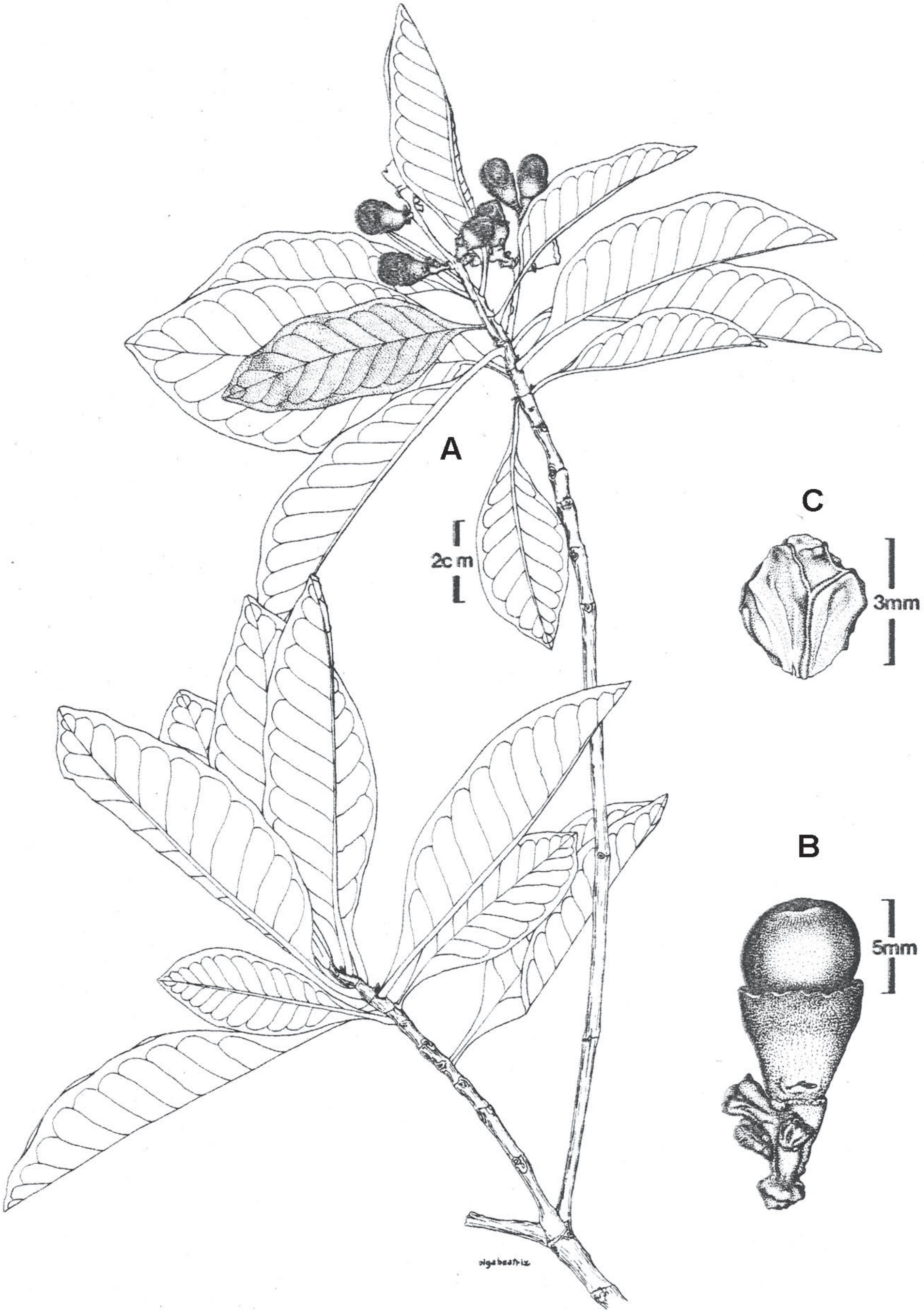

PLATE 3. *Pagamea aracaensis* Boom. A. Habitat. B. Fruit. C. Seed. Reproduced from Boom 1989, Brittonia 41, pg. 130.

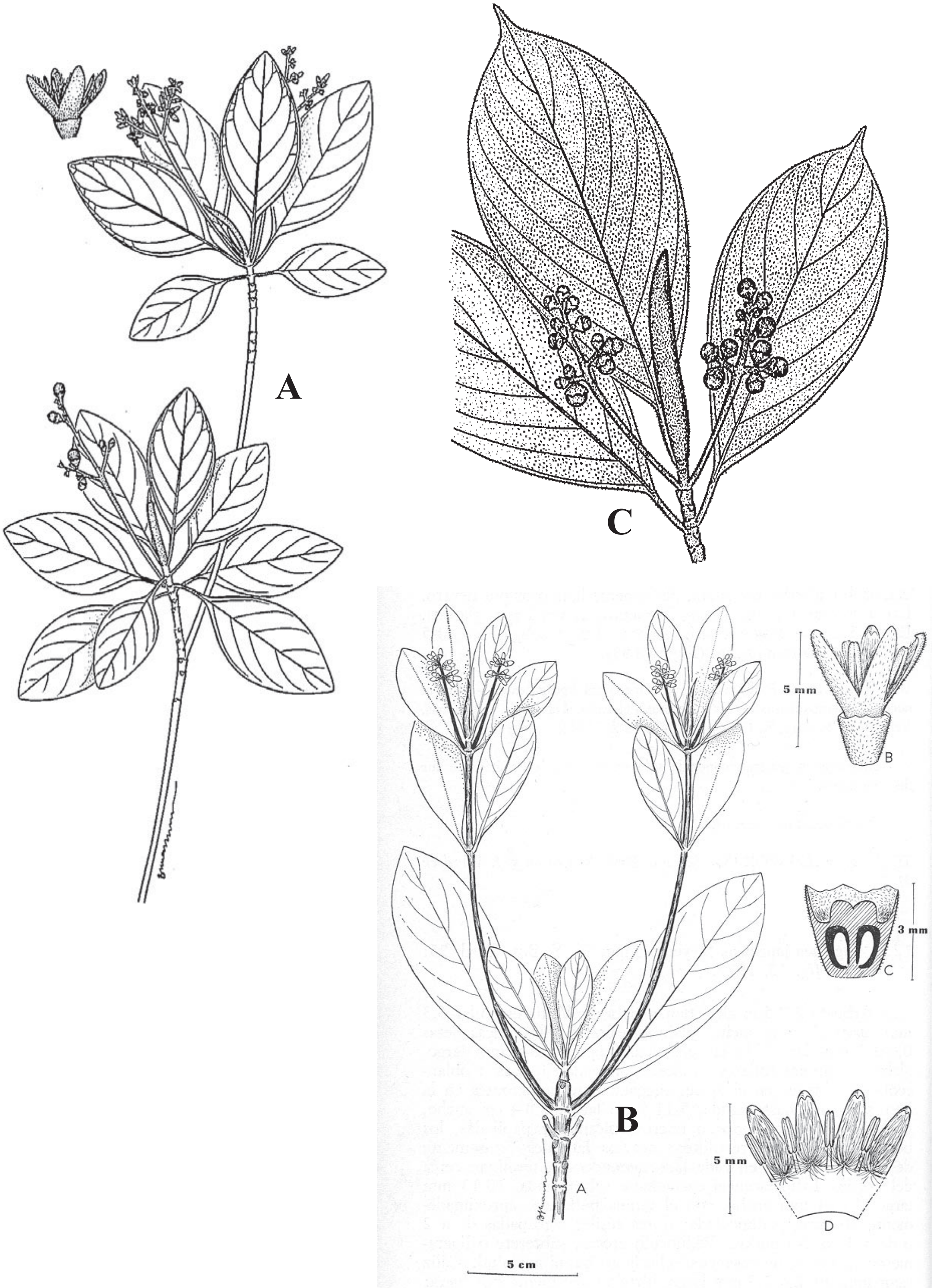

PLATE 4. A. *Pagamea anisophylla*. B. *Pagamea jauaensis*. C. *Pagamea velutina*. A and C reproduced from Vicentini and Steyermark 2004, B from Steyemark 1974.

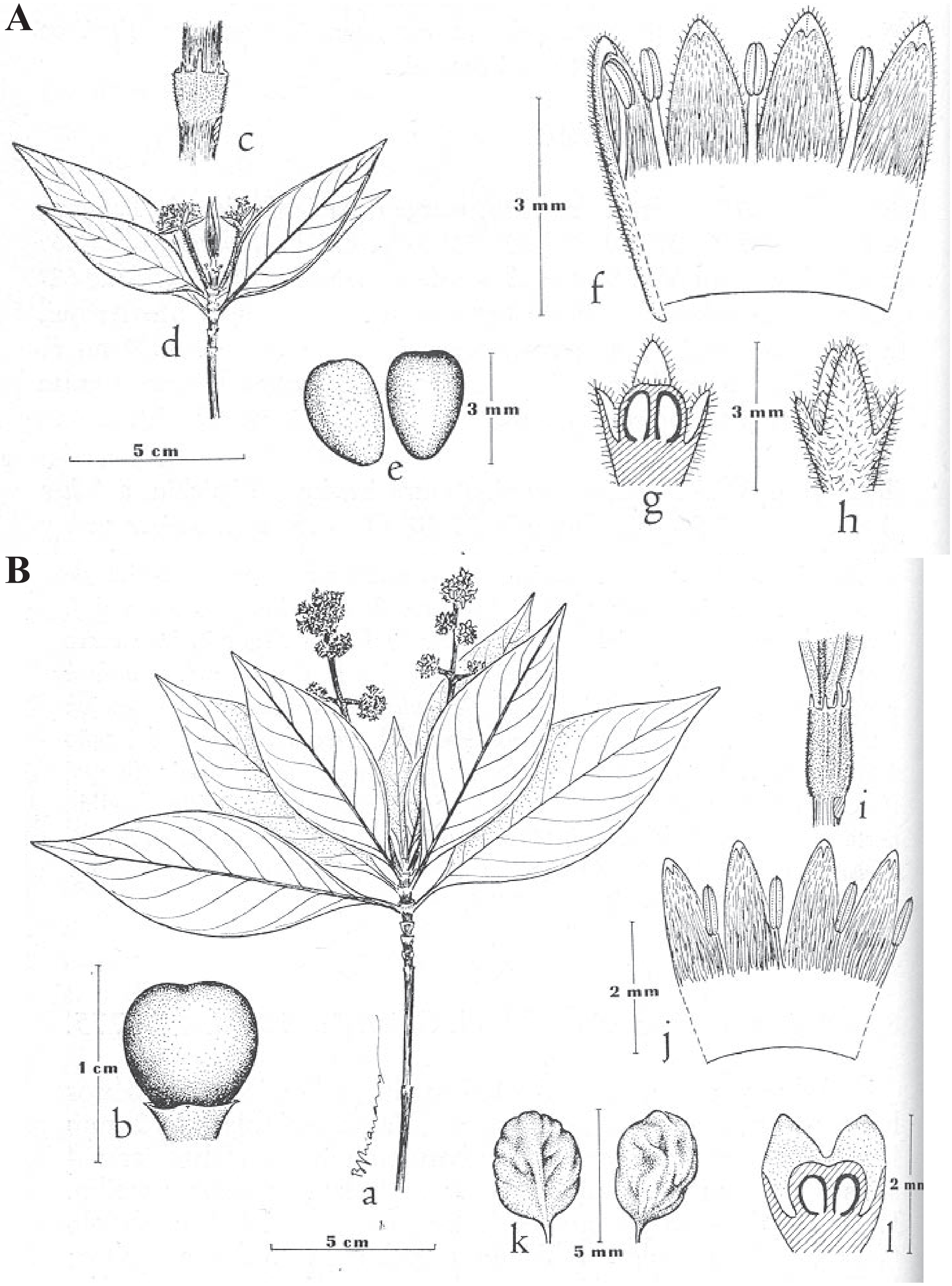

PLATE B. A. *Pagamea capitata:* c - stipule; d - habit; e - seeds; f - corolla; g - longitudinal section of ovary and calyx; h - outer view of calyx. B. *Pagamea occulta*: a - habit; b - fruit; i - stipule; j - corolla; k - seeds; i - longitudinal section of ovary and calyx. Both reproduced from Steyermark 1974.

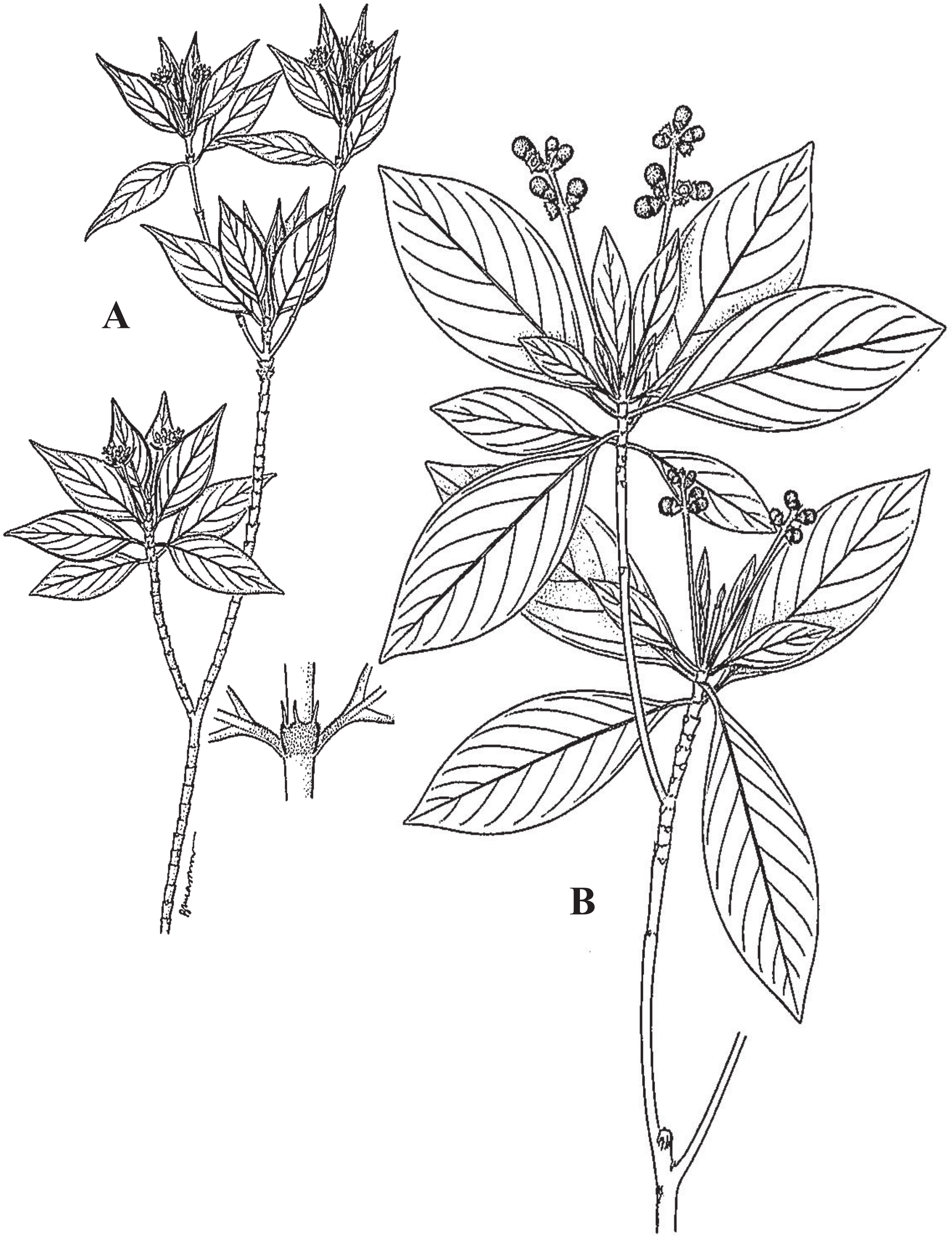

PLATE 6. A. *Pagamea capitata* habit and stipule. B. *Pagamea occulta* habit of plant with fruits. Both reproduced from Vicentini and Steyermark 2004.

PLATE 7. A. *Pagamea coriacea*. B. *Pagamea plicata.* Reproduced from Vicentini and Steyermark 2004.

PLATE 8. Reproduction of plate from Flora Brasiliensis. I. *Pagamea thyrsiflora*. II. *Pagamea plicata.* III. *Pagamea coriacea*, only parts of flowers and fruits.

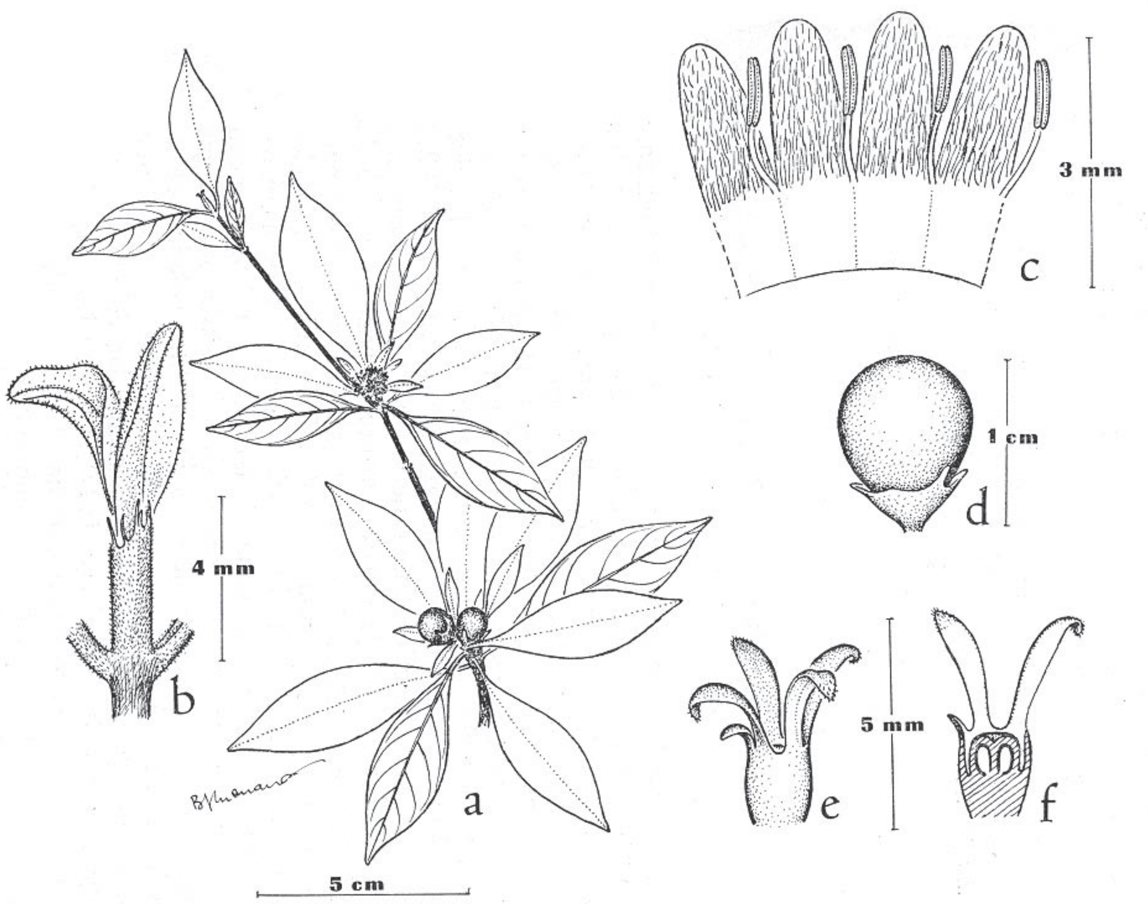

PLATE 9. *Pagamea sessiliflora*: a - habit; b - stipule; c - corolla; d - fruit; e - calyx; f - longitudinal section of ovary and calyx. Reproduced from Steyermark 1974.

APPENDIX A

Specimens

All specimens measured and seen are listed below for each species. Locality information was simplified to reduce space, but geographical coordinates were obtained (from maps and gazetteer databases) for all specimens and are given below. Elevation in m above sea level (m.a.s.l.) are also listed for all specimens. Elevation values that were not available from the collection label were estimated as the average elevation of all pixels in a Digital Elevation Model (DEM) image within a circle of 10 km radius around the collection point (pixels of 30 arc seconds or ~ 1 km; GTOP30 from the U.S. Geological Survey). A database with the information listed here is available upon request.

01. *Pagamea bahiana* Vicentini

Specimens measured — **BRASIL**. **Bahia**. Alcobaça: Rodovia BR 255 ca. 6 km a NW de Alcobaça, 17° 31' 10” S, 39° 11' 44” W, 9 m.a.s.l., 17 Sep 1978, Buds, *Mori 10604* (CEPEC, NY, US); Ilhéus: rd from Olivença to Maruim, 5.4 km SW of Olivença, 14° 59' 0” S, 39° 3' 0” W, 1 m.a.s.l., 29 Jan 1992, FR, *Thomas 8930* (CEPEC, MO, NY); Fazenda Barra do Manguinho, km 12 da Rodovia Pontal/Olivença, 14° 54' 58” S, 39° 2' 0” W, 85 m.a.s.l., 30 Jun 2000, FR, *Vicentini 1578* (INPA, MO); Fazenda Barra do Manguinho, km 12 da Rodovia Pontal/Olivença, 14° 54' 56” S, 39° 2' 0” W, 82 m.a.s.l., 30 Jun 2000, FL-old, *Vicentini 1579* (MO); Fazenda Barra do Manguinho, km 12 da Rodovia Pontal/Olivença, 14° 54' 54” S, 39° 1' 59” W, 86 m.a.s.l., 30 Jun 2000, Sterile, *Vicentini 1580* (MO); Fazenda Barra do Manguinho, km 12 da Rodovia Pontal/Olivença, 14° 54' 55” S, 39° 2' 0” W, 111 m.a.s.l., 30 Jun 2000, Sterile, *Vicentini 1582* (MO); Fazenda Barra do Manguinho, km 12 da Rodovia Pontal/Olivença, 14° 54' 58” S, 39° 2' 1” W, 81 m.a.s.l., 30 Jun 2000, Sterile, *Vicentini 1583* (MO); km 8 Olivença-Una, 14° 55' 0” S, 39° 2' 0” W, 80 m.a.s.l., 10 May 2000, FR, *Mattos 4081* (NY); Nova Viçosa: Copuva, 17° 54' 32” S, 39° 21' 49” W, 2 m.a.s.l., 9 Dec 1984, FL, *Hatschbach 48761* (CEPEC, MBM, MO, NY, US); Olivença: Estrada de terra Olivença-Vila Brasil, ca. 1 km SW, 14° 57' 14” S, 39° 0' 50” W, 70 m.a.s.l., 30 Jun 2000, Sterile, *Vicentini 1561* (MO); Estrada de terra Olivença-Vila Brasil, ca. 1 km SW, 14° 57' 14” S, 39° 0' 46” W, 70 m.a.s.l., 30 Jun 2000, Sterile, *Vicentini 1562* (MO); Estrada de terra Olivença-Vila Brasil, ca. 1 km SW, 14° 57' 14” S, 39° 0' 45” W, 72 m.a.s.l., 30 Jun 2000, FR, *Vicentini 1563* (INPA, MO); Estrada de terra Olivença-Vila Brasil, ca. 1 km SW, 14° 57' 19” S, 39° 0' 42” W, 80 m.a.s.l., 30 Jun 2000, FR, *Vicentini 1564* (MO); Estrada de terra Olivença-Vila Brasil, ca. 1 km SW, 14° 57' 13” S, 39° 0' 41” W, 76 m.a.s.l., 30 Jun 2000, Sterile, *Vicentini 1565* (MO); Estrada de terra Olivença-Vila Brasil, ca. 1 km SW, 14° 57' 14” S, 39° 0' 41” W, 70 m.a.s.l., 30 Jun 2000, FL-FR, *Vicentini 1566* (MO); Estrada de terra Olivença-Vila Brasil, ca. 1 km SW, 14° 57' 15” S, 39° 0' 38” W, 66 m.a.s.l., 30 Jun 2000, FR, *Vicentini 1567* (MO); Estrada de terra Olivença-Vila Brasil, ca. 1 km SW, 14° 57' 15” S, 39° 0' 41” W, 66 m.a.s.l., 30 Jun 2000, FR, *Vicentini 1568* (MO); Porto Seguro: km 3 da estrada Porto Seguro-Cabrália, 16° 23' 59” S, 39° 3' 36” W, 74 m.a.s.l., 1 Jul 2000, FL-old, *Vicentini 1590* (HUESF, MO); km 3 da estrada Porto Seguro-Cabrália, 16° 23' 59” S, 39° 3' 34” W, 70 m.a.s.l., 1 Jul 2000, FR, *Vicentini 1591* (HUEFS, INPA, MO); km 3 da estrada Porto Seguro-Cabrália, 16° 24' 1” S, 39° 3' 33” W, 50 m.a.s.l., 1 Jul 2000, FR, *Vicentini 1593* (MO); km 3 da estrada Porto Seguro-Cabrália, 16° 24' 1” S, 39° 3' 33” W, 41 m.a.s.l., 1 Jul 2000, Buds-FR, *Vicentini 1596* (INPA, MO); km 3 da estrada Porto Seguro-Cabrália, 16° 23' 57” S, 39° 4' 6” W, 60 m.a.s.l., 1 Jul 2000, FR, *Vicentini 1598* (HUEFS, INPA); km 3 da estrada Porto Seguro-Cabrália, 16° 23' 56” S, 39° 4' 9” W, 58 m.a.s.l., 1 Jul 2000, FL-FR, *Vicentini 1600* (HUEFS, INPA, MO); km 3 da estrada Porto Seguro-Cabrália, 16° 23' 54” S, 39° 4' 12” W, 52 m.a.s.l., 1 Jul 2000, FL-old, *Vicentini 1604* (MO); km 3 da estrada Porto Seguro-Cabrália, 16° 23' 55” S, 39° 4' 11” W, 44 m.a.s.l., 1 Jul 2000, Sterile, *Vicentini 1605* (MO); km 3 da estrada Porto Seguro-Cabrália, 16° 23' 56” S, 39° 4' 10” W, 41 m.a.s.l., 1 Jul 2000, FR, *Vicentini 1606* (HUEFS, INPA, MO); Prado: 4.5 km N of Prado on coast rd to Cumuruxatiba, 17° 20' 0” S, 39° 15' 0” W, 1 m.a.s.l., 21 Oct 1993, FL, *Thomas 10059* (CEPEC, MO, NY); Santa Cruz de Cabrália: km 4 estrada à Estação Ecológica do Pau-Brasil, 16° 18' 36” S, 39° 2' 0” W, 50 m.a.s.l., 19 Jun 1980, FR, *Mattos 934* (CEPEC, F, HUEFS, UNB); Una: Reserva Biológica de Una, 15° 11' 20” S, 39° 3' 52” W, 60 m.a.s.l., 30 Jun 2000, Sterile, *Vicentini 1560* (MO); **Espírito Santo**. 19° 25' 26” S, 39° 44' 00” W, 5 m.a.s.l., 1814, FR, *Sellow 17* (F, US); 19° 23' 47” S, 39° 43' 17” W, 5 m.a.s.l., 1815, FR, *Sellow 649985BM* (BM); 19° 15' 21.59” S, 39° 42' 19.46” W, 3 m.a.s.l., 1815, FR, *Sellow 796* (BM); 19° 19' 31.45” S, 39° 41' 41” W, 1 m.a.s.l., 1815, FR, *Sellow 964* (BM); Linhares: Reserva Florestal da CVRD, 19° 10' 0” S, 40° 0' 0” W, 39 m.a.s.l., 14 Apr 1997, FR, *Folli 2991* (NY); Reserva Florestal da CVRD, 19° 10' 0” S, 40° 0' 0” W, 39 m.a.s.l., 23 Nov 1988, FL, *Folli 820* (NY, SP); Reserva Florestal da CVRD, 19° 10' 0” S, 40° 0' 0” W, 39 m.a.s.l., 13 Nov 1991, FL, *Folli 1480* (NY); Reserva Florestal da CVRD, 19° 10' 0” S, 40° 0' 0” W, 39 m.a.s.l., 30 Mar 1993, FR, *Folli 1848* (NY); Reserva Florestal da CVRD, 19° 10' 0” S, 40° 0' 0” W, 37 m.a.s.l., 12 Mar 1972, FR, *Sucre 8637* (US).

Specimens seen but not measured — **BRASIL**. **Bahia**. Cairu: Fazenda Parafuso, 13° 29' 06” S, 39° 01' 44.21” W, 1 m.a.s.l., 20 Sep 1988, FR, *Mattos 2540* (CEPEC, MAC, SPF); Ilhéus: 2 km W of junction rd to Vila Brasil and rd Ilhéus to Una, 15° 6' 0” S, 39° 0' 0” W, 2 m.a.s.l., 10 May 1993, FR, *Thomas 9831* (MO); Itanagra: Fazenda Brejo Verde, 12° 16' 0” S, 38° 3' 0” W, 65 m.a.s.l., 22 Jun 1975, FR, *Gusmão 133A* (SPF); Porto Seguro: 6 km na estrada antiga de Arraial Dajuda-Trancoso, 16° 29' 42” S, 39° 7' 17” W, 16 m.a.s.l., 2 Feb 2002, FR, *de 1033* (CEPEC, MO); Santa Cruz de Cabrália: 15-20 km N of Porto Seguro, 16° 20' 0” S, 39° 5' 0” W, 40 m.a.s.l., 20 Feb 1988, FR, *Thomas 6185* (SPF); km 4 estrada à Estação Ecológica do Pau-Brasil, 16° 18' 36” S, 39° 2' 0” W, 50 m.a.s.l., 19 Jun 1980, FR, *Mattos 919* (CEPEC, F, IBGE, UNB).

02. *Pagamea harleyi* Steyerm.

Specimens measured — **BRASIL**. **Bahia**. Belmonte: Estrada Belmonte-Itapebi, 26 km SW of Belmonte, 16° 3' 0” S, 39° 2' 0” W, 70 m.a.s.l., 25 Mar 1974, FL-old, *Harley 17423* (MO, NY, P, US); Estrada Belmonte-Itapebi, 5 km da entrada para Cabrália, 16° 2' 24” S, 38° 58' 20” W, 47 m.a.s.l., 2 Jul 2000, Buds, *Vicentini 1616* (INPA, MO); Estrada Belmonte-Itapebi, 5 km da entrada para Cabrália, 16° 2' 12” S, 38° 58' 27” W, 43 m.a.s.l., 2 Jul 2000, Sterile, *Vicentini 1619* (MO); Estrada Belmonte-Itapebi, 7 km da entrada para Cabrália, 16° 2' 3” S, 38° 58' 37” W, 51 m.a.s.l., 2 Jul 2000, Buds, *Vicentini 1621* (INPA, MO); Estrada Cabrália-Belmonte, 3 km antes da entrada para Belmonte-Itapebi, 16° 9' 23” S, 38° 57' 40” W, 15 m.a.s.l., 2 Jul 2000, FL, *Vicentini 1609* (INPA, MO); Estrada Cabrália-Belmonte, 3 km antes da entrada para Belmonte-Itapebi, 16° 9' 26” S, 38° 57' 42” W, 3 m.a.s.l., 2 Jul 2000, FL, *Vicentini 1611* (HUEFS, INPA, MO); Estrada Cabrália-Belmonte, 3 km antes da entrada para Belmonte-Itapebi, 16° 9' 29” S, 38° 57' 45” W, 10 m.a.s.l., 2 Jul 2000, FL, *Vicentini 1613* (HUEFS, INPA, MO); Estrada Cabrália-Belmonte, 3 km antes da entrada para Belmonte-Itapebi, 16° 9' 30” S, 38° 57' 46” W, 10 m.a.s.l., 2 Jul 2000, FL, *Vicentini 1614* (HUEFS, INPA, MO); Camaçari: BA-099, Estrada do Côco, entre Arembepe e Monte Gordo, 12° 44'

0” S, 38° 9' 0” W, 1 m.a.s.l., 14 Jul 1983, Buds, *Bautista 807* (CEPEC, HALCB, IBGE, NY); Canavieiras: 23 km E de Santa Luzia-Una/Canavieiras, 15° 41' 27” S, 39° 1' 0” W, 5 m.a.s.l., 14 Dec 1991, FL, *Sant'Ana 142* (CEPEC, HUEFS, MBM, MO, NY); 30 km W de Canavieiras, rd. Camacan, 15° 33' 30” S, 39° 30' 24” W, 100 m.a.s.l., 12 Apr 1965, FL-FR, *Belem 831* (CEPEC, NY); 32 km W de Canavieiras, rd. Camacan, 15° 33' 30” S, 39° 30' 24” W, 100 m.a.s.l., 8 Sep 1965, FL, *Belem 1736* (CEPEC); Ilhéus: Fazenda Barra do Manguinho, km 12 da Rodovia Pontal/Olivença, 14° 55' 0” S, 39° 2' 0” W, 1 m.a.s.l., 11 Feb 1993, FR, *Mattos 2914* (CEPEC); Fazenda Barra do Manguinho, km 12 da Rodovia Pontal/Olivença, 14° 54' 58” S, 39° 2' 3” W, 86 m.a.s.l., 30 Jun 2000, FL-FR, *Vicentini 1570* (INPA, MO); Fazenda Barra do Manguinho, km 12 da Rodovia Pontal/Olivença, 14° 54' 59” S, 39° 2' 1” W, 75 m.a.s.l., 30 Jun 2000, Sterile, *Vicentini 1571* (MO); Fazenda Barra do Manguinho, km 12 da Rodovia Pontal/Olivença, 14° 55' 1” S, 39° 2' 0” W, 89 m.a.s.l., 30 Jun 2000, Sterile, *Vicentini 1573* (MO); Fazenda Barra do Manguinho, km 12 da Rodovia Pontal/Olivença, 14° 55' 1” S, 39° 2' 0” W, 80 m.a.s.l., 30 Jun 2000, Buds-FR, *Vicentini 1574* (INPA, MO); Fazenda Barra do Manguinho, km 12 da Rodovia Pontal/Olivença, 14° 55' 2” S, 39° 1' 59” W, 73 m.a.s.l., 30 Jun 2000, Sterile, *Vicentini 1575* (MO); Fazenda Barra do Manguinho, km 12 da Rodovia Pontal/Olivença, 14° 55' 2” S, 39° 1' 58” W, 68 m.a.s.l., 30 Jun 2000, Buds, *Vicentini 1576* (HUEFS, INPA, MO); Fazenda Barra do Manguinho, km 12 da Rodovia Pontal/Olivença, 14° 54' 59” S, 39° 2' 0” W, 82 m.a.s.l., 30 Jun 2000, Sterile, *Vicentini 1577* (MO); Fazenda Barra do Manguinho, km 12 da Rodovia Pontal/Olivença, 14° 54' 55” S, 39° 2' 0” W, 111 m.a.s.l., 30 Jun 2000, Sterile, *Vicentini 1581* (MO); Fazenda Guanabara, km 10 Ilhéus/Olivença, 14° 55' 0” S, 39° 2' 0” W, 50 m.a.s.l., 7 Mar 1985, FR, *Mattos 1848* (CEPEC, NY, US); Itacaré: Estrada Itacaré-Serra Grande, Campinho Cheiroso, 14° 23' 0” S, 39° 0' 30” W, 2 m.a.s.l., 26 Aug 1992, FL, *Amorin 699* (CEPEC); Maraú: 14° 6' 0” S, 39° 0' 0” W, 2 m.a.s.l., 6 Oct 1965, FL, *Belem 1865* (CEPEC, NY); 14° 6' 0” S, 39° 0' 0” W, 2 m.a.s.l., 6 Oct 1965, FL-FR, *Belem 1875* (CEPEC, NY); BR030, a 5 km ao S de Maraú, 14° 8' 0” S, 39° 0' 0” W, 4 m.a.s.l., 27 Feb 1980, FL-FR, *Santos 3520A* (CEPEC, F); Estrada Ubaitaba-Ponta do Mutã, km 71, 14° 0' 0” S, 39° 0' 0” W, 3 m.a.s.l., 2 Feb 1983, FR, *Carvalho 1398* (F); Porto Seguro: km 7 et 8 de la route Porto Seguro-Santa Cruz Cabrália, 16° 22' 0” S, 39° 3' 0” W, 7 m.a.s.l., 9 Dec 1986, FR, *Loizeau 565* (CEPEC); km 3 da estrada Porto Seguro-Cabrália, 16° 23' 59” S, 39° 3' 34” W, 70 m.a.s.l., 1 Jul 2000, Buds, *Vicentini 1592* (HUEFS, INPA, MO); km 3 da estrada Porto Seguro-Cabrália, 16° 24' 1” S, 39° 3' 33” W, 50 m.a.s.l., 1 Jul 2000, FL, *Vicentini 1594* (HUEFS, INPA, MO); km 3 da estrada Porto Seguro-Cabrália, 16° 24' 0” S, 39° 3' 31” W, 48 m.a.s.l., 1 Jul 2000, FL, *Vicentini 1595* (HUEFS, INPA, MO); km 3 da estrada Porto Seguro-Cabrália, 16° 23' 57” S, 39° 4' 4” W, 51 m.a.s.l., 1 Jul 2000, FL, *Vicentini 1597* (HUEFS, INPA, MO); km 3 da estrada Porto Seguro-Cabrália, 16° 23' 55” S, 39° 4' 10” W, 54 m.a.s.l., 1 Jul 2000, FL, *Vicentini 1602* (HUEFS, INPA, MO); km 3 da estrada Porto Seguro-Cabrália, 16° 23' 54” S, 39° 4' 10” W, 46 m.a.s.l., 1 Jul 2000, Sterile, *Vicentini 1603* (HUEFS, INPA, MO); 12 km N of Porto Seguro, 16° 20' 0” S, 39° 2' 0” W, 5 m.a.s.l., 27 Jul 1984, FL, *Webster 25092* (CEPEC, MO); Salvador: Dunas de Itapoã, 12° 55' 32” S, 38° 21' 11” W, 51 m.a.s.l., 21 Jun 2000, FL, *Vicentini 1512* (MO); Dunas de Itapoã, 12° 55' 32” S, 38° 21' 9” W, 45 m.a.s.l., 21 Jun 2000, FL, *Vicentini 1514* (INPA); Dunas de Itapoã, 12° 55' 32” S, 38° 21' 11” W, 54 m.a.s.l., 21 Jun 2000, FL, *Vicentini 1518* (MO); Santa Cruz de Cabrália: BR367, 18.7 km N de Porto Seguro, 16° 20' 0” S, 39° 2' 0” W, 2 m.a.s.l., 27 Jul 1978, FL, *Mori 10337* (NY); 11 km S of Santa Cruz Cabrália, 16° 22' 0” S, 39° 1' 0” W, 1 m.a.s.l., 17 Mar 1974, FL, *Harley 17069* (K, MO, NY, P, US); BR367, 18.7 km N de Porto Seguro, 16° 20' 0” S, 39° 2' 0” W, 2 m.a.s.l., 6 Jul 1979, FL, *Mori 12127* (CEPEC, US); Santa Luzia: 19 km estrada para Canavieiras, 15° 33' 20” S, 39° 4' 0” W, 22 m.a.s.l., 12 Oct 1998, FL-FR, *de 724* (CEPEC, MO); Santa Luzia-Canavieiras, 15° 33' 20” S, 39° 4' 34” W, 81 m.a.s.l., 28 Jun 2000, Buds, *Vicentini 1546* (MO); Santa Luzia-Canavieiras, 15° 33' 16” S, 39° 4' 36” W, 92 m.a.s.l., 28 Jun 2000, FL-old, *Vicentini 1549* (MO); Santa Luzia-Canavieiras, 15° 33' 16” S, 39° 4' 35” W, 89 m.a.s.l., 28 Jun 2000, FL, *Vicentini 1551* (MO); Santa Luzia-Canavieiras, 15° 33' 21” S, 39° 4' 34” W, 78 m.a.s.l., 28 Jun 2000, Sterile, *Vicentini 1553* (MO).

Specimens seen but not measured — **BRASIL**. **Bahia**. Belmonte: 15° 51' 0” S, 38° 53' 0” W, 1 m.a.s.l., 23 Sep 1970, FL, *Santos 1138* (CEPEC); Estrada Belmonte-Itapebi, 5 km da entrada para Cabrália, 16° 2' 22” S, 38° 58' 22” W, 56 m.a.s.l., 2 Jul 2000, Sterile, *Vicentini 1617* (INPA); Estrada Belmonte-Itapebi, 5 km da entrada para Cabrália, 16° 2' 15” S, 38° 58' 26” W, 45 m.a.s.l., 2 Jul 2000, Sterile, *Vicentini 1618* (INPA); Estrada Belmonte-Itapebi, 7 km da entrada para Cabrália, 16° 2' 3” S, 38° 58' 35” W, 49 m.a.s.l., 2 Jul 2000, FL, *Vicentini 1620* (INPA); Estrada Belmonte-Itapebi, 7 km da entrada para Cabrália, 16° 2' 4” S, 38° 58' 38” W, 51 m.a.s.l., 2 Jul 2000, Buds, *Vicentini 1622* (INPA); Estrada Belmonte-Itapebi, 7 km da entrada para Cabrália, 16° 2' 2” S, 38° 58' 39” W, 43 m.a.s.l., 2 Jul 2000, Buds, *Vicentini 1623* (INPA); Estrada Cabrália-Belmonte, 3 km antes da entrada para Belmonte-Itapebi, 16° 9' 28” S, 38° 57' 37” W, 9 m.a.s.l., 2 Jul 2000, Buds, *Vicentini 1607* (INPA); Estrada Cabrália-Belmonte, 3 km antes da entrada para Belmonte-Itapebi, 16° 9' 22” S, 38° 57' 38” W, 18 m.a.s.l., 2 Jul 2000, Sterile, *Vicentini 1608* (INPA); Estrada Cabrália-Belmonte, 3 km antes da entrada para Belmonte-Itapebi, 16° 9' 24” S, 38° 57' 41” W, 6 m.a.s.l., 2 Jul 2000, Sterile, *Vicentini 1610* (HUEFS); Estrada Cabrália-Belmonte, 3 km antes da entrada para Belmonte-Itapebi, 16° 9' 26” S, 38° 57' 44” W, 15 m.a.s.l., 2 Jul 2000, FL, *Vicentini 1612* (HUEFS, INPA); Estrada Cabrália-Belmonte, 3 km antes da entrada para Belmonte-Itapebi, 16° 9' 32” S, 38° 57' 48” W, 7 m.a.s.l., 2 Jul 2000, FL, *Vicentini 1615* (INPA); Canavieiras: 32 km W de Canavieiras, rd. Camacan, 15° 33' 30” S, 39° 30' 24” W, 100 m.a.s.l., 8 Sep 1965, FL, *Belem 1697* (CEPEC, NY); Ilhéus: 10 km S of Ilhéus airport on rd to Olivença, 14° 59' 0” S, 39° 3' 0” W, 1 m.a.s.l., 3 Feb 1993, FL, *Thomas 9724* (MO); Fazenda Barra do Manguinho, km 12 da Rodovia Pontal/Olivença, 14° 55' 51” S, 39° 2' 30” W, 50 m.a.s.l., 29 Sep 1980, FL, *Mattos 1131* (CEPEC, HALCB, IBGE); Fazenda Barra do Manguinho, km 12 da Rodovia Pontal/Olivença, 14° 54' 59” S, 39° 2' 1” W, 77 m.a.s.l., 30 Jun 2000, Sterile, *Vicentini 1572* (INPA); Itacaré: Campo Cheiroso, 14 km N of Serra Grande, 14° 22' 0” S, 39° 4' 0” W, 26 m.a.s.l., 15 Nov 1992, FL, *Thomas 9457* (MO); Maraú: 14° 6' 0” S, 39° 0' 0” W, 2 m.a.s.l., 6 Oct 1965, FL-old, *Belem 1861A* (CEPEC); 14° 6' 0” S, 39° 0' 0” W, 2 m.a.s.l., 7 Aug 1967, Buds, *Vinha 64* (INPA); BR030, Ubaitaba-Maraú, 14° 9' 0” S, 39° 0' 0” W, 4 m.a.s.l., 13 Dec 1967, FL, *Vinha 67* (CEPEC); BR-030 Saquaíra/Campinhos 4-8 km., 13° 59' 18” S, 38° 57' 8” W, 33 m.a.s.l., 6 Sep 1999, FL, *Carvalho 6780* (MO); Olivença: Parque dos Orixás, 14° 57' 0” S, 39° 1' 0” W, 1 m.a.s.l., 16 Oct 1998, FL, *Hatschbach 68572* (MBM, US); Porto Seguro: 16° 26' 0” S, 39° 5' 0” W, 1 m.a.s.l., 1 Nov 1985, FR, *Bautista 1153* (HALCB, HUEFS, IBGE); km 3 da estrada Porto Seguro-Cabrália, 16° 24' 0” S, 39° 3' 37” W, 60 m.a.s.l., 1 Jul 2000, Buds, *Vicentini 1589* (INPA); km 3 da estrada Porto Seguro-Cabrália, 16° 23' 56” S, 39° 4' 7” W, 56 m.a.s.l., 1 Jul 2000, FL, *Vicentini 1599* (HUEFS, INPA); km 3 da estrada Porto Seguro-Cabrália, 16° 23' 56” S, 39° 4' 9” W, 58 m.a.s.l., 1 Jul 2000, FL-FR, *Vicentini 1601* (HUEFS, INPA); Santa Cruz de Cabrália, 16° 17' 0” S, 39° 2' 0” W, 1 m.a.s.l., 25 Jan 1980, Sterile, *Perruci 23* (IPA); Salvador: Dunas de Itapoã, 12° 54' 32” S, 38° 19' 43” W, 2 m.a.s.l., 8 Jan 1993, FR, *Guedes 2543* (HALCB); Dunas de Itapoã, 12° 55' 0” S, 38° 21' 0” W, 4 m.a.s.l., 5 Apr 1988, FL, *Gusmão 510* (HUEFS, IBGE); Dunas de Itapoã, 12° 55' 0” S, 38° 21' 0” W, 4 m.a.s.l., 7 Jul 1987, FL, *Gusmão snB* (HALCB); Dunas de Itapoã, 12° 55' 0” S, 38° 21' 0” W, 4 m.a.s.l., 6 Jun 1984, FR, *Pereira 31/84* (IBGE); Dunas de Itapoã, 12° 55' 33” S, 38° 21' 11” W, 50 m.a.s.l., 21 Jun 2000, Sterile, *Vicentini 1513* (INPA); Dunas de Itapoã, 12° 55' 33” S, 38° 21' 10” W, 45 m.a.s.l., 21 Jun 2000, Sterile, *Vicentini 1515* (INPA); Dunas de Itapoã, 12° 55' 34” S, 38° 21' 9” W, 41 m.a.s.l., 21 Jun 2000, Sterile, *Vicentini 1516* (INPA); Dunas de Itapoã, 12° 55' 32” S, 38° 21' 11” W, 56 m.a.s.l., 21 Jun 2000, Sterile, *Vicentini 1517* (INPA); Dunas do Abaeté, 12° 55' 0” S, 38° 21' 0” W, 4 m.a.s.l., 5 Sep 1995, FL, *Guedes 5036* (HALCB); Dunas perto do aeroporto, 12° 55' 0” S, 38° 21' 0” W, 4 m.a.s.l., 11 Dec 1986, FR, *Alunos sn* (HALCB); Santa Cruz de Cabrália: 16° 17' 0” S, 39° 2' 0” W, 1 m.a.s.l., 25 Aug 1994, FR, *Guedes 3471* (HALCB); 4km S rd to Porto Seguro, 16° 19' 0” S, 39° 2' 0” W, 1 m.a.s.l., 21 Jan 1977, FR, *Harley 18159* (NY); 5-10 km S rd to Porto Seguro, 16° 19' 0” S, 39° 2' 0” W, 1 m.a.s.l., 18 Sep 1989, FR, *Hatschbach 53478* (CEPEC, MBM, US); Porto Seguro-St. Cruz Cabrália, km 18, 16° 20' 0” S, 39° 2' 0” W, 2 m.a.s.l., 24 Aug 1988, FL, *Mattos 2489* (CEPEC, HUEFS, IBGE); Santa Luzia: Santa Luzia-Canavieiras, 15° 33' 32” S, 39° 4' 35” W, 83 m.a.s.l., 28 Jun 2000, Sterile, *Vicentini 1555* (MO); Santa Luzia-Canavieiras, 15° 33' 30” S, 39° 4' 34” W, 78 m.a.s.l., 28 Jun 2000, Buds, *Vicentini 1556* (MO); Santa Luzia-Canavieiras, 15° 33' 29” S, 39° 4' 34” W, 82 m.a.s.l., 28 Jun 2000, Sterile, *Vicentini 1557* (MO); Santa Luzia-Canavieiras, 15° 33' 27” S, 39° 4' 34” W, 79 m.a.s.l., 28 Jun 2000, Sterile, *Vicentini 1559* (MO).

03. *Pagamea duidana* Standl. & Steyerm.

Specimens measured — VENEZUELA. **Amazonas**. Alto Orinoco: Duida tepui, 3° 36' 0” N, 65° 42' 30” W, 1675 m.a.s.l., 31 Aug 1944, FR, *Steyermark 58116* (NY); Duida tepui, 3° 36' 0” N, 65° 42' 0” W, 1463 m.a.s.l., 30 Dec 1928, FL, *Tate 567* (F, NY, US); Duida tepui, 3° 36' 0” N, 65° 40' 0” W, 1725 m.a.s.l., 5 Dec 1929, FR, *Tate 448* (NY, US); Atabapo: San Fernando de Atabapo, 3° 35' 0” N, 65° 23' 0” W, 1550 m.a.s.l., 11 Mar 1985, FR, *Liesner 18529* (MO, NY, VEN).

04. *Pagamea thyrsiflora* Spruce ex Benth.

Specimens measured — **BOLIVIA**. **Beni**. Cachuela Esperanza: rio Beni, 10° 32' 0” S, 65° 33' 49” W, 120 m.a.s.l., 17 Apr 1924, FL-old, *Meyer 76* (NY); Guayaramerin: rd to Riberalta, 10° 59' 0” S, 65° 23' 0” W, 200 m.a.s.l., 7 Feb 1978, FL, *Anderson 11991* (F, INPA, NY); **BRASIL**. **Amazonas**. Presidente Figueiredo: Manaus-Caracaraí rd, km 183, 3° 7' 12” S, 60° 1' 12” W, 34 m.a.s.l., 3 Apr 1975, FL, *Loureiro 48405INPA* (INPA, US); Rio Preto da Eva: rio Urubu, 10 km N of Manaus-Itacoatiara hwy, 2° 50' 0” S, 59° 1' 0” W, 87 m.a.s.l., 11 Jun 1968, FR, *Prance 5150* (F, NY, P); São Gabriel da Cachoeira: rio Içana, acima de Peraiauara, 1° 0' 0” N, 68° 0' 0” W, 99 m.a.s.l., 10 May 1973, FL, *Silva 1523* (INPA); Serra Tunuhy, rio Issana, 1° 30' 0” N, 68° 8' 30” W, 500 m.a.s.l., 13 Nov 1945, FL-old, *Froes 21371* (K, NY, US); **Mato Grosso**. entre Mutum e Nhambiquarahin, 12° 51' 0” S, 59° 18' 0” W, 409 m.a.s.l., May 1918, FL-FR, *Hoehne 2346* (F); **Pará**. Itaituba: Serra do Cachimbo, BR-163, km 823, 8° 41' 30” S, 54° 54' 0” W, 570 m.a.s.l., 7 Nov 1977, Buds, *Prance 24975* (MO, NY, US); Serra do Cachimbo, BR-163, km 825.5, 8° 55' 0” S, 54° 54' 0” W, 520 m.a.s.l., 19 Feb 1977, FR, *Kirkbride 2914* (F, INPA, MO, NY, P, UNB, US); Oriximiná: rio Trombetas, Campinas do Achipica, 1° 11' 19” S, 56° 40' 15” W, 91 m.a.s.l., 20 Sep 1910, FL, *Ducke 10934* (F); estrada entre Porto Trombetas e aeroporto, km 10, 1° 12' 0” S, 56° 40' 15” W, 84 m.a.s.l., 31 May 1978, FL, *Silva 4687* (NY); rio Trombetas, campina do Monte Branco., 1° 11' 30” S, 56° 40' 40” W, 86 m.a.s.l., 11 Jul 1980, FL, *Cid 1465* (INPA, NY); Porto de Moz: rio Xingú inferior, 1° 45' 0” S, 52° 14' 0” W, 30 m.a.s.l., 13 Mar 1923, FL, *Ducke 18835* (P, US); **Rondônia**. Costa Marques: W of rio Gautarinho, 6 km N of hwy BR429, 12° 1' 0” S, 63° 27' 0” W, 200 m.a.s.l., 25 Mar 1987, FL, *Nee 34489* (F, MO, NY, SP); Porto Velho: Along hwy 364, 92 km NE of junction with hwy 425 at Abuna, 9° 22' 0” S, 64° 40' 0” W, 115 m.a.s.l., 20 Apr 1987, FR, *Nee 34959* (F, INPA, MO, NY, SP); **COLOMBIA**. **Caquetá**. 0° 56' 15” N, 72° 42' 0” W, 635 m.a.s.l., 22 Nov 1992, FR, *Velayos 6332* (MO); 0° 50' 41” N, 72° 40' 24” W, 640 m.a.s.l., 30 Nov 1992, FR, *Velayos 6482* (COL, MO); Araracuara: Puerto Santander, SW de Araracuara, Sabana de Aduche, 0° 55' 0” S, 72° 20' 0” W, 200 m.a.s.l., 21 Nov 1993, FL, *Cárdenas 4147* (COAH, MO); **Guainia**. Cacagual: rio Atabapo, 4° 2' 16” N, 67° 42' 28” W, 125 m.a.s.l., 13 Jul 1957, FR, *Maguire 41450* (NY); Maimachi: Serranía del Naquén, Caño Culebra, Cerro del Helipuerto, 2° 6' 0” N, 68° 11' 0” W, 325 m.a.s.l., 2 Apr 1993, FL, *Madriñan 869* (MO); **Vaupés**. rio Karurú, Mesa de Yambí, Goo-ran-hoo-dá, 1° 20' 0” N, 71° 20' 0” W, 300 m.a.s.l., 15 Apr 1953, FL, *Schultes 19155* (BM, F, P, US); río Kuduyarí, Yapobodá, 1° 20' 0” N, 70° 30' 0” W, 300 m.a.s.l., Apr 1953, FL, *Schultes 19969* (F, NY, US); Mitú: Along lower rio Kubiyú, 1° 15' 0” N, 70° 13' 0” W, 161 m.a.s.l., 5 Jul 1975, FL, *Zarucchi 1386* (COL, F, INPA); Sierra de Chiribiquete: 0° 7' 0” N, 72° 50' 0” W, 525 m.a.s.l., 7 Dec 1990, FL, *Cardiel 1050* (COL, MO); 0° 55' 0” N, 72° 45' 0” W, 375 m.a.s.l., 13 Dec 1990, Sterile, *Palacios 2370* (MO, NY); mesa Norte, 1° 5' 0” N, 72° 40' 0” W, 600 m.a.s.l., 17 Aug 1992, FL-old, *Franco 3754* (MO); **ECUADOR**. **Zamora-Chinchipe**. Nagaritza: Cordillera del Condor, 04° 29' 57” S, 78° 38' 26” W, 1600 m.a.s.l., 14 Jun 2005, FR, *Quizhpe 1427* (MO, QCNE); **GUYANA**. **Cuyuni-Mazaruni**. Pakaraima Mts: Mazaruni River, 6° 2' 40” N, 60° 30' 6.1” W, 501 m.a.s.l., 10 Feb 2004, FR, *Redden 1768* (MO, US); Merume Mts, Partang river at rapids, 5° 41' 0” N, 60° 17' 0” W, 460 m.a.s.l., 17 Jun 1960, FL, *Maguire 43874* (NY); upper Mazaruni river, Membaru Creek, 5° 55' 0” N, 60° 36' 0” W, 367 m.a.s.l., 12 Feb 1939, FL, *Pinkus 210* (F, NA, NY); **Potaro-Siparuni**. Kaieteur plateau, 5° 12' 30” N, 59° 29' 30” W, 777 m.a.s.l., 2 May 1944, FR, *Maguire 23155* (F, MO, NY, P); Kaieteur plateau, 5° 11' 0” N, 59° 29' 0” W, 550 m.a.s.l., 7 Oct 1987, FR, *Kvist 138* (NY, US); Kaieteur plateau, 5° 10' 0” N, 59° 29' 0” W, 500 m.a.s.l., 29 Mar 1988, FL, *Hahn 4013* (NY, US); Mt. Ayanganna, 05° 23' 05” N, 59° 58' 33” W, 1545 m.a.s.l., 26 Jun 2001, Sterile, *Clarke 9584* (MO); **PERU**. **Amazonas**. Bagua: Imaza, Chiriaco, Cerro Tayu-Mujaji, 5° 15' 46” S, 78° 21' 52” W, 1031 m.a.s.l., 16 Feb 2004, FL, *Vicentini 2154* (HUT, INPA, MO, USM); Imaza, Chiriaco, Cerro Tayu-Mujaji, 5° 15' 46” S, 78° 21' 52” W, 1031 m.a.s.l., 16 Feb 2004, FR, *Vicentini 2157* (HUT, INPA, MO, USM); Imaza, Chiriaco, Cerro Tayu-Mujaji, 5° 15' 56” S, 78° 22' 7” W, 1200 m.a.s.l., 21 Oct 1997, FL, *Rojas 359* (HUT, MO); Imaza, Chiriaco, Soldado Oliva. Carretera Bagua-Imaza, 5° 15' 59” S, 78° 22' 10” W, 660 m.a.s.l., 7 Feb 1999, FL-FR, *Diaz 10645* (HUT, MO); **Huánuco**. Pucallpa: W part of Sira Mountains, 9° 27' 0” S, 74° 46' 0” W, 1230 m.a.s.l., 13 Jun 1988, FR, *Wallnofer 11413688* (K); **San Martin**. Tarapoto: Carretera Tarapoto-Yurimaguas, ca. km 35, 6° 26' 08" S, 76° 15' 57" W, 582 m.a.s.l., 26 Feb 2004, FL, *Vicentini 2178* (HUT, INPA, MO, USM); Carretera Tarapoto-Yurimaguas, ca. km 35, 6° 26' 08" S, 76° 15' 57" W, 582 m.a.s.l., 26 Feb 2004, FL-FR, *Vicentini 2179* (HUT, INPA, MO, USM); Carretera Tarapoto-Yurimaguas km 13, 6° 27' 54" S, 76° 18' 25" W, 806 m.a.s.l., 25 Feb 2004, Sterile, *Vicentini 2165* (HUT, INPA, MO, USM); Carretera Tarapoto-Yurimaguas km 13, 6° 27' 46" S, 76° 18' 28" W, 912 m.a.s.l., 25 Feb 2004, FL, *Vicentini 2169* (HUT, INPA, MO, USM); Carretera Tarapoto-Yurimaguas km 13, 6° 27' 44" S, 76° 18' 31" W, 912 m.a.s.l., 25 Feb 2004, FL, *Vicentini 2171* (HUT, INPA, MO, USM); Carretera Tarapoto-Yurimaguas km 13, 6° 27' 44" S, 76° 18' 31" W, 912 m.a.s.l., 25 Feb 2004, FR, *Vicentini 2172* (HUT, INPA, MO, USM); **VENEZUELA**. **Amazonas**. Alto Orinoco: Duida tepui, plateau above Culebra, 3° 41' 27" N, 65° 38' 11" W, 1400 m.a.s.l., 20 Nov 1950, FL, *Maguire 29588* (NY, VEN); Duida tepui, plateau above Culebra, 3° 41' 27" N, 65° 38' 11" W, 1400 m.a.s.l., 20 Nov 1950, FL, *Maguire 29590* (NY, VEN); Duida tepui, plateau above Culebra, 3° 41' 27" N, 65° 38' 11" W, 1000 m.a.s.l., 21 Nov 1950, FL, *Maguire 29627* (NY, VEN); Serrania del Vinilla, 2° 20' N, 65° 22' W, 760 m.a.s.l., 13 Jun 1981, FL, *Huber 6181* (NY, VE); Atabapo: Cerro Carishe, 3° 6' 26" N, 66° 30' 0" W, 350 m.a.s.l., 29 Jul 1959, FL, *Adderley 43660* (NY, VEN); Cerro Huachamacari, 3° 49' 0" N, 65° 42' 0" W, 650 m.a.s.l., 3 Nov 1988, FL, *Liesner 25748* (MO, NY); Autana: San Pedro, rio Sipapo, 4° 33' 39" N, 67° 32' 44" W, 100 m.a.s.l., 19 Dec 1948, FR, *Maguire 27855* (NY, VEN); Manapiare: Serranía Paru, laguna Asisa, Cerro Asisa (La Momia), 4° 15' N, 65° 55' W, 110 m.a.s.l., 6 May 1973, FL, *Hoyos 30* (VEN); Cerro Moriche, 4° 44' 44" N, 66° 17' 35" W, 1000 m.a.s.l., 15 Jan 1951, FR, *Maguire 30953* (NY, VEN); Serranía Parú, near Caño Asísa, 4° 41' 27" N, 65° 41' 27" W, 200 m.a.s.l., 15 Feb 1951, FR, *Cowan 31482* (NY, VEN); Maroa: Yavita, 1 km rd to Pimichín, 2° 55' 0" N, 67° 27' 0" W, 125 m.a.s.l., 21 Apr 1970, FL, *Steyermark 102880* (NY, VEN); Yavita,, 2° 55' 16" N, 67° 26' 17" W, 110 m.a.s.l., 28 Nov 1995, FR, *Berry 5706* (MO, TFVA, VEN); Rio Negro: Canal de Cassiquiare, 2° 0' 7" N, 67° 6' 42" W, 103 m.a.s.l., 12 Dec 1945, FR, *Froes 21510* (F, K, NY, US); Neblina tepui, 15 km NNE of Pico Phelps, 0° 51' 0" N, 65° 57' 0" W, 780 m.a.s.l., 15 Mar 1984, FL, *Liesner 16633* (MO, NY, VEN); Neblina tepui, slope above rio Marawinuma, 0° 50' 0" N, 66° 7' 0" W, 500 m.a.s.l., 26 Apr 1984, FL, *Thomas 3256* (MO, NY, US, VEN); Neblina tepui, rio Mawarinuma, 0° 50' 0" N, 66° 5' 0" W, 500 m.a.s.l., 25 Apr 1984, FL-FR, *Stein 1661* (MO, NY, VEN); San Carlos de Rio Negro, 1° 55' 0" N, 67° 4' 0" W, 98 m.a.s.l., Apr 1853, FL-FR, *Spruce 2957* (BM, F, K, NY); **Bolívar**. Gran Sabana: 17 km E of El Paují by rd and 64 km W of Santa Elena, 4° 30' 0" N, 61° 30' 0" W, 850 m.a.s.l., 29 Oct 1985, FR, *Liesner 19105* (MO, NY); Cerro de Las Guacamayas, rio Arequi, 5° 57' 57" N, 62° 25' 26.5" W, 900 m.a.s.l., 6 Sep 1954, FL, *Bernardi 1664* (NY); between Ptari-tepui and Sororopán-tepui, 5° 45' 0" N, 61° 43' 0" W, 1615 m.a.s.l., 15 Nov 1944, FL, *Steyermark 60264* (F); Raul Leoni: Sierra Auraima, rio Paragua, 6° 32' 0" N, 63° 33' 0" W, 400 m.a.s.l., 16 Jan 1962, FR, *Steyermark 90836* (NY, VEN).

Specimens seen but not measured — **BOLIVIA**. **Beni**. Cachuela Esperanza: rio Beni, 10° 32' 44" S, 65° 33' 49" W, 121 m.a.s.l., 12 Apr 1924, FR, *Meyer 71* (MO); Vaca Diez: rd to Riberalta, 11° 02' 52.13" S, 65° 23' 26.04" W, 168 m.a.s.l., 23 Sep 1993, Sterile, *Michel 2175* (LPB, MO); **BRASIL**. **Amazonas**. São Gabriel da Cachoeira: rio Içana, acima de Peraiauara, 1° 0' 0" N, 68° 0' 20" W, 99 m.a.s.l., 10 May 1973, FL, *Silva 1519* (US); Serra Tunuhy, rio Issana, 1° 26' 19" N, 68° 9' 29" W, 551 m.a.s.l., 25 Jun 2004, Sterile, *Vicentini 2247* (INPA); Serra Tunuhy, rio Issana, 1° 26' 28" N, 68° 9' 28" W, 652 m.a.s.l., 25 Jun 2004, FL, *Vicentini 2250* (INPA); Serra Tunuhy, rio Issana, 1° 26' 28" N, 68° 9' 28" W, 652 m.a.s.l., 25 Jun 2004, FL, *Vicentini 2254* (INPA); Serra Tunuhy, rio Issana, 1° 26' 28" N, 68° 9' 28" W, 652 m.a.s.l., 25 Jun 2004, FL, *Vicentini 2255* (INPA); **Pará**. Tapajoz, Bella vista, campina do Perdido, 22 Feb 1917, FR, *Ducke 16786* (F); **Rondônia**. Furnas P-13, 9° 34' 55.44" S, 64° 59' 45" W, 96 m.a.s.l., , ?, *Cohn-Haft 03* (MO); Costa Marques: BR-429, 12° 5' 0" S, 63° 35' 0" W, 206 m.a.s.l., 24 Mar 1987, FL, *Cid 8662* (INPA, MO); **COLOMBIA**. **Amazonas**. rio Vaupés, Caño Aceite, 1° 47' 00" N, 71° 18' W, 235 m.a.s.l., 6 Dec 1975, FR, *Roa 271* (COL); La Pedrera: río Caquetá, Cerro Yupatí, 01° 17' 49" S, 69° 37' 03" W, 300 m.a.s.l., 6 Aug 1997, FL, *Cárdenas 8534* (COAH); **Caquetá**. Borde de la quebrada, 1° 20' 26" N, 72° 55' 43" W, 635 m.a.s.l., 26 Nov 1992, FR, *Velayos 6384* (COAH, COL, MO); Araracuara: rio Caqueta, Caño Paujil, 10 km NO de Araracuara, 0° 46' 30" S, 72° 22' 30" W, 175 m.a.s.l., 19 Oct 1992, FR, *Arbelaez 230* (COAH, HUA); rio Caqueta, Caño Paujil, 10 km NO de Araracuara, 0° 47' 30" S, 72° 22' 30" W, 225 m.a.s.l., 24 Jul 1992, FL, *Arbelaez 165* (COAH, COL); Sabanas del Yari, 40 min del chorro de Gamitana, 00° 30' S, 72° 40' W, 101 m.a.s.l., 5 Mar 1997, FL, *Arbelaez 773* (HUA); detrás de la base militar, 0° 37' S, 72° 24' W, 100 m.a.s.l., 18 Oct 1990, FL, *Duivenvoorden 310* (COAH); **Guainia**. Caño Guarinuma: río Guainía, 2° 15' N, 69° 10' W, 150 m.a.s.l., 10 Oct 1977, FL, *Espina-M 135* (COL); Cerro Caño Minas: 2° 38' 13.7” N, 69° 14' 38.7” W, 300 m.a.s.l., 16 Feb 1995, FL-old, *Córdoba 116* (COAH, COL); Maimachi: Serrania de Naquén, 2° 13' 0” N, 68° 14' 0” W, 950 m.a.s.l., 13 Jul 1992, Buds, *Cortés 88* (COL, MO); Serranía del Naquén, Cerro Minas, alrrededores del helipuerto, 2° 13' N, 68° 14' W, 730 m.a.s.l., 29 Jul 1992, FL, *Cortés 171* (UDBC); Serranía del Naquén, Cerro Minas, alrrededores del helipuerto, 2° 12' 0” N, 68° 13' 0” W, 900 m.a.s.l., 7 Apr 1993, FL, *Barbosa 8390* (MO); **Vaupés**. río Kuduyarí, Yapobodá, 1° 20' 0” N, 70° 30' 0” W, 175 m.a.s.l., 25 Jun 1958, FL, *Barriga 15836* (COL, K); río Kuduyarí, Yapobodá, 1° 20' 0” N, 70° 30' 0” W, 300 m.a.s.l., Apr 1953, FL, *Schultes 20015* (US); Sierra de Chiribiquete: 0° 55' 0” N, 72° 45' 0” W, 300 m.a.s.l., 7 Dec 1990, FL, *Estrada 640A* (COL, MO); Estación Puerto Abeja, 0° 4' 27” N, 72° 27' 05” W, 224 m.a.s.l., 24 Jun 1999, FL, *Eusse 328* (COAH); Estación Puerto Abeja, 0° 4' 27” N, 72° 27' 05” W, 224 m.a.s.l., 30 Jul 1999, FR, *Eusse 431* (COAH); cerca del río Guaviare, 1° 5' 48” N, 72° 44' 17” W, 919 m.a.s.l., 22 Aug 1992, FR, *Barbosa 7733 (415)* (COAH); Macaya-Ajaju river confluence, 1° 5' 0” N, 72° 40' 00” W, 600 m.a.s.l., 15 May 1943, FL-old, *Schultes 5483* (COL); río Cuñaré, 20 min de la boca del río Amu, 0° 13' 25.6” N, 72° 26' 12.8” W, 350 m.a.s.l., 15 Feb 2001, ?, *Mendoza 10344* (FMB); cuenca media del río Cuñare, 0° 30' 30” N, 72° 37' 47” W, 350 m.a.s.l., 15 Nov 2000, ?, *Mendoza 9439* (FMB); cuenca media del río Cuñare, 0° 31' 44.7” N, 72° 37' 50.6” W, 350 m.a.s.l., 15 Nov 2000, ?, *Mendoza 9617* (FMB); rio Sararamano, 0° 11' 11” N, 72° 36' 20” W, 350 m.a.s.l., 15 Apr 2001, ?, *Mendoza 8264* (FMB); rio Sararamano, 0° 11' 11” N, 72° 36' 20” W, 350 m.a.s.l., 15 Apr 2001, ?, *Mendoza 8704* (FMB); 0° 55' 0” N, 72° 45' 0” W, 300 m.a.s.l., 12 Dec 1990, Sterile, *Palacios 2336* (COL); mesa Norte, 1° 5' 0” N, 72° 40' 0” W, 580 m.a.s.l., 15 Aug 1992, Sterile, *Franco 3682* (COL, MO); Valle de las Abejas, 0° 3' 55” N, 72° 27' 36” W, 223 m.a.s.l., 20 Jun 1992, Sterile, *Pedrol 4659* (COL, MO); **GUYANA**. **Cuyuni-Mazaruni**. Pakaraima Mts: Chi-Chi Mts, 2 km W of Chi-Chi falls, 5° 34' 0” N, 60° 13' 0” W, 550 m.a.s.l., 17 Feb 1987, FR, *Pipoly 10240* (MO, NY, P, US); Wayalayeng Village, falls of the Ataro river, 5° 14' 25.4” N, 60° 30' 57.9” W, 628 m.a.s.l., 5 Jun 2004, Buds, *Clarke 11429* (MO, US); Imbaimadai, 5° 42' N, 60° 30' 6.1” W, 587 m.a.s.l., 23 Jan 2004, FR, *Redden 2181* (MO, US); Kamarang river - Wenamu trail, Samwarakna Creek, 5° 52' 0” N, 60° 36' 30” W, 1100 m.a.s.l., 11 Nov 1951, FR, *Maguire 32567* (NY); Imbaimadai, Karowrieng river, 5° 40' 29” N, 60° 13' 35” W, 719 m.a.s.l., 20 Nov 2002, FR, *Redden 1583* (MO, US); upper Mazaruni river, 5° 39' 0” N, 60° 17' 0” W, 600 m.a.s.l., 11 Oct 1992, FR, *Hoffman 2863* (MO, NY); Latipú mt., 5° 57' 0” N, 60° 38' 0” W, 363 m.a.s.l., 8 Nov 1979, FR, *Maas 4174* (MO, NY, P); Vicinity of Chinoweing Village., 5° 32' 0” N, 60° 7' 0” W, 660 m.a.s.l., 21 Feb 1987, FL-old, *Pipoly 10486* (MO, NY, P, US); **Potaro-Siparuni**. Kaieteur plateau, 5° 10' 50” N, 59° 29' 0” W, 430 m.a.s.l., 6 May 1989, FR, *Gillespie 1305* (COL, MO, NY); Kaieteur plateau, 1-2 km of Tukeit trail, 5° 11' 20” N, 59° 29' 0” W, 450 m.a.s.l., 31 Mar 1989, FL, *Gillespie 968* (COL, MO, NY); Kaieteur plateau, 1-2 km of Tukeit trail, 5° 11' 30” N, 59° 29' 0” W, 360 m.a.s.l., 22 Jul 1993, FR, *Henkel 2413* (MO, NY); Kaieteur plateau, around airstrip, 5° 10' 0” N, 59° 29' 0” W, 300 m.a.s.l., 11 Feb 1962, FR, *Cowan 1803* (NY); **GUYANE FRANCAISE**.Petite Montagne Tortue, bassin de L’Approuague, 4° 18' 0” N, 52° 13' 0” W, 290 m.a.s.l., 31 Oct 1999, Sterile, *Granville 13833* (MO); **PERU**. **Amazonas**. Bagua: Imaza, Chiriaco, Cerro Tayu-Mujaji, 5° 15' 46” S, 78° 21' 52” W, 1031 m.a.s.l., 16 Feb 2004, FR, *Vicentini 2159* (HUT, INPA, MO, USM); Imaza, Chiriaco, Cerro Tayu-Mujaji, 5° 15' 25” S, 78° 21' 41” W, 800 m.a.s.l., 23 Oct 1997, FL, *Rojas 419* (HUT, MO); Imaza, Chiriaco, Cerro Tayu-Mujaji, 5° 15' 56” S, 78° 22' 7” W, 1200 m.a.s.l., 21 Oct 1997, FL, *Vasquez 24618* (MO); Imaza, Chiriaco, Cerro Tayu-Mujaji, 05° 15' 56” S, 78° 22' 07” W, 1030 m.a.s.l., 22 Mar 2001, FR, *vanderWerff 16334* (MO, USM); **San Martin**. Tarapoto: Carretera Tarapoto-Yurimaguas km 13, 6° 27' 48” S, 76° 18' 27” W, 905 m.a.s.l., 25 Feb 2004, Sterile, *Vicentini 2168* (HUT, INPA, MO, USM); Cerro de Isco, río Huallaga, 6° 29' 06” S, 76° 15' 41” W, 1000 m.a.s.l., Mar 1903, FL, *Ule 64* (F); **VENEZUELA**. **Amazonas**. Alto Orinoco: 2° 31' 0” N, 65° 23' 0” W, 500 m.a.s.l., 1 Mar 1984, FL-old, *Steyermark 130356* (MO, VEN); Serrania del Vinilla, 20 km al SW de Mavaca, 2° 20' 0” N, 65° 22' 0” W, 760 m.a.s.l., 13 Jun 1981, FL, *Huber 3967A* (NY, VEN); Atabapo: 20 km SE from San Fernando de Atabapo, 3° 50' 0” N, 67° 47' 0” W, 110 m.a.s.l., 10 Jan 1988, FR, *Aymard 6320* (MO, PORT, VEN); 20 km SE from San Fernando de Atabapo, 3° 50' 0” N, 67° 47' 0” W, 110 m.a.s.l., 10 Jan 1988, Buds, *Aymard 6529* (MO, PORT, VEN); Cerro Huachamacari, 3° 39' 0” N, 65° 42' 0” W, 850 m.a.s.l., 6 Mar 1985, FL, *Liesner 18343* (MO, VEN); Río Cuchaken, 3° 31' 0” N, 67° 22' 0” W, 100 m.a.s.l., Oct 1989, FR, *Velazco 795* (MO, NY, PORT); Autana: San Pedro, 20 km S río Guayapo, 4° 10' 0” N, 67° 31' 0” W, 100 m.a.s.l., 29 Jun 1979, Buds, *Huber 3967* (NY, VEN); San Pedro, rio Sipapo, 4° 36' 0” N, 67° 12' 0” W, 120 m.a.s.l., 28 Jul 1980, FL, *Huber 5593* (MO, NY, VEN); Manapiare: Cerro Moriche, E slopes, 4°

44' 40” N, 66° 17' 35” W, 300 m.a.s.l., 13 Jan 1951, FR, *Maguire 30861* (NY, VEN); Cerro Moriche, N slopes, 4° 44' 57” N, 66° 22' 40” W, 171 m.a.s.l., 20 Mar 2002, FL-old, *Aymard 12248* (INPA); Maroa: Yavita, río Guainia, 10 km al W del Caño Pimichín, 5 km al N de Tonina, 2° 53' 0” N, 67° 44' 0” W, 100 m.a.s.l., 1 Mar 1980, FL-old, *Huber 4887* (NY, VEN); Yavita, río Temi, rd to Pimichín, 2° 53' N, 67° 27' W, 130 m.a.s.l., 10 Jul 1969, FL, *Bunting 3705* (VEN); Yavita, 1 km N of Niñal, mouth of rio Atacavi., 3° 15' 0” N, 67° 21' 0” W, 100 m.a.s.l., 9 Nov 1992, FR, *Berry 5357* (MO, TFVA); Yavita, 1 km N of Niñal, mouth of rio Atacavi., 3° 15' 0” N, 67° 21' 0” W, 100 m.a.s.l., 9 Nov 1992, FR, *Berry 5363* (MO, TFVA); Yavita, cabeceras caño Pimichín, 03° 01' N, 67° 33' W, 120 m.a.s.l., 11 Feb 1981, FR, *Huber 5966* (VEN); Rio Negro: Neblina tepui, rio Mawarinuma, 0° 50' 30” N, 66° 4' 0” W, 350 m.a.s.l., 14 Jul 1984, FR, *Davidse 27254* (MO, NY, PORT, VEN); Neblina tepui, mouth of Caño Grande, 0° 50' 0” N, 66° 6' 0” W, 600 m.a.s.l., 15 Jul 1984, FR, *Davidse 27400* (MO, NY, VEN); Neblina tepui, south slope of north rio Mawarinuma, 0° 50' 0” N, 66° 7' 0” W, 550 m.a.s.l., 14 Feb 1984, FR, *Liesner 15926* (MO, NY, PORT); Sedukerawa tepui, río Metacuni, 03° 15' N, 64° 56' W, 335 m.a.s.l., 29 Jan 1990, FL, *Stergios 14449* (MO); **Bolívar**. Gran Sabana: Cerro Erepuchi, río Caroní, 4° 47' 0” N, 62° 16' 0” W, 700 m.a.s.l., May 1945, Sterile, *Cardona 1212* (NY, US, VEN); Río Caroni. Sabana de Arekuna, 6° 31' 0” N, 62° 53' 0” W, 520 m.a.s.l., 29 Aug 1983, FR, *Prance 28338* (MO, NY); Sierra de Lema, cabeceras de río Chicanán, 6° 5' 0” N, 62° 0' 0” W, 700 m.a.s.l., 29 Aug 1961, Buds, *Steyermark 89630* (NY, VEN).

05. *Pagamea pauciflora* Standl. & Steyerm.

Specimens measured — **GUYANA**. **Cuyuni-Mazaruni**. Pakaraima Mts: Mt. Ayanganna., 5° 23' 0” N, 59° 58' 0” W, 1575 m.a.s.l., 1 Nov 1992, FL-old, *Hoffman 3145* (MO, US); **VENEZUELA**. **Bolívar**. Gran Sabana: Carrao-tepuí, 5° 24' 0” N, 62° 24' 0” W, 2490 m.a.s.l., 7 Dec 1944, FL-FR, *Steyermark 60888* (F, NY, US); Cerro Tereké-Yurén, 5° 52' 0” N, 62° 2' 0” W, 2135 m.a.s.l., 26 May 1986, FR, *Liesner 21067* (F, MO, NY, PORT); Churi-tepuí (Muru-tepuí), 5° 13' 0” N, 61° 54' 0” W, 1400 m.a.s.l., 24 Jan 1953, FR, *Wurdack 34183* (COL, NY, VEN); Ilu-Tepu, 5° 27' 16” N, 60° 57' 49” W, 2500 m.a.s.l., 15 Mar 1952, Buds, *Maguire 33427* (NY, VEN); Macizo del Chimantá, 5° 12' 0” N, 62° 5' 0” W, 1950 m.a.s.l., 8 Feb 1985, FR, *Huber 10138* (MO, NY, TFVA, US, VEN); Macizo del Chimantá, 5° 19' 0” N, 62° 7' 0” W, 2150 m.a.s.l., 6 Feb 1984, FL, *Huber 8885* (MO, NY, US, VEN); Macizo del Chimantá, 5° 20' 0” N, 62° 12' 0” W, 2200 m.a.s.l., 1 Feb 1983, FR, *Steyermark 128436* (F, MO, NY, VEN); Macizo del Chimantá, 5° 16' 0” N, 62° 9' 0” W, 2100 m.a.s.l., 11 Feb 1985, FL, *Huber 10235* (NY, VEN); Macizo del Chimantá, 5° 25' 0” N, 62° 11' 0” W, 2350 m.a.s.l., 4 Feb 1984, FL, *Huber 8721* (NY, VEN); Macizo del Chimantá, 5° 8' 0” N, 62° 16' 0” W, 2100 m.a.s.l., 5 Mar 1986, FR, *Huber 11402* (NY); Macizo del Chimantá, 5° 24' 0” N, 62° 0' 0” W, 2170 m.a.s.l., 9 Feb 1955, FR, *Steyermark 664* (F, NY, VEN); Ptari-tepuí, 5° 46' 0” N, 61° 46' 0” W, 2100 m.a.s.l., 2 Nov 1944, FL, *Steyermark 59769* (NY, US); Roraima, 5° 0023' 47” N, 61° 00' 55” W, 2100 m.a.s.l., Jan 1910, FL, *Ule 8764* (K).

Specimens seen but not measured — **VENEZUELA**. **Bolívar**. Gran Sabana: Aparaman range, 5° 54' 0” N, 62° 7' 0” W, 2100 m.a.s.l., 27 Mar 1987, FR, *Holst 3655* (MO, NY); Macizo del Chimantá, 5° 16' 0” N, 62° 9' 0” W, 2100 m.a.s.l., 11 Feb 1985, FR, *Huber 10209* (MO, NY, TFVA, VEN); Macizo del Chimantá, 5° 15' 0” N, 61° 58' 0” W, 2250 m.a.s.l., 26 Mar 1984, FR, *Huber 9238* (MO, NY, VEN); Macizo del Chimantá, 5° 11' 0” N, 62° 0' 0” W, 1920 m.a.s.l., 14 Feb 1984, FR, *Luteyn 9541* (MO, NY, VEN); Macizo del Chimantá, 5° 15' 0” N, 61° 58' 0” W, 2250 m.a.s.l., 5 Feb 1985, FR, *Pipoly 7132* (MO, NY); Macizo del Chimantá, 5° 18' 0” N, 62° 9' 0” W, 2000 m.a.s.l., 27 Jan 1983, FR, *Steyermark 127981* (MO, VEN); Macizo del Chimantá, 5° 10' 0” N, 62° 7' 0” W, 1850 m.a.s.l., 2 Feb 1983, Sterile, *Steyermark A128471* (VEN); Aparaman range, 5° 53' 0” N, 62° 3' 0” W, 2200 m.a.s.l., 24 Mar 1987, FR, *Holst 3551* (COL, INPA, MO, VEN).

06. *Pagamea montana* Gleason & Standley

Specimens measured — **BRASIL**. **Amazonas**. Barcelos: Serra do Aracá, surrounding lowlands, 0° 57' 0” N, 63° 20' 0” W, 79 m.a.s.l., 6 Feb 1978, FR, *Rosa 2387* (NY); Serra do Aracá, summit, 0° 60' 0” N, 63° 19' 0” W, 1200 m.a.s.l., 13 Feb 1984, FR, *Prance 29049* (INPA, MO, NY, UNB); **VENEZUELA**. Alto Orinoco: Duida tepui, 3° 15' 16” N, 65° 31' 38” W, 1350 m.a.s.l., Feb 1975, FL, *Tillett 752250* (K, NY, VEN); Duida tepui, slopes of Aguita, 3° 25' 0” N, 65° 40' 0” W, 1140 m.a.s.l., 1929, FL-old, *Tate 926* (K, NY, US); Duida tepui, 3° 36' 0” N, 65° 41' 0” W, 1341 m.a.s.l., 1928, Buds, *Tate 803* (F, NY); Autana: San Pedro, Sipapo tepui, 4° 53' 34” N, 67° 21' 0” W, 1500 m.a.s.l., 25 Jan 1949, Buds, *Maguire 28586* (NY, VEN); San Pedro, Sipapo tepui, 4° 53' 0” N, 67° 21' 0” W, 1500 m.a.s.l., 25 Jan 1949, Buds, *Maguire 28589* (NY, VEN); San Pedro, Sipapo tepui, 4° 53' 34” N, 67° 21' 26” W, 1500 m.a.s.l., 25 Jan 1949, FL, *Maguire 28585* (NY, VEN); San Pedro, Sipapo tepui, 4° 53' 10” N, 67° 21' 26” W, 1500 m.a.s.l., 26 Jan 1949, FL, *Maguire 28632* (NY, VEN); Manapiare: Serranía Paru, laguna Asisa, Cerro Asisa (La Momia), 4° 14' N, 65° 56' W, 1310 m.a.s.l., 7 May 1973, FR, *Hoyos 39* (VEN); Serrania Yutaye, Cerro Guanay, 5° 55' 00” N, 66° 18' 0” W, 1800 m.a.s.l., 2 Feb 1951, FL, *Maguire 31682* (NY, VEN); Serrania Yutaye, Cerro Coro-Coro, 5° 39' 16” N, 66° 8' 44” W, 1500 m.a.s.l., 2 Mar 1953, FL, *Maguire 35433* (NY, US, VEN); Cerro Yutaje, 5° 39' 16” N, 66° 8' 44” W, 1500 m.a.s.l., 21 Feb 1953, FL, *Maguire 35348* (NY, VEN); Serrania Parú, 5° 41' 30” N, 65° 54' 30” W, 1250 m.a.s.l., 12 Feb 1953, FL, *Maguire 35198* (NY, VEN); Rio Negro: Neblina tepui, southern extension of range, 0° 47' 0” N, 66° 11' 0” W, 1600 m.a.s.l., 18 Apr 1984, FR, *Stein 1623* (F, MO, NY, VEN); Neblina tepui, summit, Caño Grande, 0° 47' 0” N, 66° 12' 0” W, 1500 m.a.s.l., 16 Jan 1954, FL, *Maguire 37341* (NY, VEN); Neblina tepui, summit, Caño Grande, 0° 50' 0” N, 66° 10' 0” W, 1850 m.a.s.l., 16 Jan 1954, FL, *Maguire 37339* (NY, VEN); **Bolívar**. Cedeño: Serrania Guanay, 5° 55' 0” N, 66° 23' 0” W, 1700 m.a.s.l., 25 Oct 1985, Buds, *Huber 10990* (NY, VEN); Heres: Cerro Marutani, a lo largo del rio Carla, 3° 50' 0” N, 62° 15' 0” W, 950 m.a.s.l., 11 Feb 1981, FL, *Steyermark 124080* (MO, NY, VEN); Raul Leoni: Cerro Guaiquinima, 5° 5' N, 63° 0' W, 1440 m.a.s.l., 13 Feb 1990, FL, *Boom 9549* (MO, VEN); Sucre: Meseta del Jaua, Cerro Sarisariñama, 4° 41' 40” N, 64° 13' 20” W, 1320 m.a.s.l., 13 Feb 1974, FL, *Steyermark B109054* (VEN).

Specimens seen but not measured — **BRASIL**. **Amazonas**. Barcelos: Serra do Aracá, summit, 0° 57' 0” N, 63° 23' 32” W, 1309 m.a.s.l., 25 Aug 2001, FL, *Vicentini 1819* (INPA); Serra do Aracá, summit, 0° 54' 59” N, 63° 21' 25” W, 1250 m.a.s.l., 27 Aug 2001, Buds, *Vicentini 1864* (INPA); Serra do Aracá, summit, 0° 55' 20” N, 63° 26' 49” W, 1102 m.a.s.l., 28 Aug 2001, Sterile, *Vicentini 1894* (INPA); Serra do Aracá, summit, 0° 56' 54” N, 63° 23' 28” W, 1261 m.a.s.l., 26 Aug 2001, Sterile, *Vicentini 1857* (INPA); **VENEZUELA**. Alto Orinoco: Duida tepui, plateau above Culebra, 3° 36' 0” N, 65° 42' 0” W, 1250 m.a.s.l., 13 Mar 1985, FR, *Liesner 18628* (MO, VEN); Cerro Marahuaca, 3° 43' 0” N, 65° 31' 0” W, 1140 m.a.s.l., 21 Feb 1985, FL, *Steyermark 130550* (MO, NY, VEN); Cerro Marahuaca, between rio Yameduaka, 3° 38' 0” N, 65° 28' 0” W, 1300 m.a.s.l., 20 Feb 1985, FR, *Liesner 17756* (MO, NY); Cerro Marahuaca, 3° 43' 0” N, 65° 30' 0” W, 1200 m.a.s.l., 16 Oct 1988, FL, *Liesner 24906* (MO, NY); Autana: Caño Piedra. 115 km al SE de Puerto Ayacucho., 4° 54' 0” N, 66° 54' 0” W, 1500 m.a.s.l., Sep 1989, FR, *Sanoja-Angel 2956* (MO, PORT); Manapiare: Serrania de Yutaje, 1-2 km E of rio Coro-Coro, 5° 42' 0” N, 66° 7' 30” W, 600 m.a.s.l., 28 Feb 1987, FL, *Liesner 21488* (MO, VEN); Serrania de Yutaje, rio Coro-coro, 5° 41' 30” N, 66° 7' 30” W, 650 m.a.s.l., 21 Feb 1987, FL, *Holst 3105* (MO, NY, VEN); Serrania Parú, 4° 14' 0” N, 65° 58' 0” W, 1250 m.a.s.l., Feb 1992, FL, *Chaviel 395* (MO, PORT); Rio Negro: Cerro Aracamuni, 1° 32' 0” N, 65° 49' 0” W, 1400 m.a.s.l., 29 Oct 1987, FR, *Liesner 22629* (MO, VEN).

07. *Pagamea standleyana* Steyerm.

Specimens measured — **GUYANA**. **Cuyuni-Mazaruni**. Pakaraima Mts: Mt. Maringma, 5° 12' 24.3” N, 60° 35' 30.1” W, 1710 m.a.s.l., 14 Jun 2004, FR, *Clarke 11638* (MO, US); **VENEZUELA**. **Bolívar**. Gran Sabana: Auyán tepui, 5° 55' 0” N, 62° 38' 0” W, 1860 m.a.s.l., 20 Oct 1986, Sterile, *Huber 11241* (MO, NY, TFVA, VEN); Auyán tepui, 5° 47' 0” N, 62° 33' 0” W, 2080 m.a.s.l., 20 Oct 1986, FL-old, *Huber*

11263 (MO, NY, TFVA, VEN); Auyán tepui, 5° 55' 0” N, 62° 32' 40” W, 1690 m.a.s.l., 2 May 1964, FL, *Steyermark 93222* (F, NY, P, US, VEN); Auyán tepui, 5° 55' 0” N, 62° 32' 20” W, 1800 m.a.s.l., 10 May 1964, FL, *Steyermark 93600* (F, NY, P, US); Camarcaibarai-Tepuí, 5° 52' 0” N, 62° 1' 0” W, 1800 m.a.s.l., 22 May 1986, FL, *Steyermark 132064* (MO, NY, VEN); Auyán tepui, 5° 48' 0” N, 62° 34' 0” W, 2200 m.a.s.l., Jan 1949, FL, *Cardona 2729* (NY, VEN); Cerro Uaipán, cumbre. rio Caroní, Guayana, 5° 36' 0” N, 62° 32' 0” W, 1920 m.a.s.l., 26 Nov 1946, FL, *Cardona 2072* (NY); Uaipán tepuí, 5° 36' 0” N, 62° 32' 0” W, 1900 m.a.s.l., 7 Feb 1948, Buds, *Phelps 366* (NY, VEN); Cerro Venamo, 5° 57' 0” N, 61° 23' 0” W, 1575 m.a.s.l., 2 Jan 1964, FL, *Steyermark 92564* (F, NY, P, US, VEN); Macizo del Chimantá, 5° 13' 0” N, 62° 15' 0” W, 2200 m.a.s.l., 13 Apr 1953, FL-FR, *Steyermark 74877* (NY, VEN); Macizo del Chimantá, 5° 10' 0” N, 62° 7' 0” W, 1850 m.a.s.l., 2 Feb 1983, FL, *Steyermark 128471* (MO, NY, VEN); Ptari-tepuí, 5° 50' 11” N, 61° 55' 38” W, 1600 m.a.s.l., 1 Nov 1944, FL-FR, *Steyermark 59634* (F, NY, US, VEN); Sarvén-tepuí,, 5° 18' 0” N, 62° 10' 0” W, 1750 m.a.s.l., 15 Jan 1953, Buds-FR, *Wurdack 34149* (K, NY, VEN); Uei-tepuí, 5° 15' 0” N, 61° 43' 0” W, 1200 m.a.s.l., 19 Apr 1960, FR, *Steyermark 323* (F, NY, US, VEN); Raul Leoni: Cerro Guaiquinima, 5° 44' 0” N, 63° 40' 0” W, 1560 m.a.s.l., 26 Jan 1977, FL, *Steyermark 113526* (F, NY, VEN).

Specimens seen but not measured — **VENEZUELA**. **Bolívar**. Gran Sabana: Macizo del Chimantá, 5° 10' N, 62° 07' W, 1850 m.a.s.l., 2 Feb 1983, Sterile, *Huber 7105* (VEN).

08. *Pagamea aracaensis* Boom

Specimens measured — **BRASIL**. **Amazonas**. Barcelos: Serra do Aracá, surrounding lowlands, 0° 19' 23” N, 63° 15' 55” W, 40 m.a.s.l., 28 Aug 2001, FL, *Vicentini 1918* (INPA, MO); Serra do Aracá, surrounding lowlands, 0° 19' 22” N, 63° 15' 57” W, 35 m.a.s.l., 28 Aug 2001, FL, *Vicentini 1925* (INPA, MO); On river Padauiri, 0° 15' 0” S, 64° 5' 0” W, 52 m.a.s.l., 28 Jun 1874, FL, *Traill 447* (K); Parque Nacional do Jaú, campina do Patauá, 1° 49' 10” S, 61° 46' 5” W, 50 m.a.s.l., 23 Jul 2001, Sterile, *Vicentini 1769* (INPA); Parque Nacional do Jaú, campina do Seringalzinho, 1° 54' 48” S, 61° 35' 25” W, 37 m.a.s.l., 27 Jul 2001, Sterile, *Vicentini 1777* (INPA); Serra do Aracá, surrounding lowlands, 0° 1' 25” S, 63° 13' 7” W, 44 m.a.s.l., 23 Aug 2001, FL, *Vicentini 1792* (INPA, MO); rio Negro, margem direita, 0° 40' S, 63° 00' W, 44 m.a.s.l., 4 Jul 1976, FL, *Coelho 557* (INPA); Serra do Aracá, surrounding lowlands, 0° 49' 0” N, 63° 19' 0” W, 60 m.a.s.l., 19 Mar 1984, FR, *Rodrigues 10553* (NY); Serra do Aracá, surrounding lowlands, 0° 49' 0” N, 63° 19' 0” W, 60 m.a.s.l., 13 Mar 1984, FL-old, *Rodrigues 10659* (INPA); Serra do Aracá, surrounding lowlands, 0° 49' 0” S, 63° 19' 0” W, 60 m.a.s.l., 28 Feb 1984, FR, *Amaral 1667* (INPA, MO, NY); Serra do Aracá, surrounding lowlands, 0° 49' 0” N, 63° 17' 0” W, 203 m.a.s.l., 20 Jul 1985, FR, *Prance 29704* (INPA); Serra do Aracá, surrounding lowlands, 0° 25' 0” N, 63° 23' 0” W, 80 m.a.s.l., 26 Aug 1985, FR, *Prance 29773* (INPA); Borba: Campo de Flores, 4° 23' 0” S, 59° 35' 0” W, 30 m.a.s.l., 25 Jun 1983, FR, *Zarucchi 2867* (F, INPA, K, NY, US); Campo de Flores, 4° 24' 18” S, 59° 34' 53” W, 31 m.a.s.l., 10 Apr 2004, FR, *Vicentini 2207* (INPA); km 41, rd to Mapiá, 4° 34' 71” S, 59° 33' 49” W, 29 m.a.s.l., 10 Apr 2004, FR, *Vicentini 2203* (INPA); Nova Aripuanã: Nova Prainha, 5° 7' 13” S, 60° 22' 44” W, 40 m.a.s.l., 24 Jul 1976, FL, *Mota 60737INPA* (INPA); Nova Olinda do Norte: Bacia do rio Madeira, Vila dos Indios Mundurucus, rio Marimari, 3° 58' 00” S, 58° 49' 00” W, 50 m.a.s.l., 2 Jul 1983, FL, *Cid 3996* (MO, NY).

Specimens seen but not measured — **BRASIL**. **Amazonas**. Barcelos: Serra do Aracá, surrounding lowlands, 0° 19' 4” N, 63° 16' 0” W, 38 m.a.s.l., 28 Aug 2001, FL, *Vicentini 1915* (INPA, MO); Serra do Aracá, surrounding lowlands, 0° 04' 40” N, 63° 12' 51” W, 69 m.a.s.l., , ?, *Cid 11905* (INPA); Serra do Aracá, surrounding lowlands, 0° 49' 0” N, 63° 19' 0” W, 206 m.a.s.l., 13 Mar 1984, Sterile, *Rodrigues sn* (NY); Serra do Aracá, surrounding lowlands, 0° 49' 0” N, 63° 19' 0” W, 206 m.a.s.l., 9 Feb 1984, FR, *Prance 28911* (INPA, NY); Serra do Aracá, surrounding lowlands, 0° 30' 0” N, 63° 30' 0” W, 83 m.a.s.l., 4 Jul 1985, FR, *Cordeiro 161* (INPA, NY); Serra do Aracá, surrounding lowlands, 0° 48' 0” N, 63° 18' 0” W, 120 m.a.s.l., 18 Mar 1984, FR, *Pipoly 6850* (NY); Borba: Campo de Flores, 4° 24' 18” S, 59° 34' 53” W, 31 m.a.s.l., 9 Apr 2004, Sterile, *Vicentini 2201* (INPA); Campo de Flores, 4° 24' 18” S, 59° 34' 53” W, 31 m.a.s.l., 9 Apr 2004, Sterile, *Vicentini 2202* (INPA).

09. *Pagamea hirsuta* Spruce ex Benth.

Specimens measured — **BRASIL**. **Amazonas**. São Gabriel da Cachoeira: rio Içana, vila Jandú-Cachoeira, 1° 29' 23” N, 68° 43' 1” W, 130 m.a.s.l., 23 Jun 2004, FL-old, *Vicentini 2236* (INPA, MO); rio Içana. vila Baniwa de Juivitera, 1° 16' 17” N, 68° 33' 22” W, 112 m.a.s.l., 22 Jun 2004, FR, *Vicentini 2234* (INPA, MO); rio Içana, vila de Jauacanã, 0° 33' 47” N, 67° 24' 9” W, 73 m.a.s.l., 27 Jun 2004, FR-old, *Vicentini 2275* (INPA, MO); **COLOMBIA**. **Caquetá**. Cerro de Cupaty, río Japurá, 1° 7' 0” S, 69° 35' 0” W, 83 m.a.s.l., 24 Nov 1912, Sterile, *Ducke 12288* (F, US); **Guainia**. Cucui: río Negro, vicinity of Piedra de Cucuí, 1° 14' 0” N, 66° 49' 0” W, 217 m.a.s.l., 27 Dec 1947, FR, *Schultes 9518* (F, US); Puerto Colombia: rio Guainia, vicinity of Pt. Colombia, 2° 43' 14” N, 67° 34' 6” W, 250 m.a.s.l., 1 Nov 1952, FL, *Schultes 18158* (F, NY, US); **Vaupés**. río Kananarí, Cerro Isibukuri, 1° 5' 0” N, 70° 35' 0” W, 385 m.a.s.l., 23 Jan 1952, FL, *Schultes 15075* (F, US); Mitú: Along lower rio Kubiyú, 1° 15' 0” N, 70° 13' 0” W, 161 m.a.s.l., 28 Sep 1976, FL, *Zarucchi 2161* (COAH, F, INPA, US); **VENEZUELA**. **Amazonas**. Atabapo: San Antonio de Orinoco, 3° 27' 0” N, 66° 45' 0” W, 140 m.a.s.l., Apr 1990, FR, *Yanez 440B* (MO, PORT); Maroa: rio Guainía, 2° 44' 11” N, 67° 33' 45” W, 127 m.a.s.l., 11 Feb 1942, FR, *Williams 14265* (F, US, VEN); Yavita,, 2° 55' 19” N, 67° 26' 7” W, 130 m.a.s.l., 19 Oct 1950, FL, *Maguire 29308* (NY, VEN); 10 km N , río Guainía, 2° 49' 5” N, 67° 37' 5” W, 130 m.a.s.l., 7 Oct 1957, FL, *Maguire 41753* (NY, VEN); Yavita,, 2° 55' 19” N, 67° 26' 7” W, 128 m.a.s.l., 1942, FR, *Williams 13920* (NY); Yavita,, 2° 55' 19” N, 67° 26' 7” W, 128 m.a.s.l., 23 Jan 1942, FR, *Williams 13927* (F, NY, US, VEN); Rio Negro: 10 km NE rom San Carlos de Rio Negro, 1° 30' 0” N, 67° 3' 0” W, 120 m.a.s.l., 7 Apr 1979, FR, *Liesner 6300* (MO, VEN); 10.8 km NE rd San Carlos de Rio Negro-Solano, 1° 56' 0” N, 67° 3' 0” W, 119 m.a.s.l., 20 Oct 1978, FL, *Clark 6889* (VEN); km E of San Carlos de rio Negro, 1° 56' 0” N, 67° 4' 0” W, 120 m.a.s.l., 23 Nov 1977, FR, *Liesner 3760* (MO, VEN); San Carlos de Rio Negro, 1° 55' 0” N, 67° 4' 0” W, 98 m.a.s.l., 1853, FL-FR, *Spruce 3137* (F, K, P).

Specimens seen but not measured — **BRASIL**. **Amazonas**. São Gabriel da Cachoeira: Yútica, Orilla izquierda del río Vaupés, 1° 11' 32.13” N, 70° 00' 33.92” W, 188 m.a.s.l., 15 Nov 1952, FL, *Romero-Castañeda 3503* (COL); 0° 8' 0” S, 67° 5' 0” W, 73 m.a.s.l., 1852, FL, *Spruce 2364* (BM); rio Içana, vila Jandú-Cachoeira, 1° 29' 23” N, 68° 43' 1” W, 130 m.a.s.l., 23 Jun 2004, FL-old, *Vicentini 2238* (INPA); rio Içana, vila Jandú-Cachoeira, 1° 29' 23” N, 68° 43' 1” W, 130 m.a.s.l., 23 Jun 2004, FL-old, *Vicentini 2239* (INPA, MO); rio Içana. vila Baniwa de Juivitera, 1° 16' 17” N, 68° 33' 22” W, 112 m.a.s.l., 22 Jun 2004, FL, *Vicentini 2230* (INPA); rio Içana. vila Baniwa de Juivitera, 1° 15' 54” N, 68° 33' 18” W, 112 m.a.s.l., 22 Jun 2004, Sterile, *Vicentini 2235* (INPA); rio Içana, vila de Jauacanã, 0° 33' 32” N, 67° 23' 53” W, 69 m.a.s.l., 27 Jun 2004, FR-old, *Vicentini 2258* (INPA, MO); **COLOMBIA**. **Guainia**. Cerro Caño Minas: 2° 38' 13.7” N, 69° 14' 38.7” W, 300 m.a.s.l., 16 Feb 1995, FL-old, *Córdoba 132* (COAH, COL); Maimachi: Serranía del Naquén, Cerro Minas, alrrededores del helipuerto, 2° 12' 0” N, 68° 13' 0” W, 900 m.a.s.l., 7 Apr 1993, FR, *Barbosa 8359* (COL, MO, NY); Puerto Colombia: río Negro, 2° 43' 13” N, 67° 33' 52” W, 75 m.a.s.l., 27 Oct 1977, FL, *Pabón 425* (COL); 2° 43' N, 67° 33' W, 99 m.a.s.l., 19 Feb 1965, FR, *Pérez 6909* (COL); Puerto Inírida: Raudal Samuro, 3° 15' 10.2” N, 72° 06' 06.5” W, 250 m.a.s.l., 21 Nov 1998, FL, *Marin 628* (COAH); **Vaupés**. San José del Guaviare: PNN Nukak Guaviare, Tomachipán, rio Inírida, Cerro Cocui, 2° 8' 38.8” N, 71° 09' 45.3” W, 350 m.a.s.l., 10 Feb 1996, Sterile, *Córdoba 2170* (COAH); **VENEZUELA**. **Amazonas**. Atabapo: rio Atabapo, ca. rio Atacaví, 3° 15' 0” N, 67° 20' 10” W, 115 m.a.s.l., 9 Sep 1960, Buds, *Foldats 3811* (VEN); Río Atacavi, 3° 12' 0” N, 67° 24' 0” W, 100 m.a.s.l., Nov 1989, FL, *Velazco 1108* (MO, PORT); Maroa: Maroa-Yavita rd, 2° 45' 49” N, 67° 32' 44” W, 100 m.a.s.l., 19 Jan 1998, FR, *Campbell 523* (MO); Rio Negro: 1-2 km E and SE from San Carlos de Rio Negro, 1° 51' 0” N, 67° 3' 0” W, 120 m.a.s.l., 11 Nov 1987, FL, *Liesner 22975* (MO, NY, VEN); 1-2 km E and SE rom San Carlos de Rio Negro, 1° 56' 0” N, 67° 3' 0” W, 120 m.a.s.l., 22 Apr 1979, FR, *Liesner 6856* (MO, VEN); 10.8 km NE rd San Carlos de Rio Negro-Solano, 1° 56' 0” N, 67° 3' 0” W, 119 m.a.s.l., 9 Feb 1978, FR, *Clark 6474* (VEN); rio Pasimoni, 1° 30' 0” N, 66° 30' 0” W, 80 m.a.s.l., Apr 1991, FR, *Velazco 1953* (MO, PORT).

10. *Pagamea glabra* Vicentini

Specimens measured — **BRASIL**. **Amazonas**. São Gabriel da Cachoeira: rio Içana. vila Baniwa de Juivitera, 1° 16' 15" N, 68° 33' 24" W, 112 m.a.s.l., 22 Jun 2004, Sterile, *Vicentini 2231* (INPA); rio Içana. vila Baniwa de Juivitera, 1° 16' 15" N, 68° 33' 24" W, 112 m.a.s.l., 22 Jun 2004, Sterile, *Vicentini 2232* (INPA).

Specimens seen but not measured — **BRASIL**. **Amazonas**. São Gabriel da Cachoeira: rio Içana. vila Baniwa de Juivitera, 1° 16' 15" N, 68° 33' 24" W, 112 m.a.s.l., 22 Jun 2004, Sterile, *Vicentini 2232A* (INPA).

11. *Pagamea macrophylla* Spruce ex Benth.

Specimens measured — **BRASIL**. **Amazonas**. Manaus: Reserva Florestal Adolpho Ducke, 2° 53' 0" S, 59° 58' 0" W, 70 m.a.s.l., 30 Jul 1968, FL-old, *Aluisio 70* (INPA, US); Reserva Florestal Adolpho Ducke, 2° 53' 0" S, 59° 58' 0" W, 70 m.a.s.l., 29 Mar 1957, FR, *Coelho 5216INPA* (INPA); Reserva Florestal Adolpho Ducke, 2° 53' 0" S, 59° 58' 0" W, 70 m.a.s.l., 31 Aug 1966, FL, *Prance 2130* (F, INPA, NY, P); Reserva Florestal Adolpho Ducke, 2° 53' 10" S, 59° 58' 10" W, 70 m.a.s.l., 16 Jun 1994, FL, *Ramos 2842* (MO, NY); Reserva Florestal Adolpho Ducke, 2° 53' 70" S, 59° 58' 70" W, 70 m.a.s.l., 26 Apr 1996, FL, *Ribeiro 1821* (MO, NY); Reserva Florestal Adolpho Ducke, 2° 53' 0" S, 59° 58' 0" W, 70 m.a.s.l., 2001, FL, *Vicentini 1800* (INPA); Reserva Florestal Adolpho Ducke, 2° 53' 40" S, 59° 58' 40" W, 70 m.a.s.l., 3 Feb 1995, FR, *Vicentini 839* (F, MO, NY); São Gabriel da Cachoeira: Panuré, ad rio Uapés., 0° 30' 0" N, 68° 00' 00" W, 92 m.a.s.l., Sep 1852, FL, *Spruce 2578* (BM, F, K, NY, P); São Paulo de Olivença: 3° 27' 0" S, 68° 48' 0" W, 72 m.a.s.l., 3 Oct 1931, FR, *Ducke 23* (F); 3° 27' 0" S, 68° 48' 0" W, 72 m.a.s.l., 18 Apr 1945, FR, *Froes 20724* (K, NY, US); Platô ao sul da cidade, estrada para Bomfim, 3° 27' 0" S, 68° 48' 0" W, 72 m.a.s.l., 25 Nov 1986, FR, *Cid 8535* (INPA, MO); **COLOMBIA**. **Vaupés**. río Piraparaná, Caño Paca, río Apaporis, 0° 20' 0" S, 70° 30' 0" W, 94 m.a.s.l., 19 Sep 1952, FL-old, *Schultes 17581* (COL, F, US).

Specimens seen but not measured — **BRASIL**. **Amazonas**. Manaus: Manaus-Caracaraí rd, 2° 50' 0" S, 60° 1' 55" W, 64 m.a.s.l., 27 Jul 1961, FR, *Rodrigues 2234* (INPA); Manaus-Caracaraí rd, 2° 55' 30" S, 60° 1' 50" W, 53 m.a.s.l., 27 Jul 1961, FR, *Rodrigues 3034* (US); Manaus-Caracaraí rd, 2° 45' 0" S, 60° 1' 50" W, 75 m.a.s.l., 27 Jun 1956, FL, *Coelho 3945INPA* (INPA, US); igarapé do Riacho Grande, 3° 6' 48" S, 60° 1' 31" W, 50 m.a.s.l., 7 Nov 1956, FR, *Coelho 4305INPA* (INPA); Reserva Florestal Adolpho Ducke, 2° 53' 0" S, 59° 58' 0" W, 70 m.a.s.l., 17 Jun 1958, FL, *Coelho 15* (INPA, US); Reserva Florestal Adolpho Ducke, 2° 55' 60" S, 59° 58' 60" W, 70 m.a.s.l., 13 Mar 1996, FR, *Campos 546* (MO, NY); Reserva Florestal Adolpho Ducke, 2° 53' 50" S, 59° 58' 50" W, 70 m.a.s.l., 28 Apr 1995, FR, *Ribeiro 1616* (MO, NY); Reserva Florestal Adolpho Ducke, 2° 53' 20" S, 59° 58' 20" W, 70 m.a.s.l., 4 Jun 1993, FR, *Ribeiro 841* (MO, NY); Reserva Florestal Adolpho Ducke, 2° 53' 30" S, 59° 58' 30" W, 70 m.a.s.l., 12 May 1994, FL-FR, *Vicentini 539* (MO, NY); Reserva Florestal Adolpho Ducke, 2° 53' 0" S, 59° 58' 0" W, 70 m.a.s.l., 14 Aug 1957, FR, *Rodrigues 533* (INPA); Reserva Florestal Adolpho Ducke, 2° 53' 0" S, 59° 58' 0" W, 70 m.a.s.l., 18 Aug 1966, FL, *Rodrigues 8231* (INPA).

12. *Pagamea velutina* Steyerm.

velutina

Specimens measured — **VENEZUELA**. **Amazonas**. Autana: Caño Piedra. 115 km al SE de Puerto Ayacucho., 4° 54' 0” N, 66° 54' 0” W, 1500 m.a.s.l., Sep 1989, FR, *Sanoja-Angel 2927* (MO, PORT); San Pedro, rio Sipapo, 4° 51' 0” N, 67° 24' 0” W, 150 m.a.s.l., 21 Jan 1949, FR, *Maguire 28536* (K, NY, US, VEN); San Pedro, rio Sipapo, 4° 51' 26” N, 67° 24' 0” W, 150 m.a.s.l., 21 Jan 1949, FR, *Maguire 28538* (NY).

neblinensis

Specimens measured — **BRASIL**. **Amazonas**. São Gabriel da Cachoeira: Neblina tepui, 0° 43' 0” N, 66° 18' 0” W, 1250 m.a.s.l., 23 Apr 1964, FR, *Euvel 137* (NY); Serra Pirapucú, slope, rio Negro, rio Cauaburí, rio Maturacá, 0° 30' 0” N, 66° 15' 0” W, 1300 m.a.s.l., 26 Jan 1966, FR, *Silva 60891* (COL, F, NY); **VENEZUELA**. Rio Negro: Neblina tepui, Caño Grande, 0° 51' 0” N, 65° 57' 0” W, 780 m.a.s.l., 15 Mar 1984, FR, *Liesner 16712* (VEN).

13. *Pagamea anisophylla* Standl. & Steyerm.

Specimens measured — **VENEZUELA**. **Amazonas**. Alto Orinoco: Duida tepui, near Culebra, 3° 44' 0” N, 65° 44' 0” W, 250 m.a.s.l., 24 Feb 1985, FL-FR, *Liesner 17934* (MO, NY, VEN); Atabapo: 13 km NO desembocadura del Yurueba en el Ventuari., 4° 6' N, 66° 24' W, 180 m.a.s.l., May 1990, FL, *Marin 1110* (MO); 43 km al NE from Santa Barbara del Orinoco, 4° 16' N, 66° 42' W, 180 m.a.s.l., May 1990, FL, *Marin 1064* (MO); Kanaripó, rio Ventuari, 4° 6' 32” N, 66° 54' 32” W, 100 m.a.s.l., 22 Aug 1978, FR, *Huber 2445* (NY, VEN); Carmelitas, rio Ventuari,, 4° 13' 0” N, 66° 33' 0” W, 100 m.a.s.l., 22 Aug 1978, Buds, *Huber 2424* (COL, INPA, K, NY, VEN); Kanaripó, rio Ventuari, 4° 5' N, 66° 50' W, 125 m.a.s.l., 2 Mar 1977, FL-old, *Steyermark 113815* (VEN); NW from Santa Barbara del Orinoco, 4° 6' N, 66° 58' W, 180 m.a.s.l., May 1990, FL, *Marin 1082* (MO); río Atabapo, 30 kms de la confluencia con el Río Caname, 3° 48' 0” N, 67° 38' 0” W, 110 m.a.s.l., Nov 1989, FR, *Yanez 226* (NY, PORT); rio Ventuari, ca. 5 km por sendero en frente a la Isla Caymán, 4° 7' 41” N, 66° 40' 38” W, 126 m.a.s.l., 13 Mar 2002, Sterile, *Aymard 12192* (MO, PORT); Autana: Montaña Fría, de Puerto Ayacucho y Sanariapo, 5° 15' N, 67° 30' 0” W, 180 m.a.s.l., 27 Jul 1967, FL, *Ruiz-Teran 4320* (VEN); río Sanariapo, 5° 14' 11” N, 67° 46' 54” W, 100 m.a.s.l., 8 Sep 1944, FL, *Steyermark 58461* (F, NY, VEN); Manapiare: Cerro Moriche, SE base, 4° 22' 0” N, 66° 43' 0” W, 120 m.a.s.l., 19 Feb 1979, FR, *Huber 3207* (NY, VEN); Cerro Moriche, E base, 4° 44' 44” N, 66° 17' 27” W, 100 m.a.s.l., 13 Jan 1951, FR, *Maguire 30873* (NY, UNB, VEN); Cerro Morrocoy y Serranía Colmena, 5° 20' 0” N, 66° 10' 0” W, 275 m.a.s.l., 16 Oct 1977, FL-old, *Huber 1213* (NY, US, VEN); S-SE, Cerro Camani, a unos 20-25 km al W de San Juan, 5° 18' N, 66° 16' W, 600 m.a.s.l., 10 Oct 1979, FL-old, *Huber 4621* (VE); Serrania de Yutaje, 5° 28' 22” N, 66° 3' 16” W, 150 m.a.s.l., 30 Jan 1953, FR, *Maguire 35042* (F, NY, VEN); Yutajé, 5° 36' 51” N, 66° 6' 85” W, 377 m.a.s.l., 12 Dec 1999, FR, *Milano 1454* (VEN).

Specimens seen but not measured — **VENEZUELA**. **Amazonas**. Atabapo: Kanaripó, rio Ventuari, 4° 3' 0” N, 66° 41' 27” W, 98 m.a.s.l., 29 May 1978, FL, *Huber 1871* (NY, VEN); Cerro Gavillán, ca. La Carmelita, 4° 11' 20” N, 66° 31' 19” W, 235 m.a.s.l., 18 Mar 2002, Sterile, *Aymard 12241* (MO, PORT); Kanaripó, rio Ventuari, 4° 4' 0” N, 66° 49' 0” W, 110 m.a.s.l., 22 Mar 2002, FL-FR, *Aymard 12291* (INPA); rio Ventuari, ca. 5 km por sendero en frente a la Isla Caymán, 4° 7' 22” N, 66° 40' 49” W, 129 m.a.s.l., 13 Mar 2002, Sterile, *Aymard 12190* (MO, PORT); rio Ventuari, ca. 5 km por sendero en frente a la Isla Caymán, 4° 7' 41” N, 66° 40' 38” W, 126 m.a.s.l., 13 Mar 2002, Sterile, *Aymard 12203* (INPA); SSE trail to S. Antonio del Orinoco, 3° 45' 0” N, 67° 4' 0” W, 100 m.a.s.l., 4 Dec 1978, FR, *Huber 2842* (INPA, NY, VEN); Manapiare: Cerro Moriche, N base, 4° 44' 57” N, 66° 23' 0” W, 110 m.a.s.l., 20 Mar 2002, FR, *Aymard 12251* (INPA); Cerro Moriche, SW base, 4° 43' 42” N, 66° 20' 31” W, 132 m.a.s.l., 21 Mar 2002, FL, *Aymard 12268* (INPA); Cerro Moriche, NW base, 4° 44' 57” N, 66° 24' 0” W, 120 m.a.s.l., 20 Mar 2002, FL-FR, *Aymard 12267* (INPA).

14. *Pagamea jauaensis* Steyerm.

Specimens measured — **VENEZUELA**. **Amazonas**. Atabapo: Cabeceras del Río Yudi, 5° 29' 0” N, 65° 18' 0” W, 1600 m.a.s.l., Mar 1992, FR, *Delgado 1699* (NY, PORT); Manapiare: Serrania de Yutaje, 4 km W of rio Coro-Coro, 5° 41' 0” N, 66° 10' 0” W, 1600 m.a.s.l., 4 Mar 1987, FL, *Liesner 21635* (F, MO, NY, PORT); Sierra Maigualida, Caño Iguana, 5° 30' 0” N, 65° 15' 0” W, 2000 m.a.s.l., 1 Mar 1991, FL, *Berry 4852* (MO, NY); **Bolívar**. Sucre: Meseta del Jaua, Cerro Jáua, 4° 45' 0” N, 64° 26' 0” W, 2000 m.a.s.l., 25 Mar 1967, FL, *Steyermark 97928* (MO, NY, VEN); Meseta del Jaua, Cerro Jáua, 4° 48' 50” N, 64° 34' 10” W, 1800 m.a.s.l., 7 Mar 1974, FR, *Steyermark 109824* (MO, VEN); Meseta del Jaua, Cerro Jáua, 4° 48' 50” N, 64° 34' 10” W, 1800 m.a.s.l., 26 Feb 1974, FL, *Steyermark 109554* (VEN).

15. *Pagamea capitata* Benth.

Specimens measured — **BRASIL**. **Amazonas**. Nova Aripuanã: Nova Prainha, 5° 7' 13” S, 60° 22' 44” W, 40 m.a.s.l., 31 Jul 1976, Sterile, *Mota 60882INPA* (INPA); São Gabriel da Cachoeira: Serra Tunuhy, rio Issana, 1° 30' 0” N, 68° 8' 0” W, 164 m.a.s.l., 29 Apr 1975, Sterile, *Cavalcante 3049* (INPA, NY); **Pará**. Itaituba: Serra do Cachimbo, 8° 57' 0” S, 54° 54' 0” W, 425 m.a.s.l., 14 Dec 1956, FR, *Pires 6221* (NY, UNB); Serra do Cachimbo, Santarém-Cuiabá, BR 163, km 794, 9° 22' 0” S, 54° 54' 0” W, 379 m.a.s.l., 25 Apr 1983, FR, *Amaral 938* (INPA, MO, NY, UNB, US); Serrado Cachimbo, BR-163, km 856, 9° 40' 0” S, 54° 54' 0” W, 400 m.a.s.l., 19 Feb 1977, FR, *Kirkbride 2909* (F, INPA, MO, NY, US); Oriximiná: rio Trombetas, rio Jaranacaru, 1° 17' 29” S, 55° 56' 54” W, 51 m.a.s.l., 2 Dec 1910, FL-old, *Ducke 11269* (F, K, US); **GUYANA**. **Cuyuni-Mazaruni**. Pakaraima Mts: Arubaru river (Kako tributary), upper Mazaruni, 5° 5' 0” N, 58° 15' 0” W, 600 m.a.s.l., 5 Feb 1939, FL, *Pinkus 189* (NY, US); Imbaimadai, 5° 42' N, 60° 13' W, 587 m.a.s.l., 23 Jan 2004, FR, *Redden 2357* (MO, US); Ireng river, Kurutuik Falls, 5° 5' 0” N, 59° 59' 0” W, 800 m.a.s.l., 21 May 1998, FL, *Henkel 6543* (MO, US); **Demerara-Mahaica**. Linden hwy, 1 km N of Kuru-Kuru Creek., 6° 25' 0” N, 58° 14' 0” W, 15 m.a.s.l., 3 Jan 1992, FL, *Hoffman 696* (COL, INPA, MO, NY, US); Atkinson field, 6° 31' N, 58° 17' 30” W, 2 m.a.s.l., 12 Nov 1958, FL, *Harrison 1737* (NY); NE coastal plain W of Abary river, ca. 35 mi SE of Georgetwon., 6° 4' 0” N, 57° 44' 0” W, 15 m.a.s.l., 16 Oct 1955, FR, *Little 16886* (US); Soesdyke-Linden hwy, S of Timehri aiport, 6° 16' 0” N, 58° 15' 0” W, 25 m.a.s.l., 11 Oct 1989, FR, *Kelloff 609* (COL, MO, NY, US); Kuru Kuru Creek along the Soesdyke-Linden hwy, 6° 24' 0” N, 58° 13' 0” W, 15 m.a.s.l., 8 Dec 1989, FL-FR, *Gillespie 2651* (COL, MO, NY, US); **Potaro-Siparuni**. Iwokrama Rainforest Reserve, 4° 33' 0” N, 58° 50' 0” W, 75 m.a.s.l., 27 Sep 1995, FL-FR, *Clarke 237* (MO, US); Kaieteur plateau, 5° 9' 0” N, 59° 28' 0” W, 730 m.a.s.l., 3 May 1944, FL, *Maguire 23185* (F, MO, NY); Kaieteur plateau, above kaieteur falls, 5° 11' 0” N, 59° 29' 0” W, 450 m.a.s.l., 25 Jul 1991, FR, *Lance 82* (MO, NY, US); Kaieteur plateau, around airstrip, 5° 10' 0” N, 59° 29' 0” W, 300 m.a.s.l., 11 Jul 1993, FR, *Kelloff 889* (F, MO, US); Kaieteur plateau, 5° 10' 0” N, 59° 29' 30” W, 500 m.a.s.l., 25 Feb 1962, FR, *Cowan 1957* (NY, US); Kurupukari-Annai rd, 28 mi from Kurupukari, 4° 20' 0” N, 58° 50' 0” W, 60 m.a.s.l., 30 Sep 1996, FR, *Clarke 2668* (US); Ebini, Rupununi savanna, 3° 0' 0” N, 59° 30' 0” W, 155 m.a.s.l., 29 Oct 1963, FR, *Goodland 1079* (NY); Rupununi: base of Mt. Makarapan to Rupununi river, 3° 56' 0” N, 58° 56' 0” W, 109 m.a.s.l., 20 Sep 1988, FR, *Maas 7578* (US); **Upper Demerara-Berbice**. About 27 km from Ituni along Ituni-Kwakwani rd, 5° 22' 0” N, 58° 7' 0” W, 50 m.a.s.l., 16 Jan 1990, FL-FR, *Gillespie 2969* (COL, MO, NY, US);Berbice river; Warniabo Creek, 5° 39' 0” N, 57° 53' 0” W, 60 m.a.s.l., 28 Jun 1995, FL, *Chanderbali 117* (MO, NY, US); **SURINAME**.5° 25' 53” N, 54° 54' W, 29 m.a.s.l., 1843, FL, *Hostmann 801* (BM, F, K, MO, P); **Paramaribo**. Zanderij, 45-50 km S of Paramaribo, 5° 28' 0” N, 55° 21' 0” W, 24 m.a.s.l., 19 Sep 1976, FR, *Mori 8331* (NY, SPF, US); **Sipaliwini**. Tafelberg, 3° 54' 55” N, 56° 11' 40” W, 610 m.a.s.l., , FL-FR, *Hawkins 1966* (MO); Lisa Kreek Savanah, Tafelberg, 3° 54' 32” N, 56° 12' 44” W, 600 m.a.s.l., 26 Jun 1998, FL-old, *Hawkins 1793* (MO, umounted); Tafelberg, 3° 54' 26” N, 56° 12' 45” W, 313 m.a.s.l., 26 Jun 1998, FR, *Lohmann 165* (MO); **VENEZUELA**. **Amazonas**. Alto Orinoco: Duida tepui, 3° 15' 16” N, 65° 36' 0” W, 1000 m.a.s.l., Jan 1969, FL, *Farinas 387* (NY, VEN); Duida tepui, plateau above Culebra, 3° 35' 0” N, 65° 45' 0” W, 1600 m.a.s.l., 23 Apr 1949, Sterile, *Maguire 29125* (NY); Duida tepui, 3° 10' 0” N, 65° 31' 0” W, 1350 m.a.s.l., 29 Jan 1975, FL, *Tillett 75116* (NY, VEN); Duida tepui, plateau above Culebra, 3° 13' 0” N, 65° 58' 0” W, 1400 m.a.s.l., 20 Nov 1950, FR, *Maguire 29573* (NY, US, VEN); Duida tepui, 3° 25' 30” N, 65° 40' 0” W, 1341 m.a.s.l., 1928, FL, *Tate 794* (F, NY); Duida tepui, 3° 25' 20” N, 65° 40' 0” W, 1840 m.a.s.l., 1 Sep 1944, FR, *Steyermark 58192* (F, NY); Autana: San Pedro, rio Autana, 4° 44' 0” N, 67° 33' 0” W, 100 m.a.s.l., 2 Jul 1979, FR, *Huber 4072* (COL, K, NY, US); San Pedro, rio Autana, 4° 51' 0” N, 67° 34' 0” W, 150 m.a.s.l., 16 Jul 1980, FR, *Huber 5365* (COL, NY, US, VEN); Rio Negro: Cerro Aracamuni, 1° 32' 0” N, 65° 48' 0” W, 750 m.a.s.l., 10 Feb 1981, FR, *Huber 5916* (K, MO, NY, VEN); **Bolívar**. Gran Sabana: NE Arautá-parú y km 148 al S de El Dorado, 5° 41' 0” N, 61° 35' 0” W, 1350 m.a.s.l., 21 Dec 1970, FR, *Steyermark 104170* (NY, VEN); cabeceras occidentales del rio Urimán, 5° 43' 0” N, 62° 50' 0” W, 1050 m.a.s.l., 10 May 1987, FR, *Huber 12204* (MO, US); Auyán tepui, 5° 55' 0” N, 62° 32' 30” W, 1100 m.a.s.l., Jan 1938, FR, *Tate 1164* (NY); Auyán tepui, 5° 55' 0” N, 62° 32' 0” W, 1000 m.a.s.l., 18 May 1964, FL-old, *Steyermark 94193* (NY, US, VEN); Auyán tepui, 5° 41' 0” N, 62° 32' 0” W, 1100 m.a.s.l., Apr 1956, FR, *Vareschi 4637* (F, VEN); Between Mission of Santa Teresita de Kavanayén, 5° 38' 0” N, 61° 48' 0” W, 1220 m.a.s.l., 26 Oct 1944, FR, *Steyermark 59339* (F, US); Cerro Guanacoco, 4° 46' 30” N, 63° 55' 5” W, 1450 m.a.s.l., 3 Mar 1974, Sterile, *Steyermark 109720* (F, MO, VEN); rio Kanayeuta, ca. 15 km NW de Sta. Elena de Uairén, 4° 43' 0” N, 61° 6' 0” W, 1050 m.a.s.l., 5 Oct 1982, FR, *Huber 6674* (NY); N del Kamámeru, 5° 25' 0” N, 61° 13' 0” W, 1000 m.a.s.l., 4 Mar 1983, FR, *Huber 7304* (MO, US, VEN); ca. 2 kms. E of Kavanayen, 5° 37' 5” N, 61° 48' 0” W, 1060 m.a.s.l., 15 Dec 1984, FR, *Kral 72078* (NY, US); ierra de Lema, regíon del Río Carrao alto, 65 km N de Kavanayén, 5° 57' 0” N, 61° 46' 0” W, 950 m.a.s.l., 31 Jan 1988, FR, *Huber 12534* (US); Ilu-tepui, 5° 37' 0” N, 61° 13' 0” W, 1000 m.a.s.l., 18 Jun 1985, FL, *Huber 10615* (NY, TFVA, VEN); Río Cama. Cerca del puente sobre el rio Cama, a +/- 61 km de La Ciudadela, 5° 18' 0” N, 61° 10' 0” W, 1100 m.a.s.l., 30 Jan 1981, FR, *Berti 136981* (NY, US); surrounding of Roraima tepui, 4° 59' 13.66” N, 60° 53' 06.66” W, 1282 m.a.s.l., 1842, FL, *Schomburgk 578* (BM, K, MO, NY, P); rio Karuai and Salto de Iraba-naima along rio Karuai, at SW base of Ptari-tepui, 5° 46' 0” N, 61° 46' 0” W, 1220 m.a.s.l., 28 Nov 1944, FR, *Steyermark 60700* (F, US, VEN); Uarama tepui, 5° 3' 0” N, 61° 22' 0” W, 1200 m.a.s.l., 9 Mar 1962, FL, *Steyermark 62* (NY, VEN); Uarama tepui, 5° 3' 0” N, 61° 22' 0” W, 1220 m.a.s.l., 25 Apr 1960, FR, *Steyermark 630* (NY, US, VEN); Raul Leoni: Macizo Ichún, 4° 45' 0” N, 63° 24' 0” W, 660 m.a.s.l., 2 Sep 1988, Buds, *Fernandez 4725* (NY, PORT); Cerro Guaiquinima, 5° 44' 4” N, 63° 41' 8” W, 750 m.a.s.l., 20 Jan 1977, FR, *Steyermark 113121* (F, NY, VEN); Cerro Guaiquinima, 5° 44' 0” N, 63° 40' 10” W, 1650 m.a.s.l., 4 Jan 1952, FL, *Maguire 32982* (NY); Cerro Guaiquinima, 5° 44' 30” N, 63° 40' 20” W, 1650 m.a.s.l., 11 Jan 1952, FR, *Maguire 33070* (NY, US, VEN); Cerro Guaiquinima, 5° 54' 0” N, 63° 42' 0” W, 1350 m.a.s.l., 2 Apr 1984, FR, *Huber 9346* (MO, NY, VEN); Cerro Guaiquinima, 5° 51' 0” N, 63° 25' 0” W, 1350 m.a.s.l., 26 Sep 1985, FL-FR, *Huber 10895* (NY, TFVA, VEN); Sierra Ichún, N del Salto María Espuma (Salto Ichún), 4° 46' 0” N, 63° 18' 0” W, 675 m.a.s.l., 27 Dec 1961, FL-old, *Steyermark 90281* (NY, US); Sucre: Cerro Jáua, along rio Kanarakuni, 4° 28' 0” N, 63° 57' 0” W, 400 m.a.s.l., 17 Mar 1967, FR, *Steyermark 98207* (NY, US, VEN); Meseta del Jaua, Cerro Sarisariñama, 4° 41' 40” N, 64° 13' 20” W, 1320 m.a.s.l., 13 Feb 1974, FR, *Steyermark 109060* (VEN); Meseta del Jaua, Cerro Sarisariñama, 4° 41' 40” N, 64° 13' 20” W, 1410 m.a.s.l., 10 Feb 1974, Sterile, *Steyermark 108889* (F, US, VEN).

Specimens seen but not measured — **BRASIL**. **Amazonas**. Borba: interflúvio Madeira-Purus, 4° 18' 08” S, 60° 29' 57” W, 26 m.a.s.l., , ?, *Cohn-Haft 02* (INPA); Lábrea: 7° 16' 0” S, 64° 47' 30” W, 75 m.a.s.l., 8 Jul 1976, Sterile, *Mota sn* (IBGE, INPA); Maués: 03° 48' 38” S, 57° 36' 37” W, 50 m.a.s.l., , ?, *Carvalho 01* (INPA); 03° 48' 36” S, 57° 36' 36” W, 50 m.a.s.l., , ?, *Carvalho 02* (INPA); 03° 48' 37” S, 57° 36' 38” W, 50 m.a.s.l., , ?, *Carvalho 03* (INPA); **Pará**. Itaituba: Serra do Cachimbo, BR-163, km 823, 8° 40' 0” S, 54° 54' 0” W, 570 m.a.s.l., 7 Nov 1977, FL, *Prance 24986* (MO, NY, US); **GUYANA**. **Cuyuni-Mazaruni**. Pakaraima Mts: 0.5 to 2 km W of Waramadan village, 5° 58' 0” N, 60° 44' 0” W, 490 m.a.s.l., 8 Jun 1990, FR, *McDowell 3145* (MO, NY, Us); Ayanganna plateau, 5° 28' 0” N, 60° 4' 0” W, 675 m.a.s.l., 1 Mar 1987, FR, *Pipoly 10893* (NY, P, US); Chi-Chi Mts, 2 km W of Chi-Chi falls, 5° 34' 0” N, 60° 13' 0” W, 550 m.a.s.l., 17 Feb 1987, FR, *Pipoly 10262* (MO, NY, P); Imbaimadai, Partang river, 1 km from mouth, 5° 42' 0” N, 60° 16' 0” W, 550 m.a.s.l., 14 Dec 1989, FR, *Gillespie 2678* (COL, MO, NY); Kuroba, 3 km N of confluence of Kamarang R. with Mazaruni R., 5° 54' 0” N, 60° 36' 0” W, 580 m.a.s.l., 24 Jan 1996, FR, *Clarke 809* (MO, NY, US); Macaw Creek, hillside of Kartabo Mt., 6° 0' 0” N, 61° 5' 0” W, 580 m.a.s.l., 4 Jun 1990, FR, *McDowell 3086* (MO, NY); Imbaimadai, 5° 37' 3.6” N, 60° 13' 8.3” W, 902 m.a.s.l., 4 Dec 2002, FR, *Redden 1405* (MO, US); between Chinowieng Village and Heiba river, 5° 27' 0” N, 60° 4' 0” W, 750 m.a.s.l., 13 Nov 1992, FR, *Henkel 270* (MO, NY, US); banks of Mazaruni W of Imbaimadai, 5° 43' 0” N, 60° 20' 0” W, 488 m.a.s.l., 21 Jun 1986, FL-FR, *Pipoly 7940* (MO, NY, P); Karowrieng river, 0.5-1 km SE Maipuri falls, 5° 40' 0” N, 60° 13' 0” W, 635 m.a.s.l., 15 Oct 1992, FL, *Hoffman 3031* (MO, US); Membaru-Kurupung trail, 5° 55' 0” N, 60° 36' 0” W, 1100 m.a.s.l., 10 Nov 1951, FR, *Maguire 32534* (NY); between Sukabi river and Kurutuik falls, 5° 6' 0” N, 59° 59' 0” W, 670 m.a.s.l., 22 Oct 1994, FR, *Mutchnick 168* (BM, NY, US); 8.6 km NE Imbaimadai on Partang river, 5° 46' 0” N, 60° 15' 0” W, 650 m.a.s.l., 21 May 1992, FL, *Hoffman 1784* (MO, NY, US); 2-3 km SSW from Kukuinang peak, 5° 4' 0” N, 59° 57' 0” W, 1000 m.a.s.l., 27 Feb 1993, FR, *Henkel 1629* (COL, MO, NY, US); Imbaimadai, Partang river, 5° 42' 12” N, 60° 16' 36” W, 902 m.a.s.l., 20 Nov 2002, FR, *Redden 1195* (MO, US); Imbaimadai, Partang river, 5° 42' 10.5” N, 60° 16' 50” W, 873 m.a.s.l., 7 Dec 2002, FR, *Forbes 335* (MO, US); Paruima, 9 km W, Ararata scrub area, 5° 49' 0” N, 61° 8' 0” W, 800 m.a.s.l., 3 Jul 1997, FL, *Clarke 5246* (MO, US); Imbaimadai, near airstrip, 5° 42' 30” N, 60° 18' W, 500 m.a.s.l., 2 Jul 2004, Buds, *Clarke 12382* (MO, US); Imbaimadai, Partang river at Partang Rapids, 5° 41' 0” N, 60° 17' 0” W, 460 m.a.s.l., 17 Jun 1960, FL, *Maguire 43873* (NY); Karowrieng river, peak NW of Maipuri Falls, 5° 43' 0” N, 60° 8' 0” W, 1385 m.a.s.l., 13 Jun 1986, FL, *Pipoly 7687* (NY, P); Karowrieng river, above Maipuri falls, 5° 42' 0” N, 60° 3' 0” W, 550 m.a.s.l., 12 Jun 1986, FL, *Pipoly 7623* (MO, NY, P, US); peak N of Karowrieng river, 5° 43' 0” N, 60° 8' 0” W, 1385 m.a.s.l., 14 Jun 1986, FL, *Pipoly 7748* (MO, NY); upper Mazaruni river, Kamakusa, 5° 56' 44” N, 59° 56' 44” W, 108 m.a.s.l., 23 Nov 1922, FL, *De 2862* (MO, NY); upper Mazaruni river, 5° 40' 0” N, 60° 1' 0” W, 732 m.a.s.l., 22 Sep 1922, FR, *De 2111* (F, MO, NY); upper Mazaruni river, 5° 41' 0” N, 60° 1' 0” W, 660 m.a.s.l., 22 Sep 1922, FR, *De 2214* (MO, NY); Utshi river to Great falls trail, on Kamarang R., 5° 40' 0” N, 61° 6' 0” W, 910 m.a.s.l., 30 Jan 1996, FR, *Clarke 894* (MO); Chinoweing village, 5° 32' 0” N, 60° 7' 0” W, 660 m.a.s.l., 21 Feb 1987, FR, *Pipoly 10408* (MO, NY, P, US); Chinoweing village, 5° 32' 0” N, 60° 7' 0” W, 660 m.a.s.l., 21 Feb 1987, FR, *Pipoly 10495* (NY, P, US); **Demerara-Berbice**. 15 km E of Rochstone, on Linden-rockstone rd., 5° 58' 0” N, 58° 30' 0” W, 25 m.a.s.l., 1 Jan 1987, FL-FR, *Pipoly 9558* (MO, NY, P); 15 km E of Rochstone, on Linden-rockstone rd., 5° 58' 0” N, 58° 30' 0” W, 25 m.a.s.l., 1 Jan 1987, FL, *Pipoly 9597* (MO, NY, P); **Demerara-Mahaica**. along hwy to Timehri aiport, 6° 30' 0” N, 58° 0' 0” W, 4 m.a.s.l., 22 Mar 1987, FL-FR, *Boom 7122* (MO, NY); Linden-Soesdyke hwy, ca. 16 mi S of Georgetown, 6° 20' 0” N, 58° 15' 0” W, 25 m.a.s.l., 7 Dec 1986, FL, *Pipoly 9176* (MO, NY, P); Kuru Kuru Creek along the Soesdyke-Linden hwy, 6° 25' 0” N, 58° 15' 0” W, 20 m.a.s.l., 18 Mar 1988, FR, *Hahn 3949* (COL, MO, NY, US); 3 mi E of Atkison field., 6° 32' N, 58° 17' 45” W, 2 m.a.s.l., 16 Aug 1953, FR, *Irwin 395* (US); Timehri, St. Cuthbert’s trail, 6° 30' N, 58° 18' 10” W, 2 m.a.s.l., 5 Jan 1969, FR, *U.G 8* (NY); between Dora and Maibia Creek;, 6° 18' 0” N, 58° 14' 0” W, 35 m.a.s.l., , ?, *Pipoly 9679* (MO, NY, P); Yarawkabra settlement, 6° 28' 0” N, 58° 12' 0” W, 25 m.a.s.l., 13 Sep 1986, FL, *Pipoly 8420* (MO, NY); Yarawkabra settlement, 6° 30' 0” N, 58° 10' 0” W, 5 m.a.s.l., 23 May 1986, FR, *Pipoly 7376* (COL, MO, NY, P, SP); **East Berbice-Corentyne**. Berbice savanna near Takama Army Base, 5° 43' 0” N, 57° 57' 0” W, 100 m.a.s.l., 14 Aug 1993, FR, *Henkel 2483* (COL, INPA, MO, NY, US); **Potaro-Siparuni**. Annai-Karupukari rd, 45 km N of Surama village, 4° 20' 0” N, 58° 50' 0” W, 65 m.a.s.l., 24 Apr 1992, FR, *Hoffman 1445* (MO, NY, US); Kaieteur plateau, around airstrip, 5° 10' 0” N, 59° 29' 0” W, 395 m.a.s.l., 24 Jan 1989, FR, *Pipoly 9771* (MO, P); Kaieteur plateau, 5° 12' 0” N, 59° 30' 0” W, 540 m.a.s.l., 22 Jul 1993, FR, *Henkel 2389* (INPA, MO, NY); Kaieteur plateau, 5° 13' 0” N, 59° 27' 0” W, 692 m.a.s.l., 6 May 1944, FL, *Maguire 23281* (MO, NY); Kaieteur plateau, 5° 10' 0” N, 59° 29' 0” W, 300 m.a.s.l., 12 Jun 1994, FL, *Kelloff 1054* (MO, US); **Upper Demerara-Berbice**. 5 km E of Rockstone, on Linden-Tockstone rd, 5° 58' 0” N, 58° 35' 0” W, 60 m.a.s.l., 19 Jan 1987, FR, *Pipoly 9629* (MO, NY, P); E of Ituni, 35 mi of Mackenzie., 5° 32' 0” N, 58° 15' 0” W, 101 m.a.s.l., 17 Jan 1955, FR, *Cowan 39253* (NY); Malali, Demerara river, 5° 35' 0” N, 58° 28' 22” W, 168 m.a.s.l., 30 Oct 1922, ?, *De 2659* (MO, NY, US); Waruni-Ituni, along the Berbice-Rupununi trail, 5° 30' 00” N, 58° 20' W, 94 m.a.s.l., 8 May 1919, FL, *Abraham 126* (NY); **SURINAME**., FL, *Kappler 801* (F); **Para**. Jodensavanna, 5° 25' 0” N, 54° 59' 0” W, 20 m.a.s.l., 12 Apr 1949, FL, *Lanjouw 2979* (NY); **Sipaliwini**. Tafelberg, 3° 54' 55” N, 56° 11' 40” W, 600 m.a.s.l., 27 Jun 2001, FR, *Evans 3223* (MO); Tafelberg, 3° 54' 35” N, 56° 11' 10” W, 600 m.a.s.l., 30 Jun 2001, FR, *Evans 3253* (MO); Tafelberg, 3° 56' 00” N, 56° 11' 10” W, 600 m.a.s.l., 26 Jun 2001, FR, *Evans 3214* (MO); Tafelberg, 03° 53' 30” N, 56° 10' 05” W, 600 m.a.s.l., 7

Jul 2001, FR, *Evans 3318* (MO); Tafelberg, 3° 48' 0” N, 56° 8' 0” W, 300 m.a.s.l., 26 Feb 1961, FR, *Krames 3094* (NY); Tafelberg, 3° 45' 49” N, 56° 2' 11” W, 565 m.a.s.l., 13 Sep 1944, FR, *Maguire 24740* (MO, NY); Tafelberg, 3° 45' 49” N, 56° 0' 30” W, 364 m.a.s.l., 7 Aug 1944, FL-FR, *Maguire 24252* (MO, NY); **VENEZUELA**.Cuenca Alta del rio Karaurin, 5° 21' 00” N, 61° 08' 45” W, 1100 m.a.s.l., 3 Sep 1986, FR, *Hernandez 330* (VEN); **Amazonas**. Alto Orinoco: Duida tepui, 3° 15' 16” N, 65° 36' 0” W, 1000 m.a.s.l., Feb 1969, Sterile, *Farinas 386* (NY); Duida tepui, plateau above Culebra, 3° 36' 0” N, 65° 42' 0” W, 1250 m.a.s.l., 2 Mar 1985, FL, *Liesner 18163* (MO, NY); Sierra de Untuyan, en las cabeceras del rio Mauaca, 1° 32' 0” N, 65° 11' 0” W, 600 m.a.s.l., 26 Feb 1981, FR, *Guanchez 819* (MO, VEN); Atabapo: Caño Negro, 3° 40' 0” N, 65° 45' 0” W, 205 m.a.s.l., 8 Feb 1982, FL, *Steyermark 126124* (COL, MO, NY, VEN); Autana: San Pedro, rio Autana, 4° 51' 0” N, 67° 32' 0” W, 95 m.a.s.l., 12 Nov 1984, FL, *Guanchez 3518* (MO, VEN); **Bolívar**. Gran Sabana: 5° 40' 0” N, 61° 25' 0” W, 1300 m.a.s.l., 4 Apr 1985, FR, *Holst 2211* (MO, VEN); 1 km al NNE del puente sobre el Río Yuruaní, San Francisco de Yuruaní, 5° 6' 0” N, 61° 5' 0” W, 900 m.a.s.l., 19 Jan 1985, FR, *Huber 9946* (MO, NY, VEN); 1-3 km NW of Luepa rd to La Ciudadela, 5° 52' 0” N, 61° 29' 0” W, 1350 m.a.s.l., 14 Nov 1997, FL-FR, *Berry 6560* (MO); 10 km al E. del Cerro Venado y 25 km al ENE de Canaima, 06° 20' 57” N, 62° 42' 41” W, 950 m.a.s.l., 28 May 1995, FR, *Duno 474* (VEN); Karaurin tepui, 5° 19' 0” N, 61° 4' 0” W, 950 m.a.s.l., 1 May 1988, FL-FR, *Liesner 24118* (MO, NY, VEN); 17 km E of El Pauji by rd and 64 km W of Santa Elena, 4° 30' 0” N, 61° 30' 0” W, 850 m.a.s.l., 30 Oct 1985, FL-FR, *Liesner 19168* (MO, NY); 2 km al SW de Perai-tepui, 55 km al W de Santa Elena de Uairén, 4° 33' 0” N, 61° 30' 0” W, 1050 m.a.s.l., 13 Aug 1984, FR, *Huber 9635* (MO, NY, VEN); 50 km entre San Isidoro y Yuruaní, 4° 50' 0” N, 61° 5' 0” W, 792 m.a.s.l., 2 Mar 1984, FR, *Colonnello-Medina 709* (MO); Auyán tepui, 5° 44' 0” N, 62° 32' 0” W, 950 m.a.s.l., 25 Nov 1982, FL, *Davidse 22707* (MO, NY); Carretera fuerta Luepa-Kanavayen, entre Iwarkey y Riworiwo, 5° 43' 38” N, 61° 39' 16” W, 1538 m.a.s.l., 23 Mar 1993, FR, *Ramirez 4072* (MO, VEN); Carretera fuerta Luepa-St. Elena, 5° 46' 0” N, 61° 22' 0” W, 1210 m.a.s.l., 20 Mar 1993, FR, *Ramirez 3672* (MO, VEN); Cerro Akurimá, 2 km al N de Santa Elena de Uairén, 4° 37' 0” N, 61° 7' 0” W, 1000 m.a.s.l., 19 Aug 1984, FR, *Huber 9699* (MO, NY, VEN); En el valle de rio Guarí, W de la carretera Luepa-Santa Elena, 4° 43' 0” N, 61° 3' 0” W, 900 m.a.s.l., 25 Jul 1983, FL, *Huber 7841* (MO, NY, TFVA, VEN); Mandapai, 5° 37' 5” N, 61° 48' 30” W, 1180 m.a.s.l., 28 Mar 1946, FL, *Yasser 1782* (VEN); rd San Rafael y el río Kamúrán, 5° 36' 30” N, 61° 12' 30” W, 1150 m.a.s.l., 15 Jul 1974, FL-old, *Ruiz-Teran 11285* (VEN); Alrededores de la Quebrada del Jaspe, 4° 45' 30” N, 61° 15' 20” W, 948 m.a.s.l., 25 Feb 1983, FR, *Garofalo 1220* (INPA); rio Cuquenan, 4° 45' 00” N, 61° 15' 00” W, 1026 m.a.s.l., Dec 1909, FL, *Ule 8767* (F); ca. 25 km SSE of Canaima, 6° 2' 0” N, 62° 48' 0” W, 435 m.a.s.l., 1 Sep 1983, FL, *Prance 28475* (MO, NY); Parque Nacional Canaima, 5° 50' 26” N, 61° 27' 58” W, 1300 m.a.s.l., 21 Feb 1997, FR, *Picon 2928* (VEN); Raul Leoni: Cerro Guaiquinima, 5° 44' 36” N, 63° 38' 55” W, 833 m.a.s.l., 5 Dec 1990, FR, *Duno 341* (VEN); Sierra Auraima, rio Paragua, 6° 22' 30” N, 63° 33' 30” W, 330 m.a.s.l., 13 May 1987, FL, *Stergios 10488* (MO, PORT, VEN); Cerro Guaiquinima, 5° N, 63° W, 990 m.a.s.l., 4 Feb 1990, FL-FR, *Boom 9335* (MO); Cerro Guaiquinima, 5° 47' 0” N, 63° 48' 0” W, 1400 m.a.s.l., 30 May 1987, FL, *Huber 12243* (MO, NY, VEN); Cerro Guaiquinima, 6° 4' 0” N, 63° 22' 0” W, 500 m.a.s.l., 11 May 1987, FL, *Aymard 5980* (MO, PORT); Cerro Guaiquinima, 5° 40' 0” N, 63° 26' 0” W, 1250 m.a.s.l., 26 May 1978, FR, *Steyermark 117416* (MO, VEN); Cerro Guaiquinima, 5° 44' 4” N, 63° 41' 8” W, 800 m.a.s.l., 24 May 1978, Sterile, *Steyermark 117297* (MO, VEN); Sucre: Meseta del Jaua, Cerro Sarisariñama, 4° 41' 40” N, 64° 13' 20” W, 1320 m.a.s.l., 13 Feb 1974, FR, *Steyermark A109054* (VEN).

16. *Pagamea duckei* Standley

Specimens measured — **BRASIL**. **Amazonas**. Manaus: Manaus-Caracaraí rd, 3° 0' 10” S, 60° 1' 50” W, 52 m.a.s.l., 19 Oct 1966, FL, *Prance 2695* (F, NY, P); Manaus-Caracaraí rd, 2° 55' 10” S, 60° 1' 50” W, 59 m.a.s.l., 10 Nov 1961, FL, *Rodrigues 2773* (INPA); Manaus-Caracaraí rd, 2° 43' 0” S, 60° 1' 50” W, 82 m.a.s.l., 26 Jan 1963, FR, *Eiten 5143* (MO, NY, UNB, US); Reserva Biológica da Campina, 2° 38' 20” S, 60° 1' 50” W, 78 m.a.s.l., 8 Mar 1996, FR, *Cid 11218* (INPA); Reserva Biológica da Campina, 2° 35' 20” S, 60° 1' 50” W, 78 m.a.s.l., 31 Oct 1977, FL, *Keel 226* (NY, US); Reserva Biológica da Campina, 2° 35' 20” S, 60° 1' 50” W, 78 m.a.s.l., 26 Dec 1982, FR, *Plowman 12658* (F, INPA, US); Manaus-Caracaraí rd, 2° 40' 6”

S, 60° 2' 46” W, 67 m.a.s.l., 4 Aug 2000, FR, *Vicentini 1688* (INPA, MO); Reserva Biológica da Campina, 2° 37' 15” S, 60° 02' 27” W, 73 m.a.s.l., 28 Jul 2003, Sterile, *Vicentini 2063* (INPA, MO); igarapé Tarumã-mirin, 2° 45' 51” S, 60° 15' 57” W, 50 m.a.s.l., 14 Aug 2003, FR, *Vicentini 2064* (INPA, MO); rio Cueiras, Lago de Jaradá, ca. 40 km from the mouth at the rio Negro, 2° 41' 46” S, 60° 21' 10” W, 52 m.a.s.l., 4 Jun 1989, FR, *Mori 20349* (INPA, NY, SPF); igarapé Tarumã-mirin, 3° 0' 20” S, 60° 21' 49” W, 38 m.a.s.l., 24 Apr 1941, FR, *Ducke 696* (F, MO, NY, US).

Specimens seen but not measured — **BRASIL**. **Amazonas**. <u>Manaus</u>: Manaus-Caracaraí rd, 2° 35' 22” S, 60° 1' 50” W, 96 m.a.s.l., 28 Jan 1959, FR, *Rodrigues 193* (US); 2° 35' 20” S, 60° 1' 50” W, 80 m.a.s.l., 28 Jan 1959, FR, *Rodrigues 793* (F); Manaus-Caracaraí rd, 3° 0' 0” S, 60° 1' 50” W, 54 m.a.s.l., 17 Oct 1961, FL, *Rodrigues 2657* (INPA); Manaus-Caracaraí rd, 3° 0' 0” S, 60° 1' 50” W, 54 m.a.s.l., 18 Oct 1959, FL, *Rodrigues 1348* (F, INPA); Manaus-Caracaraí rd, 3° 0' 0” S, 60° 1' 50” W, 54 m.a.s.l., 30 Sep 1960, FL, *Rodrigues 1800* (F, INPA, US); Manaus-Caracaraí rd, 3° 0' 20” S, 60° 1' 50” W, 52 m.a.s.l., 17 Oct 1961, FL, *Rodrigues 3457* (NY, US); Manaus-Caracaraí rd, 3° 0' 30” S, 60° 1' 50” W, 52 m.a.s.l., 17 Mar 1967, FR, *Prance 4666* (F, INPA, NY, P); Manaus-Caracaraí rd, 1° 55' 0” S, 60° 1' 20” W, 110 m.a.s.l., 13 Oct 1997, FR, *Vieira 1347* (INPA); Manaus-Caracaraí rd, 2° 55' 0” S, 60° 1' 50” W, 59 m.a.s.l., 10 Nov 1961, FL, *Rodrigues 3573* (US); Reserva Biológica da Campina, 2° 35' 20” S, 60° 1' 50” W, 78 m.a.s.l., 25 Feb 1974, FR, *Albuquerque 1077* (INPA); Reserva Biológica da Campina, 2° 35' 20” S, 60° 1' 50” W, 78 m.a.s.l., 9 Oct 1974, FL, *Albuquerque 1105* (INPA); Reserva Biológica da Campina, 2° 35' 20” S, 60° 1' 50” W, 78 m.a.s.l., 11 Nov 1974, FR, *Coelho 49151INPA* (INPA, US); Reserva Biológica da Campina, 2° 35' 20” S, 60° 1' 50” W, 78 m.a.s.l., 23 May 1975, FR, *Lisboa 96* (INPA); Reserva Biológica da Campina, 2° 35' 20” S, 60° 1' 50” W, 78 m.a.s.l., 11 Apr 1975, FR, *Macedo 25* (INPA); Reserva Biológica da Campina, 2° 35' 20” S, 60° 1' 50” W, 78 m.a.s.l., 11 Apr 1972, FR, *Schultes 26158A* (INPA); Reserva Biológica da Campina, 2° 35' 20” S, 60° 1' 56” W, 70 m.a.s.l., 4 Aug 2000, Sterile, *Vicentini 1693* (INPA); Reserva Biológica da Campina, 2° 35' 26” S, 60° 1' 54” W, 77 m.a.s.l., 4 Aug 2000, Sterile, *Vicentini 1694* (INPA); Reserva Biológica da Campina, 2° 35' 22” S, 60° 1' 54” W, 109 m.a.s.l., 4 Aug 2000, Sterile, *Vicentini 1695* (INPA); Reserva Biológica da Campina, 2° 35' 22” S, 60° 1' 54” W, 94 m.a.s.l., 4 Aug 2000, Sterile, *Vicentini 1696* (INPA); Reserva Biológica da Campina, 2° 35' 23” S, 60° 1' 53” W, 90 m.a.s.l., 4 Aug 2000, Sterile, *Vicentini 1697* (INPA); Reserva Biológica da Campina, 2° 35' 25” S, 60° 1' 53” W, 90 m.a.s.l., 4 Aug 2000, Sterile, *Vicentini 1698* (INPA); Reserva Biológica da Campina, 2° 35' 26” S, 60° 1' 50” W, 113 m.a.s.l., 4 Aug 2000, Sterile, *Vicentini 1699* (INPA); Reserva Biológica da Campina, 2° 35' 27” S, 60° 1' 31” W, 77 m.a.s.l., 4 Aug 2000, Sterile, *Vicentini 1700* (INPA); Reserva Biológica da Campina, 2° 35' 27” S, 60° 1' 50” W, 80 m.a.s.l., 4 Aug 2000, Sterile, *Vicentini 1701* (INPA); Reserva Biológica da Campina, 2° 35' 27” S, 60° 1' 48” W, 78 m.a.s.l., 4 Aug 2000, Sterile, *Vicentini 1702* (INPA); Reserva Biológica da Campina, 2° 35' 20” S, 60° 1' 50” W, 78 m.a.s.l., 8 Feb 1972, FR, *Silva 057* (INPA); Reserva Biológica da Campina, 2° 35' 20” S, 60° 1' 50” W, 78 m.a.s.l., 7 Mar 1995, FR, *Vicentini 894* (ACRE, IAN, K, MO, NY, SP); Manaus-Caracaraí rd, 2° 35' 20” S, 60° 1' 50” W, 70 m.a.s.l., 22 Apr 1971, FR, *Byron 400* (INPA, US); Manaus-Caracaraí rd, 2° 35' 20” S, 60° 1' 50” W, 78 m.a.s.l., 5 Apr 1971, FR, *Prance 11325* (INPA, MO, NY, P, US); Manaus-Caracaraí rd, 2° 20' 0” S, 60° 1' 50” W, 70 m.a.s.l., 28 Jun 1976, FR, *Monteiro 1230* (INPA); 2° 40' 6” S, 60° 2' 48” W, 68 m.a.s.l., 4 Aug 2000, Sterile, *Vicentini 1686* (INPA); Manaus-Caracaraí rd, 2° 40' 8” S, 60° 2' 47” W, 80 m.a.s.l., 4 Aug 2000, Sterile, *Vicentini 1687* (INPA); Manaus-Caracaraí rd, 2° 40' 5” S, 60° 2' 46” W, 84 m.a.s.l., 4 Aug 2000, Sterile, *Vicentini 1689* (INPA); Manaus-Caracaraí rd, 2° 40' 4” S, 60° 2' 44” W, 54 m.a.s.l., 4 Aug 2000, Sterile, *Vicentini 1690* (INPA); Manaus-Caracaraí rd, 2° 40' 12” S, 60° 2' 45” W, 54 m.a.s.l., 4 Aug 2000, Sterile, *Vicentini 1691* (INPA); Manaus-Caracaraí rd, 2° 40' 10” S, 60° 2' 44” W, 67 m.a.s.l., 4 Aug 2000, FR, *Vicentini 1692* (INPA); Manaus-Caracaraí rd, 2° 45' 02” S, 60° 02' 55” W, 59 m.a.s.l., 16 Nov 1958, FL, *Aubreville 782* (INPA); igarapé Tarumã-mirin, 2° 46' 55” S, 60° 15' 20” W, 49 m.a.s.l., 14 Aug 2003, Sterile, *Vicentini 2073* (INPA); rio Cuieiras, 2° 49' 39” S, 60° 30' 33” W, 37 m.a.s.l., 30 Mar 1974, FR, *Kubitzki P21706* (INPA, NY); rio Cuieras, 1.5 hours upstream from rio Negro, 2° 49' 39” S, 60° 30' 33” W, 37 m.a.s.l., 5 Mar 1976, Buds, *Anderson 248* (INPA); rio Cuieras, below mouth of rio Branquinho, 2° 29' 1” S, 60° 20' 38” W, 71 m.a.s.l., 25 Jul 1971, Sterile, *Prance 14867* (INPA); igarapé Tarumã-mirin, 3° 0' 40” S, 60° 21' 49” W, 37 m.a.s.l., 19 Jan 1943, FL, *Ducke 1166* (MO, NY, US); igarapé Tarumã-mirin, 3° 0' 20” S, 60° 21' 49” W, 38 m.a.s.l., 22 Dec 1912, FL, *Ducke 12415* (F, MO, NY); **COLOMBIA**. cuenca rio Caquetá, 0° 50' S, 71° 50' W, 96 m.a.s.l., 20 Nov 1991, Sterile, *Duivenvoorden 1228* (COAH); Quebradón del Metá, 4.7 km desde boca en el rio Caquetá, 0° 53' 55” S, 71° 37' 08” W, 93 m.a.s.l., 16 Oct 1997, Sterile, *Sanchez 6824* (COAH); **Vaupés**. Taraira: Estación Biológica Mosico Itajura (Caparú), 1° 4' 21.8" S, 69° 31' 2.9" W, 200 m.a.s.l., 26 Apr 2004, FR, *Clavijo-R 817* (COL).

17. *Pagamea glabrescens* (Benth) Vicentini

Specimens measured — **BRASIL**. **Amazonas**. Borba: Campo de Flores, 4° 24' 18" S, 59° 34' 53" W, 31 m.a.s.l., 10 Apr 2004, FL-old, *Vicentini 2208* (INPA, MO); Estrada do Incra, 4° 25' 37" S, 59° 31' 11" W, 63 m.a.s.l., 9 Apr 2004, FR, *Vicentini 2196* (MO); Estrada do Incra, 4° 25' 37" S, 59° 31' 11" W, 63 m.a.s.l., 9 Apr 2004, FL-old, *Vicentini 2197* (INPA, MO); km 41, rd to Mapiá, 4° 34' 71" S, 59° 33' 49" W, 29 m.a.s.l., 10 Apr 2004, FR, *Vicentini 2204* (MO); Manaus: Igarapé da Cachoeira Alta do Tarumã, 3° 6' 48" S, 60° 1' 31" W, 60 m.a.s.l., 10 Feb 1958, FL-old, *Pessoal 6057INPA* (F, INPA); Igarapé da Cachoeira Alta do Tarumã, 3° 3' 0" S, 60° 4' 0" W, 46 m.a.s.l., 20 Apr 1961, FR, *Rodrigues 2403* (F, INPA, US); Igarapé da Cachoeira Alta do Tarumã, 3° 3' 0" S, 60° 4' 0" W, 46 m.a.s.l., 14 Dec 1960, FL, *Rodrigues 2001* (F); **Bahia**. rio Preto, 13° 35' 0" S, 39° 52' 0" W, 636 m.a.s.l., Sep 1839, FL, *Gardner 2891* (BM, HUES); Lençois: Serra da Chapadinha, 12° 27' 3" S, 41° 25' 7" W, 600 m.a.s.l., 6 Feb 1995, FL, *Giulietti 1588PCD* (CEPEC, HALCB, MO); Mucugê: 3 km ao S de Mucugê, estrada para Jussiape, 13° 0' 29" S, 41° 23' 27" W, 1000 m.a.s.l., 22 Dec 1979, FL, *Mori 13176* (CEPEC, NY); Mucugê-Barra da Estiva, 3 km, 13° 0' 29" S, 41° 23' 27" W, 987 m.a.s.l., 4 Jul 2000, FR, *Vicentini 1630* (HUEFS, INPA, MO); Mucugê-Barra da Estiva, 3 km, 13° 0' 29" S, 41° 23' 27" W, 986 m.a.s.l., 4 Jul 2000, Buds, *Vicentini 1631* (HUEFS, INPA, MO); Mucugê-Barra da Estiva, 3 km, 13° 0' 35" S, 41° 23' 37" W, 982 m.a.s.l., 4 Jul 2000, FL, *Vicentini 1632* (HUEFS, INPA, MO); Mucugê-Barra da Estiva, 3 km, 13° 0' 21" S, 41° 23' 21" W, 975 m.a.s.l., 4 Jul 2000, FL, *Vicentini 1633* (INPA, MO); Mucugê-Barra da Estiva, 3 km, 13° 0' 25" S, 41° 23' 22" W, 978 m.a.s.l., 4 Jul 2000, Sterile, *Vicentini 1634* (MO); Mucugê-Barra da Estiva, 3 km, 13° 0' 27" S, 41° 23' 23" W, 977 m.a.s.l., 4 Jul 2000, Sterile, *Vicentini 1635* (MO); Mucugê-Barra da Estiva, 3 km, 13° 0' 27" S, 41° 23' 24" W, 979 m.a.s.l., 4 Jul 2000, Buds, *Vicentini 1636* (HUEFS, INPA, MO); **Goiás**. Chapada dos Veadeiros: 20 km by rd S of Terezinha, 13° 55' 0" S, 47° 20' 0" W, 1200 m.a.s.l., 18 Mar 1973, Buds, *Anderson 7416* (NY, US); 35 km N of Veadeiros, 14° 5' 0" S, 47° 28' 0" W, 1000 m.a.s.l., 14 Mar 1969, FL, *Irwin 24312* (F, NY); **Mato Grosso**. Comodoro: Chapada dos Parecis, BR-364, 13° 0' 0" S, 60° 0' 0" W, 586 m.a.s.l., 31 Aug 1963, FL-FR, *Maguire 56446* (NY); **COLOMBIA**. **Caquetá**. Araracuara: near air field, 0° 25' 0" S, 72° 19' 0" W, 250 m.a.s.l., 27 Jan 1989, FL-old, *Gentry 65260* (COAH, MO); cerca de la pista aérea, 0° 37' 0" N, 72° 24' 0" W, 306 m.a.s.l., 12 Nov 1991, FL, *Duivenvoorden 2732* (COAH, NY); camino a Puerto Arturo, 0° 30' 10" S, 72° 00' W, 150 m.a.s.l., 19 Apr 1986, FR, *Galeano 970* (COAH, NY); Araracuara-Pista-Cueva de Guácharos, 0° 35' 0" S, 72° 24' 0" W, 300 m.a.s.l., 14 Nov 1993, FL, *Cárdenas 4014* (COAH, MO); **PERU**. **Loreto**. Iquitos: 3° 57' 12" S, 73° 25' 17" W, 180 m.a.s.l., , ?, *Ortiz 260* (MO); Allpahuayo, 3° 53' 0" S, 73° 25' 0" W, 140 m.a.s.l., 28 Dec 1997, Sterile, *Vasquez 25234* (MO); Allpahuayo. Estacion Experimental del IIAP, 4° 10' 0" S, 73° 30' 0" W, 150 m.a.s.l., 23 Mar 1992, Sterile, *Vasquez 18001* (MO); Carretera Iquitos-Nauta, km 22, 3° 54' 52" S, 73° 24' 15" W, 127 m.a.s.l., 5 Mar 2004, Sterile, *Vicentini 2194* (AMAZ, HUT, INPA, MO, USM); Carretera Iquitos-Nauta, km 31.5, 4° 00' 09" S, 73° 26' 02" W, 149 m.a.s.l., 29 Feb 2004, FR, *Vicentini 2180* (AMAZ, HUT, INPA, MO, USM); Carretera Iquitos-Nauta, km 31.5, 4° 00' 09" S, 73° 26' 02" W, 149 m.a.s.l., 4 Oct 2003, FL, *Zarate sn* (AMZ, MO); Iquitos-Nauta km 7.5, 3° 52' 22" S, 73° 15' 16" W, 150 m.a.s.l., 11 Dec 1987, FR, *McDaniel 29722* (MO, NY, US); Puerto Almendras, 3° 48' 0" S, 73° 25' 0" W, 122 m.a.s.l., 30 Nov 1987, Buds, *Vasquez 9650* (F, MO, NY, USM); Puerto Almendras de la UNAP, 3° 48' 0" S, 73° 25' 0" W, 123 m.a.s.l., 4 Feb 1986, Sterile, *Ruíz 802* (AMAZ, MO).

Specimens seen but not measured — **BRASIL**. **Amazonas**. Borba: Estrada do Incra, 4° 26' 57" S, 59° 33' 20" W, 65 m.a.s.l., 9 Apr 2004, Sterile, *Vicentini 2198* (INPA); Manaus: Igarapé da Cachoeira Alta do Tarumã, 3° 3' 0" S, 60° 4' 0" W, 46 m.a.s.l., 19 May 1961, FR, *Rodrigues 2619* (US); **Bahia**. Correntina: confluência do rio Cajueiro e rio Corrente, 13° 3' 36" S, 45° 29' 34" W, 660 m.a.s.l., 7 May 1990, FL, *Bautista 1521* (IBGE, MBM); Ibotirama: 12° 11' 0" S, 43° 13' 0" W, 442 m.a.s.l., Sep 1974, FL, *Andrade-Lima 747923* (IPA); Lençois: Serra da Chapadinha, 12° 27' 3" S, 41° 25' 7" W, 600 m.a.s.l., 6 Feb 1995, FR, *Giulietti 1589PCD* (CEPEC, HALCB, IBGE, SPF); **COLOMBIA**. **Amazonas**. rio Caquetá, 8 km rio arriba de la Isla del Guadual, 01° 02' 07” S, 71° 31' 11” W, 93 m.a.s.l., 4 Nov 1997, Sterile, *Duque 4007* (COAH); rio Caquetá, Quebrada el Tigre, 8 km N of mouth, 1° 15' 35” S, 70° 51' 08” W, 89 m.a.s.l., 20 Sep 1988, Sterile, *Sanchez 1350* (COAH); **Caquetá**. Araracuara: cerca de la pista aérea, 0° 25' S, 72° 21' W, 103 m.a.s.l., 27 Apr 1988, Sterile, *Sanchez 125* (COAH); cerca de la pista aérea, 0° 25' 30” S, 72° 20' 30” W, 103 m.a.s.l., 27 Apr 1988, FR, *Sanchez 126* (COAH); cerca de la pista aérea, 0° 25' S, 72° 20' W, 250 m.a.s.l., 20 Oct 1990, Buds, *Restrepo 139* (COAH); 0° 25' 0” S, 72° 19' W, 300 m.a.s.l., 21 Feb 1986, Sterile, *Palacios 894* (COAH); **Caqueta**. Puerto Santander, rio Caquetá, Ciudad Perdida, 0° 52' 30” S, 72° 22' 30” W, 175 m.a.s.l., 13 Feb 1993, FL-old, *Arbelaez 581* (HUA); **Caquetá**. río Caquetá, 0° 25' S, 72° 20' W, 104 m.a.s.l., , Sterile, *Bergeron 746116* (COAH); Sabanas del Yari, 40 min del chorro de Gamitana, 00° 14' S, 72° 26' W, 250 m.a.s.l., 20 Mar 1998, Sterile, *Arbelaez 966* (COAH); rio Caquetá, W del caño Paujil, 0° 46' 33” S, 72° 22' 15” W, 100 m.a.s.l., 29 Nov 1988, Sterile, *Sanchez 1766* (COAH); Villa Azul, resguardo indigena Muinane, 0° 32' S, 72° 06' W, 290 m.a.s.l., Jun 1992, Sterile, *Duque 297* (COL, HUA); Villazul, rio Caquetá, en frente a la isla Sumaeta, 0° 34' S, 72° 08' W, 250 m.a.s.l., 11 Aug 89, Sterile, *Londoño 1306* (COAH, JAUM); **Vaupés**. Sierra de Chiribiquete: Estación Puerto Abeja, 0° 4' 20” N, 72° 26' 50” W, 222 m.a.s.l., 23 Mar 1999, FR, *Garcia B153PA* (COAH); rio mesay, 00° 04' 16” N, 72° 26' 48” W, 300 m.a.s.l., 6 Jun 2000, Sterile, *Phillips 506* (COAH); **PERU**. **Loreto**. Iquitos: 4° 00' S, 73° 25' 45” W, 114 m.a.s.l., , ?, *Vasquez SN* (INPA); Requena: rio Blanco, 5° 85' 76.83” S, 73° 76' 03.33” W, 140 m.a.s.l., 31 Oct 2004, Buds, *Dávila 1134* (AMAZ, F).

18. *Pagamea plicata* Spruce ex Benth.

Specimens measured — **BRASIL**. **Amazonas**. Manaus: igarapé Tarumã-mirin, 2° 46' 10” S, 60° 15' 43” W, 50 m.a.s.l., 14 Aug 2003, Sterile, *Vicentini 2066* (MO); igarapé Tarumã-mirin, 2° 46' 27” S, 60° 15' 33” W, 50 m.a.s.l., 14 Aug 2003, Sterile, *Vicentini 2070* (MO); rio Cuieiras, near Jarada, 2° 41' 46” S, 60° 21' 10” W, 52 m.a.s.l., 17 Sep 1973, FL, *Prance 18046* (MO, NY, US); Presidente Figueiredo: Cachoeira da Iracema, trilha entre Iracema e Araras, 1° 55' 27” S, 60° 04' 25” W, 137 m.a.s.l., 28 Apr 2004, FR, *Vicentini 2279* (INPA, MO); Reserva Ecologica de Lajes, 1° 58' 51” S, 60° 01' 19” W, 114 m.a.s.l., 28 Jul 2003, Sterile, *Vicentini 2059* (MO); Reserva Ecologica de Lajes, 1° 58' 58” S, 60° 01' 15” W, 115 m.a.s.l., 28 Jul 2003, Sterile, *Vicentini 2061* (MO); Santa Isabel do Rio Negro: perto do aeroporto, 0° 21' 59” S, 64° 59' 48” W, 53 m.a.s.l., 3 Dec 2003, Sterile, *Vicentini 2150* (MO); São Gabriel da Cachoeira: rio Negro, 0° 7' 45” S, 67° 5' 30” W, 71 m.a.s.l., 1852, FR, *Spruce 2342* (BM, F); rio Içana, vila Jandú-Cachoeira, 1° 28' 36” N, 68° 43' 9” W, 158 m.a.s.l., 23 Jun 2004, Sterile, *Vicentini 2244* (MO); rio Içana. vila Baniwa de Juivitera, 1° 16' 47” N, 68° 32' 30” W, 111 m.a.s.l., 21 Jun 2004, FR, *Vicentini 2222* (INPA, MO); rio Içana. vila Baniwa de Juivitera, 1° 16' 59” N, 68° 32' 23” W, 121 m.a.s.l., 21 Jun 2004, FR-old, *Vicentini 2225* (INPA, MO); rio Içana, vila de Jauacanã, 0° 33' 39” N, 67° 24' 38” W, 69 m.a.s.l., 27 Jun 2004, FR, *Vicentini 2262* (INPA, MO); rio Içana, vila de Jauacanã, 0° 33' 32” N, 67° 23' 53” W, 69 m.a.s.l., 27 Jun 2004, Sterile, *Vicentini 2259* (INPA, MO); Serra Tunuhy, rio Issana, 1° 26' 19” N, 68° 9' 29” W, 551 m.a.s.l., 25 Jun 2004, Sterile, *Vicentini 2248* (MO); Serra Tunuhy, rio Issana, 1° 26' 21” N, 68° 9' 31” W, 579 m.a.s.l., 25 Jun 2004, FR, *Vicentini 2251* (INPA, MO); rio Waupés, Matapi, 0° 0' 10” N, 68° 15' 0” W, 86 m.a.s.l., 7 Dec 1978, FR, *Damiao 3011* (BM, INPA, MO); near Camanaus, 0° 9' 40” S, 66° 53' W, 68 m.a.s.l., 2 Nov 1971, Buds, *Prance 15995* (INPA, MO, NY, P); **Mato Grosso**. Agrochapada Paramatinga: Córrego Santiago, 13° 27' S, 54° 16' 48” W, 400 m.a.s.l., 30 Oct 1990, FL, *Macedo 2557* (INPA); Serra do Roncador: 160 km N of Xavantina, 13° 30' 0” S, 51° 50' 0” W, 500 m.a.s.l., 27 May 1966, FR, *Irwin 16144* (NY); Vicinity of Garapu, 13° 10' 54” S, 52° 39' 27” W, 277 m.a.s.l., 2 Oct 1964, FR, *Prance 59226* (MO, NY, UNB, US); **Pará**. Itaituba: Serra do Cachimbo, 8° 57' 0” S, 54° 54' 0” W, 425 m.a.s.l., 12 Dec 1956, FR, *Pires 6069* (NY); Jacarecanga: rio Cururú, Mundurukú village ca. 2 km N of rio Cururú, 7° 45' 0” S, 57° 20' 0” W, 200 m.a.s.l., 13 Feb 1974, FR, *Anderson 10904* (MO, NY, US); **VENEZUELA**. **Amazonas**. Alto Orinoco: 5 km N near “morocoy”, 3° 11.8' N, 65° 33' W, 130 m.a.s.l., 7 Jan 1994, FR, *Coomes 361* (VEN); Cerro Vinilla. ca. 30 km al SSw de Ocamo, 2° 31' 0” N, 65° 23' 0” W, 525 m.a.s.l., 1 Mar 1984, FR, *Steyermark 130364* (F, MO, VEN); Atabapo: Yapacana tepui, 3° 41' 27” N, 66° 49' 0” W, 700 m.a.s.l., 3 Jan 1951, FR, *Maguire 30735* (NY, VEN); Autana: San Pedro, rio Sipapo, 4° 34' 0” N, 67° 18' 0” W, 120 m.a.s.l., Jun

1989, FL-old, *Foldats 9590* (NY, PORT); San Pedro, rio Autana, 4° 49' 0” N, 67° 26' 0” W, 200 m.a.s.l., 14 Nov 1984, FL, *Guanchez 3613* (MO, TFVA, VEN); San Pedro, rio Sipapo, 4° 51' 26” N, 67° 25' 0” W, 125 m.a.s.l., 30 Dec 1948, FL-old, *Maguire 28036* (NY, VEN); Maroa: Yavita,, 2° 52' 26” N, 67° 29' 27” W, 162 m.a.s.l., 22 Feb 1998, FR, *Acevedo-Rdgz 10360* (MO, PORT, US, VEN); Yavita,, 2° 56' 0” N, 67° 21' 0” W, 128 m.a.s.l., 24 Jan 1942, FR, *Williams 13962* (F, MO, NY, P, US, VEN); Rio Negro: 10.8 km NE rd San Carlos de Rio Negro-Solano, 1° 56' 0” N, 67° 3' 0” W, 119 m.a.s.l., 22 Feb 1979, FR, *Clark 7032* (NY); ca. 20 km S of confluence of rio Negro and Brazo Casiquiare, 1° 56' 0” N, 67° 3' 0” W, 119 m.a.s.l., 18 Jan 1979, FR, *Clark 6947* (MO, NY, QCNE, VEN); Neblina tepui, rio Mawarinuma, 0° 50' 0” N, 66° 10' 0” W, 140 m.a.s.l., 8 Feb 1985, FR, *Boom 5697* (MO, VEN); Neblina tepui, rio Mawarinuma, 0° 50' 0” N, 66° 11' 0” W, 140 m.a.s.l., 2 May 1984, FR, *Gentry 47099* (F, MO, NY); Neblina tepui, rio Baria, 0° 50' 0” N, 66° 10' 0” W, 140 m.a.s.l., 12 Apr 1974, FR, *Plowman 13574* (F, MO, NY, VEN); Neblina tepui, rio Baria, 0° 50' 0” N, 66° 10' 0” W, 140 m.a.s.l., 12 Apr 1974, FR, *Plowman 13574* (F, MO, NY, VEN); **Bolívar**. Gran Sabana: rio Arequi, region Urimãn, 5° 21' 0” N, 62° 29' 0” W, 360 m.a.s.l., 5 Sep 1954, FR, *Bernardi 1690* (NY, P, VEN).

Specimens seen but not measured — **BRASIL**. **Amazonas**. Manaus: Manaus-Caracaraí rd, 3° 0' 0” S, 60° 1' 50” W, 54 m.a.s.l., 18 Feb 1955, Buds, *Chagas 819INPA* (INPA); São Gabriel da Cachoeira: Estrada SGC-Camanaus, km 20, ramal do Quidaban, 0° 9' 2” S, 66° 56' 53” W, 36 m.a.s.l., 17 Jun 2004, Sterile, *Vicentini 2212* (INPA, MO); Estrada SGC-Camanaus, km 20, ramal do Quidaban, 0° 9' 22” S, 66° 59' 6” W, 87 m.a.s.l., 17 Jun 2004, FL-old, *Vicentini 2215* (INPA); 0° 8' 0” S, 67° 5' 0” W, 73 m.a.s.l., 1852, FR, *Spruce 2243* (NY); **COLOMBIA**. **Guainia**. Cerro Caño Minas: 2° 38' 13.7” N, 69° 14' 38.7” W, 300 m.a.s.l., 16 Feb 1995, FL-old, *Córdoba 114* (COAH); Puerto Inírida: Resguardo La Ceiba-Caranacoa, carretera Huesito-El Pato, km 6-10, 3° 25' 24” N, 67° 53' 37.7” W, 125 m.a.s.l., 28 Apr 2004, FR, *Cárdenas 14778* (COL); **VENEZUELA**. **Amazonas**. Alto Orinoco: 8 km al E from La Esmeralda, 3° 11' 0” N, 65° 27' 0” W, 140 m.a.s.l., 20 Feb 1990, FR, *Aymard 8096* (MO, PORT); Cerro Vinilla, 2° 31' 0” N, 65° 23' 0” W, 525 m.a.s.l., 12 Mar 1984, Sterile, *Steyermark 130417* (MO, VEN); Atabapo: 44 km al SE from Santa Barbara del Orinoco, 3° 50' 0” N, 66° 44' 0” W, 130 m.a.s.l., May 1990, FR, *Marin 1187A* (MO, PORT); San Antonio de Orinoco, 3° 27' 0” N, 66° 45' 0” W, 140 m.a.s.l., Apr 1990, FR, *Yanez 440A* (MO, PORT); Autana: San Pedro, rio Autana, 4° 52' 0” N, 67° 27' 0” W, 110 m.a.s.l., 10 Nov 1984, Sterile, *Guanchez 3449* (MO, TFVA); Maroa: rio Guainía, 2° 44' 50” N, 67° 34' 30” W, 127 m.a.s.l., 14 Feb 1942, FR, *Williams 14351* (F, NY, US, VEN); rio Guainía, 2° 44' 30” N, 67° 34' 0” W, 127 m.a.s.l., 1942, FR, *Williams 15351* (NY, US); Yavita,, 2° 53' 39” N, 67° 27' 57” W, 110 m.a.s.l., 23 May 1996, FR, *Aymard 10986* (MO, PORT, VEN); Yavita,, 2° 55' 16” N, 67° 26' 17” W, 110 m.a.s.l., 28 Nov 1995, FR, *Berry 5718* (MO, VEN); Yavita,, 2° 51' 0” N, 67° 29' 30” W, 110 m.a.s.l., 28 May 1996, Sterile, *Berry 6337* (MO, VEN); Rio Negro: 1.5 km SE de San Carlos, caño Marimajari, 1° 54' 55” N, 67° 3' 5” W, 120 m.a.s.l., 28 Mar 2000, Sterile, *Berry 7283* (MO, PORT); ca. 20 km S of confluence of rio Negro and Brazo Casiquiare, 1° 56' 0” N, 67° 3' 0” W, 119 m.a.s.l., 20 Oct 1978, FL, *Clark 6887* (MO, NY, QCNE); Neblina tepui, rio Mawarinuma, 0° 50' 0” N, 66° 10' 0” W, 140 m.a.s.l., 27 Jan 1985, Sterile, *Boom 5375* (MO, VEN); Neblina tepui, rio Mawarinuma, 0° 50' 0” N, 66° 10' 0” W, 140 m.a.s.l., 6 Mar 1984, FR, *Liesner 16463* (MO, NY, VEN); carretera San Carlos de Rio Negro-Solano, 1° 55' 0” N, 67° 3' 0” W, 96 m.a.s.l., 17 Mar 1979, FR, *Marcano-Berti 124979* (US, VEN); rio Pasimoni, 1° 30' 0” N, 66° 30' 0” W, 80 m.a.s.l., Apr 1991, Sterile, *Velazco 2066* (MO, PORT); San Carlos de Rio Negro, 1° 55' 0” N, 67° 4' 0” W, 100 m.a.s.l., , ?, *Aymard 11497* (INPA).

19. *Pagamea coriacea* Spruce ex Benth.

Specimens measured — **BRASIL**. **Amazonas**. Apuí: Transamazon hwy, 9 km W of rio dos Pombos, 7° 15' 0” S, 60° 10' 40” W, 100 m.a.s.l., 17 Jun 1979, FR, *Calderon 2543* (INPA, NY, US); Transamazon hwy, 9 km W of rio dos Pombos, 7° 15' 0” S, 60° 10' 20” W, 100 m.a.s.l., 18 Jun 1979, FR, *Calderon 2567* (INPA, NY, US); Barcelos: 0° 30' 39” N, 63° 14' 13” W, 78 m.a.s.l., , ?, *Carneiro 3* (INPA, MO); Cemitério do Castelo, acima de Barcelos, abaixo de Tapuruquara, 0° 31' 26.15” S, 63° 32' 45.43” W, 41 m.a.s.l., 29 Jun 1979, FR, *Maia 181* (INPA); Serra do Aracá, surrounding lowlands, 0° 19' 12” N, 63° 15' 59” W, 32 m.a.s.l., 28 Aug 2001, FR, *Vicentini 1916* (INPA, MO); Serra do Aracá, surrounding lowlands, 0° 19' 22” N, 63° 15' 57” W, 35 m.a.s.l., 28 Aug 2001, FR, *Vicentini 1917* (INPA, MO); Serra do Aracá, surrounding lowlands, 0° 19' 2” N, 63° 16' 0” W, 38 m.a.s.l., 28 Aug 2001, FR, *Vicentini 1924* (INPA, MO); Parque Nacional do Jaú, campina do Patauá, 1° 48' 29” S, 61° 45' 24” W, 37 m.a.s.l., 23 Jul 2001, Sterile, *Vicentini 1760* (INPA, MO); Parque Nacional do Jaú, campina do Patauá, 1° 49' 10” S, 61° 46' 5” W, 50 m.a.s.l., 23 Jul 2001, Sterile, *Vicentini 1768* (INPA); Parque Nacional do Jaú, campina do Patauá, 1° 48' 29” S, 61° 45' 24” W, 37 m.a.s.l., 23 Jul 2001, Sterile, *Vicentini 1761* (INPA, MO); Parque Nacional do Jaú, campina do Seringalzinho, 1° 54' 56” S, 61° 35' 38” W, 36 m.a.s.l., 27 Jul 2001, Sterile, *Vicentini 1775* (INPA, MO); Parque Nacional do Jaú, campina do Seringalzinho, 1° 54' 48” S, 61° 35' 25” W, 37 m.a.s.l., 27 Jul 2001, Sterile, *Vicentini 1776* (INPA, MO); Serra do Aracá, surrounding lowlands, 0° 1' 25” S, 63° 13' 7” W, 44 m.a.s.l., 23 Aug 2001, FR, *Vicentini 1801* (INPA, MO); Serra do Aracá, surrounding lowlands, 0° 13' 58” S, 63° 9' 36” W, 41 m.a.s.l., 23 Aug 2001, FR, *Vicentini 1788* (INPA, MO); Serra do Aracá, surrounding lowlands, 0° 13' 58” S, 63° 9' 38” W, 39 m.a.s.l., 23 Aug 2001, FR, *Vicentini 1789* (INPA, MO); São Tomé, rio Negro, between Manaus and São Gabriel, 0° 25' 0” S, 64° 25' 0” W, 49 m.a.s.l., 29 Jun 1979, FR, *Alencar 181* (NY, US); Serra do Aracá, surrounding lowlands, 0° 49' 0” S, 63° 19' 0” W, 38 m.a.s.l., 28 Feb 1984, FL-old, *Amaral 1661* (F, INPA, NY); Serra do Aracá, surrounding lowlands, 0° 49' 0” N, 63° 19' 0” W, 60 m.a.s.l., 28 Feb 1984, FR, *Rodrigues 10476* (F, INPA, MO, NY, UNB, US); Serra do Aracá, surrounding lowlands, 0° 49' 0” N, 63° 20' 0” W, 191 m.a.s.l., 25 Nov 1977, FR, *Rosa 1650* (NY, SPF); Serra do Aracá, surrounding lowlands, 0° 49' 0” N, 63° 19' 0” W, 206 m.a.s.l., 6 Feb 1984, FR, *Prance 28830* (F, INPA, MO, NY, UNB, US); Serra do Aracá, surrounding lowlands, 0° 30' 0” N, 63° 30' 0” W, 83 m.a.s.l., 2 Jul 1985, Buds, *Cordeiro 123* (INPA, NY); Serra do Aracá, surrounding lowlands, 0° 49' 0” N, 63° 23' 0” W, 197 m.a.s.l., 1 Mar 1977, FL, *Rosa 1709* (NY, US); Borba: Campo de Flores, 4° 24' 22” S, 59° 35' 15” W, 33 m.a.s.l., 9 Apr 2004, FR, *Vicentini 2199* (INPA, MO); Campo de Flores, 4° 24' 23” S, 59° 35' 19” W, 32 m.a.s.l., 9 Apr 2004, Buds, *Vicentini 2200* (INPA, MO); rio Madeira, 4° 23' 20” S, 59° 35' 37” W, 30 m.a.s.l., 22 Jan 1930, FL, *Ducke 22946* (US); km 8, rd to Mapiá, 4° 21' 49” S, 59° 37' 5” W, 30 m.a.s.l., 22 Jun 1983, FR, *Cid 3867* (INPA, MO, NY); km 41, rd to Mapiá, 4° 34' 71” S, 59° 33' 49” W, 29 m.a.s.l., 10 Apr 2004, FR, *Vicentini 2205* (INPA, MO); km 41, rd to Mapiá, 4° 34' 71” S, 59° 33' 49” W, 29 m.a.s.l., 10 Apr 2004, FR, *Vicentini 2206* (INPA, MO); Humaitá: BR230, Reserva Indígena dos Tenharim, 7° 55' 0” S, 62° 13' 0” W, 100 m.a.s.l., 13 Apr 1985, FR, *Cid 5462* (F, INPA, MO, NY, UNB); BR230, Reserva Indígena dos Tenharim, 8° 1' 0” S, 62° 5' 0” W, 99 m.a.s.l., 15 Apr 1985, FR, *Cid 5581* (MO, NY, UNB, US); Iranduba: rio Negro, Praia Grande, 3° 2' 4” S, 60° 32' 35” W, 36 m.a.s.l., 31 Jul 2000, FL, *Vicentini 1680* (INPA, MO); rio Negro, Praia Grande, 3° 2' 4” S, 60° 32' 46” W, 34 m.a.s.l., 31 Jul 2000, FL, *Vicentini 1683* (INPA, MO); rio Negro, Praia Grande, 3° 2' 4” S, 60° 32' 20” W, 33 m.a.s.l., 11 Sep 1987, FL, *Kawasaki 103* (NY); rio Negro, Acajutuba, 3° 3' 0” S, 60° 35' 0” W, 40 m.a.s.l., 22 Mar 1941, FL, *Ducke 683* (MO, NY, US); Itacoatiara: Manaus-Itacoatiara rd, km 200, 2° 38' 0” S, 59° 1' 0” W, 100 m.a.s.l., 19 Nov 1965, FL, *Rodrigues 7283* (INPA, US); Manaus: igarapé Tarumã-mirin, 2° 46' 20” S, 60° 15' 00” W, 50 m.a.s.l., 14 Aug 2003, Sterile, *Vicentini 2067* (MO); igarapé Tarumã-mirin, 2° 46' 26” S, 60° 15' 32” W, 51 m.a.s.l., 14 Aug 2003, Sterile, *Vicentini 2069* (MO); igarapé Tarumã-mirin, 2° 46' 15” S, 60° 15' 40” W, 50 m.a.s.l., 14 Aug 2003, Sterile, *Vicentini 2071* (MO); Ponta Negra, 3° 2' 0” S, 60° 6' 0” W, 34 m.a.s.l., 24 Jan 1962, FR, *Rodrigues 4126* (NY, US); Ponta Negra, 3° 2' 0” S, 60° 6' 0” W, 34 m.a.s.l., 12 May 1961, FR, *Rodrigues 2587* (INPA, US); Manicoré: ig. Copaíba, afluente do Matupiri, 5° 27' 53.4” S, 61° 07' 17” W, 47 m.a.s.l., 14 Apr 2004, FR, *Vicentini 2209* (INPA, MO); ig. Copaíba, afluente do Matupiri, 5° 27' 53.4” S, 61° 07' 17” W, 47 m.a.s.l., 14 Apr 2004, FR, *Vicentini 2210* (INPA, MO); ig. Copaíba, afluente do Matupiri, 5° 27' 53.4” S, 61° 07' 17” W, 47 m.a.s.l., 14 Apr 2004, FR, *Vicentini 2211* (INPA, MO); Presidente Figueiredo: Reserva Biológica de Lajes, 1° 59' 3” S, 60° 1' 20” W, 101 m.a.s.l., 5 Aug 2000, Sterile, *Vicentini 1716* (MO); Reserva Biológica de Lajes, 1° 59' 3” S, 60° 1' 20” W, 97 m.a.s.l., 5 Aug 2000, Sterile, *Vicentini 1717* (MO); Reserva Biológica de Lajes, 1° 59' 3” S, 60° 1' 21” W, 120 m.a.s.l., 5 Aug 2000, Sterile, *Vicentini 1718* (MO); Reserva Biológica de Lajes, 1° 58' 55” S, 60° 1' 22” W, 124 m.a.s.l., 5 Aug 2000, Sterile, *Vicentini 1719* (MO); Reserva Biológica de Lajes, 1° 59' 13” S, 60° 1' 35” W, 110 m.a.s.l., 5 Aug 2000, Sterile, *Vicentini 1705* (MO); Reserva Biológica de Lajes, 1° 59' 16” S, 60° 1' 34” W, 118 m.a.s.l., 5 Aug 2000, Sterile, *Vicentini 1707* (MO); Reserva Biológica de Lajes, 1° 59' 18” S, 60° 1' 34” W, 116 m.a.s.l., 5 Aug 2000, Sterile, *Vicentini 1708* (MO); Reserva Biológica de Lajes, 1° 59' 14” S, 60° 1' 33” W, 123 m.a.s.l., 5 Aug 2000, Sterile, *Vicentini 1709* (MO); Reserva Biológica de Lajes, 1° 59' 15” S, 60° 1' 23” W, 127 m.a.s.l., 5 Aug 2000, Sterile, *Vicentini 1711* (MO); Reserva Biológica de Lajes, 1° 59' 7” S, 60° 1' 18”

W, 124 m.a.s.l., 5 Aug 2000, Sterile, *Vicentini 1712* (MO); Reserva Biológica de Lajes, 1° 59' 5” S, 60° 1' 18” W, 124 m.a.s.l., 5 Aug 2000, Sterile, *Vicentini 1713* (MO); Reserva Biológica de Lajes, 1° 59' 1” S, 60° 1' 18” W, 124 m.a.s.l., 5 Aug 2000, Sterile, *Vicentini 1714* (MO); Manaus-Caracaraí rd, km 140, 1° 39' 16” S, 60° 8' 44” W, 93 m.a.s.l., 21 Feb 1974, FR, *Steward 20398P* (INPA, US); Manaus-Caracaraí rd, km 130, 1° 50' 0” S, 60° 1' 20” W, 110 m.a.s.l., 13 Nov 1973, Buds, *Berg 19540P* (INPA, MO, NY, P, US); Cachoeira da Iracema, trilha entre Iracema e Araras, 1° 56' 42” S, 60° 04' 35” W, 141 m.a.s.l., 28 Jul 2003, Sterile, *Vicentini 2052* (MO); Cachoeira da Iracema, trilha entre Iracema e Araras, 1° 56' 27” S, 60° 04' 44” W, 139 m.a.s.l., 28 Jul 2003, Sterile, *Vicentini 2054* (MO); Cachoeira da Iracema, trilha entre Iracema e Araras, 1° 57' 10” S, 60° 04' 25” W, 130 m.a.s.l., 28 Jul 2003, Sterile, *Vicentini 2056* (MO); Cachoeira da Iracema, trilha entre Iracema e Araras, 1° 57' 05” S, 60° 04' 25” W, 135 m.a.s.l., 28 Jul 2003, Sterile, *Vicentini 2057* (MO); margem direita do rio Uatumã, acima da barragem, 1° 59' 06” S, 59° 35' 02” W, 134 m.a.s.l., 31 Oct 1983, FL, *Lima 594* (INPA); Reserva Ecologica de Lajes, 1° 58' 59” S, 60° 01' 20” W, 107 m.a.s.l., 28 Jul 2003, Sterile, *Vicentini 2060* (MO); Reserva Ecologica de Lajes, 1° 59' 07” S, 60° 01' 12” W, 111 m.a.s.l., 28 Jul 2003, Sterile, *Vicentini 2062* (MO); rio Uatumã, a montante da barragem, igarapé Catitu, 1° 54' 33” S, 59° 39' 16” W, 100 m.a.s.l., 29 Mar 1986, FL-FR, *Cid 7020* (INPA, MO, NY, US); Rio Negro: Taracuá, 0° 6' 0” N, 68° 28' 0” W, 50 m.a.s.l., 28 Feb 1959, FR, *Rodrigues 159* (NY); Rio Preto da Eva: rio Urubu, 10 km N of Manaus-Itacoatiara hwy, 2° 50' 0” S, 59° 1' 0” W, 87 m.a.s.l., 5 Apr 1967, FR, *Prance 4780* (F, NY, P); Santa Isabel do Rio Negro: rio Uneixi, 0° 28' 21.6” S, 65° 10' 14.2” W, 50 m.a.s.l., 3 Dec 2003, FL, *Vicentini 2147* (INPA, MO); São Gabriel da Cachoeira: Boca do rio Içana, Boa Vista, 0° 30' 0” N, 67° 21' 0” W, 89 m.a.s.l., 12 Nov 1987, FL, *Kawasaki 109* (F, INPA, MO, NY, US); Estrada SGC-Camanaus, km 20, ramal do Quidaban, 0° 8' 58” S, 66° 57' 8” W, 66 m.a.s.l., 17 Jun 2004, FR, *Vicentini 2213* (MO); Estrada SGC-Camanaus, km 20, ramal do Quidaban, 0° 9' 22” S, 66° 59' 6” W, 87 m.a.s.l., 17 Jun 2004, Sterile, *Vicentini 2216* (INPA); perto do aeroporto de Uaupés, 0° 9' 31” S, 66° 59' 37” W, 76 m.a.s.l., 17 Jun 2004, FR, *Vicentini 2217* (INPA, MO); perto do aeroporto de Uaupés, 0° 9' 31” S, 66° 59' 37” W, 76 m.a.s.l., 17 Jun 2004, FR, *Vicentini 2218* (INPA, MO); perto do aeroporto de Uaupés, 0° 9' 31” S, 66° 59' 37” W, 76 m.a.s.l., 17 Jun 2004, FL-old, *Vicentini 2219* (INPA, MO); rio Curicuriary super cataractas, 0° 14' 21” N, 66° 52' 30” W, 78 m.a.s.l., 24 Nov 1936, FL, *Ducke 35061* (F); rio Içana, vila Jandú-Cachoeira, 1° 29' 23” N, 68° 43' 1” W, 130 m.a.s.l., 23 Jun 2004, FR, *Vicentini 2237* (INPA, MO); rio Içana, vila Jandú-Cachoeira, 1° 28' 36” N, 68° 43' 9” W, 158 m.a.s.l., 23 Jun 2004, FR, *Vicentini 2245* (INPA, MO); rio Içana. vila Baniwa de Juivitera, 1° 17' 7” N, 68° 32' 22” W, 148 m.a.s.l., 21 Jun 2004, FR, *Vicentini 2229* (INPA, MO); rio Içana. vila Baniwa de Juivitera, 1° 16' 15” N, 68° 33' 24” W, 112 m.a.s.l., 22 Jun 2004, FR, *Vicentini 2233* (INPA, MO); rio Içana. vila Baniwa de Juivitera, 1° 16' 47” N, 68° 32' 30” W, 111 m.a.s.l., 21 Jun 2004, FR, *Vicentini 2221* (INPA, MO); rio Içana. vila Baniwa de Juivitera, 1° 16' 59” N, 68° 32' 23” W, 121 m.a.s.l., 21 Jun 2004, FR, *Vicentini 2226* (INPA, MO); rio Içana. vila Baniwa de Juivitera, 1° 17' 7” N, 68° 32' 22” W, 148 m.a.s.l., 21 Jun 2004, FR, *Vicentini 2228* (INPA, MO); rio Içana, vila de Jauacanã, 0° 33' 47” N, 67° 24' 9” W, 73 m.a.s.l., 27 Jun 2004, FL-old, *Vicentini 2273* (INPA, MO); rio Içana, vila de Jauacanã, 0° 33' 39” N, 67° 24' 38” W, 69 m.a.s.l., 27 Jun 2004, FR, *Vicentini 2261* (INPA, MO); rio Içana, vila de Jauacanã, 0° 33' 32” N, 67° 23' 53” W, 69 m.a.s.l., 27 Jun 2004, FR, *Vicentini 2257* (INPA, MO); Serra Tunuhy, rio Issana, 1° 3' 17” N, 67° 32' 50” W, 97 m.a.s.l., 20 Jun 2004, FL-old, *Vicentini 2220* (INPA, MO); Serra Tunuhy, rio Issana, 1° 26' 21” N, 68° 9' 31” W, 579 m.a.s.l., 25 Jun 2004, FR, *Vicentini 2252* (INPA, MO); Tapuruquara, rio Negro, 0° 31' 38.75” S, 64° 58' 32.41” W, 41 m.a.s.l., 29 Nov 1978, FL, *Damiao 2918* (BM); rio Tikié, basin of rio Negro, 0° 5' 0” N, 68° 25' 0” W, 88 m.a.s.l., 29 Apr 1942, FR, *Krukoff 12533/227* (F); Uanauáca, 0° 33' 47” N, 67° 24' 15” W, 81 m.a.s.l., Jan 1852, FR, *Spruce 2026* (BM, K, NY, P); **Mato Grosso**. Sararé: 13° 50' 0” S, 58° 55' 0” W, 590 m.a.s.l., 4 Aug 1978, Buds, *Pires 16404* (F, NY); **Pará**. Oriximiná: rio Mapuera, 10 km upriver from Cachoeira Porteira, campina das onças, 1° 5' 0” S, 57° 30' 0” W, 80 m.a.s.l., 30 Jun 1980, FL-old, *Davidson 10608* (INPA, NY); **Roraima**. Boa Vista: estrada para Colônia Apiaui, 2° 50' 0” N, 60° 40' 0” W, 76 m.a.s.l., 7 Aug 1986, FL, *Silva 646* (INPA, MO, NY); Caracaraí: BR-174, 7 km ao sul do equador, 0° 5' 0” S, 60° 43' 38” W, 100 m.a.s.l., 14 Jun 1985, FL, *Cordeiro 25* (INPA, MO, NY, US); BR-174, km 345-360, 0° 1' 0” S, 60° 43' 0” W, 98 m.a.s.l., 15 Mar 1984, FL, *Santos 673* (INPA, MO, NY, US); BR-174, entre a estrada da perdida e rotatoria, ca. 5-6 km da rotatória, 1° 18' 36” N, 60° 35' 57” W, 96 m.a.s.l., 6 Aug 2000, Sterile, *Vicentini 1729* (MO); BR-174, entre a estrada da perdida e rotatoria, ca. 5-6 km da rotatória, 1° 18' 44” N, 60° 35' 28” W, 74 m.a.s.l., 6 Aug 2000, Sterile, *Vicentini 1732* (MO); estrada da Perdida, 4 km da BR-174, 1° 26' 23” N, 60° 58' 52” W, 58 m.a.s.l., 7 Aug 2000, Sterile, *Vicentini 1734* (MO); estrada da Perdida, 4 km da BR-174, 1° 26' 19” N, 60° 58' 57” W, 58 m.a.s.l., 7 Aug 2000, FL-old, *Vicentini 1737* (MO); estrada da Perdida, 4 km da BR-174, 1° 26' 18” N, 60° 59' 3” W, 62 m.a.s.l., 7 Aug 2000, Sterile, *Vicentini 1739* (MO); estrada da Perdida, 4 km da BR-174, 1° 26' 19” N, 60° 59' 4” W, 62 m.a.s.l., 7 Aug 2000, Sterile, *Vicentini 1740* (MO); Manaus-Caracaraí rd, próximo ao entrocanamento com a Perimetral Norte (BR-210), 1° 18' 0” N, 60° 35' 0” W, 113 m.a.s.l., 25 Aug 1987, FR, *Cid 9156* (INPA, MO); Roranópolis: Manaus-Caracaraí rd, km 350, 0° 2' 0” S, 60° 38' 0” W, 100 m.a.s.l., 30 Jun 1985, FL-old, *Huber 10648* (INPA, NY); **COLOMBIA**. **Amazonas**. río Apaporis, Raudal de Jerijerimo, 0° 8' 0” N, 70° 39' 0” W, 158 m.a.s.l., Mar 1951, FL-old, *Schultes 12108* (COL, US); La Pedrera: rio Caquetá, frente al Cerro Yupati., 1° 18' 1” S, 69° 33' 50” W, 260 m.a.s.l., 9 Mar 1990, FL, *Galeano 2012* (COL, HUA, NY); **Vaupés**. Cerro E-ree-eé-kö-mee-ö-kee, río Piraparaná, río Apaporis, 0° 20' 0” S, 70° 30' 0” W, 94 m.a.s.l., 18 Sep 1952, FR, *Schultes 17537* (F, US); río Apaporis, Cachivera de Jirijirimo, 0° 8' 0” N, 70° 39' 0” W, 250 m.a.s.l., 16 Sep 1951, FR, *Schultes 14012* (F, US); río Apaporis, raudal Jirijirimo, below mouth of Kananarí, 0° 8' 0” N, 70° 39' 0” W, 158 m.a.s.l., 27 Nov 1951, FL, *Schultes 14646* (F, NY); río Apaporis, raudal Jirijirimo, below mouth of Kananarí, 0° 5' 0” N, 70° 40' 0” W, 270 m.a.s.l., 15 Mar 1952, FR, *Schultes 15931* (COL, F, US); río Apaporis, raudal Jirijirimo, below mouth of Kananarí, 0° 5' 0” N, 70° 40' 0” W, 270 m.a.s.l., 21 Jan 1952, FL, *Schultes 14953* (COL, US); rio Karurú, Mesa de Yambí, Goo-ran-hoo-dá, 1° 20' 0” N, 71° 20' 0” W, 300 m.a.s.l., 15 Apr 1953, FL-old, *Schultes 19169* (COL, US); río Kuduyarí, Yapobodá, 1° 20' 0” N, 70° 30' 0” W, 175 m.a.s.l., 16 Aug 1960, FR, *Schultes 22680* (COL, NY); rio Paraná Pichuna, 1° 10' 0” N, 70° 30' 0” W, 210 m.a.s.l., Jun 1953, FR, *Schultes 19921* (BM, F, US); Mitú: río Vaupés: between Mitú and Javareté, 1° 15' 0” N, 70° 13' 0” W, 161 m.a.s.l., 15 May 1953, FL-old, *Schultes 19367* (F, US); Sierra de Chiribiquete: arriba de la cascada grande, 0° 55' 0” N, 72° 45' 0” W, 300 m.a.s.l., 1 Dec 1990, FL, *Estrada 640* (BM, COL, MO); **GUYANA**. **Potaro-Siparuni**. Rupununi: Kuyuwini Landing, 2° 10' 0” N, 59° 15' 0” W, 200 m.a.s.l., 6 Feb 1991, FR, *Jansen-Jacobs 2432* (NY, P, US); Kuyuwini Landing, 2° 5' 0” N, 59° 15' 0” W, 200 m.a.s.l., 29 Oct 1992, FL, *Jansen-Jacobs 3166* (MO, NY, P, US); **VENEZUELA**. **Amazonas**. Alto Orinoco: 10-12 km from La Esmeralda al W along río Orinoco, 3° 11' 0” N, 65° 37' 0” W, 130 m.a.s.l., 5 Mar 1980, FL, *Huber 5015* (NY, VEN); 10-12 km from La Esmeralda, al W along río Orinoco, 3° 11' 0” N, 65° 37' 0” W, 125 m.a.s.l., 7 Mar 1980, FR, *Huber 5046* (NY, VEN); Duida tepui, 3° 10' 21” N, 65° 33' 0” W, 150 m.a.s.l., 1929, FR, *Tate 943* (INPA, MBM, NY, US); entre las rocas cercanas a La Esmeralda, 3° 10' 54” N, 65° 32' 44” W, 126 m.a.s.l., Jan 1969, FR, *Farinas 627* (F, MO, NY, VEN); on La Esmeralda Ridge, 3° 10' 20” N, 65° 33' 20” W, 100 m.a.s.l., 6 Oct 1928, FL, *Tate 196* (NY); La Esmeralda, 3° 10' 20” N, 65° 33' 40” W, 130 m.a.s.l., 1942, FR, *Williams 15420* (F, MO, NY, US, VEN); Atabapo: Chipital, Caño Yagua, 3° 29' 0” N, 66° 41' 0” W, 120 m.a.s.l., 6 Dec 1978, FL, *Huber 2922* (NY, VEN); Caño Guacamaya, 03° 54' 48” N, 67° 33' 07” W, 75 m.a.s.l., 25 May 2001, Buds, *Diaz 5242* (MO); Caño Perro de Agua, 30 km SE mouth of Ventuari river, 3° 34' 17” N, 66° 42' 51” W, 100 m.a.s.l., 4 Dec 1978, FL, *Huber 2812* (NY, VEN); Caño Perro de Agua, 30 km SE mouth of Ventuari river, 3° 47' N, 67° 00' W, 100 m.a.s.l., 30 Nov 1978, FL, *Huber 2774* (VEN); Yapacana tepui, 3° 41' 27” N, 66° 51' 0” W, 125 m.a.s.l., 20 Nov 1953, FL, *Maguire 36587* (COL, NY, USM, VEN); margen N del río Orinoco, ca. Santa Bárbara del Orinoco, 4° 2' 0” N, 67° 15' 0” W, 100 m.a.s.l., 23 Aug 1978, FL-old, *Huber 2467* (NY, VEN); Autana: Reserva Forestal El Sipapo, 4° 33' 46” N, 67° 32' 46” W, 663 m.a.s.l., May 1971, FR, *Blanco 1131* (VEN); San Pedro, rio Autana, 4° 44' 0” N, 67° 33' 0” W, 100 m.a.s.l., 2 Jul 1979, FR, *Huber 4066* (VEN); San Pedro, rio Sipapo, 4° 53' 0” N, 67° 47' 0” W, 90 m.a.s.l., 17 Feb 1979, FR, *Huber 3150* (NY, VEN); San Pedro, rio Autana, 4° 45' 0” N, 67° 35' 0” W, 100 m.a.s.l., 26 Jun 1979, FR, *Huber 3826* (NY, VEN); San Pedro, rio Sipapo, 4° 51' 0” N, 67° 25' 50” W, 200 m.a.s.l., 8 Feb 1949, FL-FR, *Maguire 28826* (NY, VEN); San Pedro, rio Sipapo, 4° 51' 26” N, 67° 25' 43” W, 125 m.a.s.l., 25 Dec 1948, FR, *Maguire 27967* (NY, VEN); San Pedro, rio Sipapo, 4° 50' 0” N, 67° 25' 40” W, 125 m.a.s.l., 28 Dec 1948, FL, *Maguire 27976* (NY, VEN); San Pedro, rio Sipapo, 4° 33' 49” N, 67° 32' 44” W, 100 m.a.s.l., 19 Dec 1948, FL, *Maguire 27858* (NY, VEN); San Pedro, rio Sipapo, 4° 33' 44” N, 67° 32' 48” W, 100 m.a.s.l., 19 Dec 1948, FL, *Maguire 27859* (NY); San Pedro, 110 km arriba río Guayapo, 4° 18' 0” N, 67° 28' 0” W, 120 m.a.s.l., May 1989, FL, *Foldats 9300* (NY, PORT); Manapiare: SW del Cerro Morrocoy, Caño Camaní, 5° 15' 0” N, 66° 9' 0” W, 130 m.a.s.l., 20 Aug 1978, FR, *Huber 2350* (COL, K, NY, TFVA, VEN); Cerro Moriche, NW base, 4° 45' 49” N, 66° 21' 49” W, 150 m.a.s.l., 17 Jan 1951, FL-old, *Maguire 30982* (NY, VEN); Cerro Moriche, NW base, 4° 45' 49” N, 66° 21' 49” W, 150 m.a.s.l., 17 Jan 1951, FR, *Maguire 30988* (NY, UNB, VEN); Cerro Moriche, NW base, 4° 45' 49” N, 66° 21' 49” W, 150 m.a.s.l., 17 Jan 1951, FL, *Maguire 31009* (NY, VEN); Maroa: 1 km E, 2° 45' 0” N, 67° 35' 0” W, 125 m.a.s.l., 20 Apr 1970, FL, *Steyermark 102820* (NY, VEN); south on río Guainía, 2° 42' 33” N, 67° 32' 44”

W, 130 m.a.s.l., 28 Dec 1953, FL, *Maguire 36458* (NY, VEN); Rio Negro: 10-11 km carretera San Carlos de Rio Negro-Solano, 1° 56' 0” N, 67° 3' 0” W, 100 m.a.s.l., 30 Oct 1987, Buds, *Carnevali 2590* (VEN); 2 km E rd San Carlos de Rio Negro-Solano, 1° 55' 17” N, 67° 2' 46” W, 120 m.a.s.l., 3 Apr 2000, FL, *Berry 7556* (MO, PORT, TFVA); Santa Rosa de Amanadona, 1° 29' 14” N, 66° 54' 41” W, 100 m.a.s.l., 31 Jan 1968, FR, *Ruiz-Teran 5185* (NY); mouth of rio Pasimoni, 1° 55' 54” N, 66° 36' 33” W, 29 m.a.s.l., 15 Jan 1989, FR, *Stergios 13127* (NY, PORT); Cerro Aracamuni, 1° 32' 0” N, 65° 48' 0” W, 750 m.a.s.l., 10 Feb 1981, FL-FR, *Huber 5915* (NY, VEN); rio Pasimoni, 1° 35' 0” N, 66° 30' 0” W, 66 m.a.s.l., 3 Feb 1992, FR, *Stergios 15555* (MO, PORT, US, VEN); rio Pasimoni, Pedra de Arapacoa, 1° 32' 0” N, 66° 20' 0” W, 150 m.a.s.l., 24 Jul 1982, FL, *Stergios 4072* (VEN); rio Pasimoni, entre la boca y piedra Arapacoa, 1° 30' 0” N, 66° 10' 0” W, 130 m.a.s.l., 4 Dec 1984, FL, *Stergios 7587* (NY); río Casiquiare, Hechimoni, 2° 0' 7” N, 67° 6' 42” W, 115 m.a.s.l., 25 Jul 1959, FL, *Wurdack 43623* (MO, NY, USM, VEN).

Specimens seen but not measured — **BRASIL**. **Amazonas**. Barcelos: Parque Nacional do Jaú, campina do Patauá, 1° 48' 47” S, 61° 45' 39” W, 37 m.a.s.l., 23 Jul 2001, FL, *Vicentini 1762* (INPA); Parque Nacional do Jaú, campina do Seringalzinho, 1° 54' 24” S, 61° 35' 11” W, 32 m.a.s.l., 26 Jul 2001, FL, *Vicentini 1772* (INPA); Parque Nacional do Jaú, campina do Seringalzinho, 1° 54' 28” S, 61° 35' 11” W, 60 m.a.s.l., 26 Jul 2001, FL, *Vicentini 1773* (INPA); Serra do Aracá, surrounding lowlands, 00° 18' 16” N, 63° 01' 35” W, 75 m.a.s.l., , ?, *Cid 11887* (INPA); Serra do Aracá, surrounding lowlands, 00° 04' 40” N, 63° 12' 51” W, 69 m.a.s.l., , ?, *Cid 11894* (INPA); rio Univini [Unini], 1° 40' 54” S, 61° 31' 04” W, 35 m.a.s.l., 23 Apr 1974, FL, *Pires 14197* (INPA); Serra do Aracá, surrounding lowlands, 0° 48' 0” N, 63° 21' 0” W, 100 m.a.s.l., Jul 1985, FL, *Huber 10725* (INPA, MO, NY, SP, US); Serra do Aracá, surrounding lowlands, 0° 49' 0” N, 63° 19' 0” W, 206 m.a.s.l., 28 Feb 1984, FR, *Amaral 1681* (INPA, MO, NY, UNB); Serra do Aracá, surrounding lowlands, 0° 49' 0” N, 65° 17' 0” W, 100 m.a.s.l., 18 Jul 1985, FR, *Prance 29664* (NY); Serra do Aracá, surrounding lowlands, 0° 49' 0” N, 65° 17' 0” W, 100 m.a.s.l., 18 Jul 1985, FR, *Prance 29678* (INPA, NY); Serra do Aracá, surrounding lowlands, 0° 49' 0” N, 63° 20' 0” W, 191 m.a.s.l., 12 Jul 1985, FL, *Prance 29488* (INPA, NY); Serra do Aracá, surrounding lowlands, 0° 49' 0” N, 63° 20' 0” W, 191 m.a.s.l., 12 Jul 1985, FR, *Prance 29508* (INPA, NY); Serra do Aracá, surrounding lowlands, 0° 42' 0” N, 63° 22' 0” W, 98 m.a.s.l., 2 Jul 1985, Buds, *Silva 210* (INPA, NY); Serra do Aracá, surrounding lowlands, 0° 25' 0” N, 63° 23' 0” W, 80 m.a.s.l., 25 Jul 1985, FL, *Prance 29759* (INPA, MO, NY, SP, US); Borba: interflúvio Madeira-Purus, 4° 18' 33” S, 60° 25' 26” W, 46 m.a.s.l., , ?, *Cohn-Haft 01* (INPA); Iranduba: rio Negro, Acajutuba, igarapé do Inglês, 3° 3' 0” S, 60° 36' 0” W, 40 m.a.s.l., 22 Jun 1985, FL, *Mesquita 893* (HALCB); rio Negro, Praia Grande, 3° 2' 0” S, 60° 30' 0” W, 40 m.a.s.l., 15 Jun 1990, FR, *Mori 21321* (INPA, MO, NY); rio Negro, Praia Grande, 3° 2' 0” S, 60° 32' 0” W, 33 m.a.s.l., 27 Mar 1978, FR, *Revilla 4048* (INPA); rio Negro, Praia Grande, 3° 2' 0” S, 60° 32' 30” W, 33 m.a.s.l., 13 Feb 1979, FR, *Revilla 4161* (INPA); rio Negro, Praia Grande, 3° 2' 6” S, 60° 32' 33” W, 32 m.a.s.l., 31 Jul 2000, FL, *Vicentini 1679* (INPA); rio Negro, Praia Grande, 3° 2' 5” S, 60° 32' 37” W, 37 m.a.s.l., 31 Jul 2000, FR, *Vicentini 1681* (INPA); rio Negro, Praia Grande, 3° 2' 4” S, 60° 32' 39” W, 33 m.a.s.l., 31 Jul 2000, Buds, *Vicentini 1682* (INPA); rio Negro, Praia Grande, 3° 2' 4” S, 60° 32' 47” W, 28 m.a.s.l., 31 Jul 2000, FR, *Vicentini 1684* (INPA); rio Negro, Acajutuba, 3° 3' 0” S, 60° 36' 0” W, 40 m.a.s.l., 20 Apr 1986, FL, *Prance 29948* (MO, NY); Itacoatiara: Manaus-Itacoatiara, km 227, rd to Silves, rio Carú, 2° 38' 0” S, 59° 1' 0” W, 100 m.a.s.l., 9 Mar 2000, FR, *Anunciação 836* (INPA); Manaus: Ponta Negra, 3° 2' 0” S, 60° 6' 0” W, 34 m.a.s.l., 26 Jun 1929, FR, *Ducke sn* (INPA); Ponta Negra, 3° 2' 0” S, 60° 6' 0” W, 34 m.a.s.l., 12 May 1961, FR, *Rodrigues 2594* (INPA); Presidente Figueiredo: Manaus-Caracaraí rd, km 114, 1° 58' 3” S, 60° 1' 20” W, 120 m.a.s.l., 17 Dec 1997, FR, *Cid 11516* (INPA); Reserva Biológica de Lajes, 1° 59' 14” S, 60° 1' 36” W, 105 m.a.s.l., 5 Aug 2000, FL-FR, *Vicentini 1703* (INPA); Reserva Biológica de Lajes, 1° 59' 15” S, 60° 1' 35” W, 103 m.a.s.l., 5 Aug 2000, Sterile, *Vicentini 1704* (INPA); Reserva Biológica de Lajes, 1° 59' 13” S, 60° 1' 29” W, 133 m.a.s.l., 5 Aug 2000, FR, *Vicentini 1710* (INPA); Reserva Biológica de Lajes, 1° 59' 1” S, 60° 1' 19” W, 100 m.a.s.l., 5 Aug 2000, FR, *Vicentini 1715* (INPA); Presidente figueiredo: Manaus-Caracaraí rd, km 125, 1° 55' 0” S, 60° 1' 20” W, 110 m.a.s.l., 13 Feb 1974, FR, *Loureiro 47891INPA* (US); Presidente Figueiredo: Manaus-Caracaraí rd, km 125, 1° 55' 0” S, 60° 1' 20” W, 110 m.a.s.l., 20 Feb 1979, FR, *Coelho 943* (INPA, MBM); Manaus-Caracaraí rd, km 125, 1° 55' 0” S, 60° 1' 20” W, 110 m.a.s.l., 22 Sep 1977, FR, *Rodrigues 9761* (INPA); Cachoeira da Iracema, trilha entre Iracema e Araras, 1° 57' 26” S, 60° 04' 27” W, 130 m.a.s.l., 28 Apr 2004, FR, *Vicentini 2278* (INPA); Cachoeira da Iracema, trilha entre Iracema e Araras, 1° 55' 28” S, 60° 04' 26” W, 130 m.a.s.l., 28 Apr 2004, FR, *Vicentini 2280* (INPA); Cachoeira da Iracema, trilha entre

Iracema e Araras, 1° 54' 32” S, 60° 03' 59” W, 133 m.a.s.l., 28 Apr 2004, FR, *Vicentini 2285* (INPA); Cachoeira da Iracema, trilha entre Iracema e Araras, 1° 54' 33” S, 60° 03' 59” W, 135 m.a.s.l., 28 Apr 2004, FR, *Vicentini 2286* (INPA); Cachoeira da Iracema, trilha entre Iracema e Araras, 1° 56' 10” S, 60° 04' 32” W, 135 m.a.s.l., 28 Jul 2003, Sterile, *Vicentini 2050* (INPA); Cachoeira das Orquídeas, 1° 58' 04” S, 59° 59' 20” W, 150 m.a.s.l., 29 Apr 2004, FR, *Vicentini 2281* (INPA); Cachoeira das Orquídeas, 1° 58' 03” S, 59° 59' 22” W, 148 m.a.s.l., 29 Apr 2004, FR, *Vicentini 2282* (INPA); Cachoeira das Orquídeas, 1° 58' 10” S, 59° 59' 15” W, 140 m.a.s.l., 29 Apr 2004, FR, *Vicentini 2283* (INPA); Cachoeira das Orquídeas, 1° 58' 03” S, 60° 00' 00” W, 145 m.a.s.l., 29 Apr 2004, FR, *Vicentini 2284* (INPA); Reserva Ecologica de Lajes, 1° 59' 1” S, 60° 1' 36” W, 110 m.a.s.l., 28 Jul 2003, Sterile, *Vicentini 2058* (INPA); rio Uatumã, margem direita a 300 m da cachoeira Morena, 2° 6' 33” S, 59° 15' 16” W, 96 m.a.s.l., 12 Aug 1979, FL, *Cid 237* (INPA, MO, NY); Santa Isabel do Rio Negro: 0° 21' 59” S, 64° 59' 48” W, 60 m.a.s.l., , ?, *Amaral 03* (INPA); São Gabriel da Cachoeira: Alto rio Negro, rio Tuari, afluente do rio Negro, Piraiauara, 1° 0' 10” N, 68° 0' 30” W, 99 m.a.s.l., 13 Nov 1987, FL, *Lima 3173* (MO, NY); Alto rio Negro, rio Waupés, 0° 9' 34” S, 66° 59' 36” W, 71 m.a.s.l., 20 May 1975, FL-old, *Coelho 19* (US); Camanáus, 0° 9' 10” S, 66° 56' 59” W, 71 m.a.s.l., 16 Feb 1963, Sterile, *Lanna 328* (K); Estrada SGC-Camanaus, km 20, ramal do Quidaban, 0° 8' 52” S, 66° 57' 8” W, 65 m.a.s.l., 17 Jun 2004, Sterile, *Vicentini 2214* (INPA); Iauaretê, 0° 38' 0” N, 69° 12' 0” W, 60 m.a.s.l., 12 Dec 1975, FL, *Coelho 219* (INPA); rio Cubate, afluente do Içana, 0° 33' 0” N, 67° 23' 0” W, 86 m.a.s.l., 3 Nov 1987, Buds, *Daly 5564* (INPA, MO, NY); rio Tauari, lago Uirauaçu, 0° 20' 0” N, 67° 0' 0” W, 115 m.a.s.l., 13 Nov 1987, FL, *Kawasaki 139* (F, INPA, MO, NY); **Mato Grosso**. entre 17 de fevereiro e Mingáo affl. do Cantario (rio Cautário em Rondônia), 11° 23' 0” S, 63° 25' 0” W, 362 m.a.s.l., Feb 1919, FL, *Kuhlmann 2232* (SP); Reserva Indígena Mambikwara, rio Camararé, 12° 15' 0” S, 59° 30' 0” W, 400 m.a.s.l., 22 Apr 1977, FR, *Oliveira 154* (IBGE); **Rondônia**. VIlhena: 12° 43' 0” S, 60° 7' 0” W, 600 m.a.s.l., 3 Apr 1977, Sterile, *Silva 25* (IBGE); **Roraima**. Caracaraí: BR-174, km 350-355, 0° 1' 0” N, 60° 43' 38” W, 97 m.a.s.l., 21 Aug 1987, FL, *Cid 9078* (INPA, MO); BR-174, km 530-540, 1° 25' 0” N, 60° 45' 0” W, 101 m.a.s.l., 27 Aug 1987, FL-FR, *Cid 9240* (INPA, MO); BR-174, entre a estrada da perdida e rotatoria, ca. 5-6 km da rotatória, 1° 18' 37” N, 60° 35' 35” W, 82 m.a.s.l., 6 Aug 2000, Sterile, *Vicentini 1730* (INPA); BR-174, entre a estrada da perdida e rotatoria, ca. 5-6 km da rotatória, 1° 18' 37” N, 60° 35' 37” W, 81 m.a.s.l., 6 Aug 2000, Sterile, *Vicentini 1731* (INPA); estrada da Perdida, 4 km da BR-174, 1° 26' 21” N, 60° 58' 53” W, 58 m.a.s.l., 7 Aug 2000, FR, *Vicentini 1735* (INPA); estrada da Perdida, 4 km da BR-174, 1° 26' 20” N, 60° 58' 54” W, 53 m.a.s.l., 7 Aug 2000, FL-old, *Vicentini 1736* (INPA); estrada da Perdida, 4 km da BR-174, 1° 26' 18” N, 60° 58' 59” W, 56 m.a.s.l., 7 Aug 2000, Sterile, *Vicentini 1738* (INPA); estrada da Perdida, 4 km da BR-174, 1° 26' 21” N, 60° 59' 2” W, 51 m.a.s.l., 7 Aug 2000, Sterile, *Vicentini 1741* (INPA); estrada da Perdida, 4 km da BR-174, 1° 26' 24” N, 60° 58' 59” W, 71 m.a.s.l., 7 Aug 2000, Sterile, *Vicentini 1742* (INPA); **COLOMBIA**. **Amazonas**. rio Caquetá, Quebrada el Tigre, 1° 15' 35” S, 70° 51' 08” W, 89 m.a.s.l., 20 Sep 1988, Sterile, *Sanchez 1348* (COAH); **Caquetá**. 0° 04' 16” N, 72° 26' 48” W, 120 m.a.s.l., 18 Jun 1993, Sterile, *Hernández CHI1296* (COL); rio Caquetá, W del caño Paujil, 0° 46' 31” S, 72° 21' 30” W, 100 m.a.s.l., 3 Dec 1988, Sterile, *Sanchez 1911* (COAH); rio Caquetá, W del caño Paujil, 0° 46' S, 72° 22' 00” W, 100 m.a.s.l., 3 Dec 1988, Sterile, *Sanchez 1928* (COAH); Extremo norte del parque cerca de 2 Rios Guaviare., 1° 5' 48” S, 72° 44' 17” W, 112 m.a.s.l., 16 Aug 1992, FL-FR, *Barbosa 7393A (75A)* (COAH); Araracuara: 0° 25' 10” S, 72° 20' 10” W, 103 m.a.s.l., 11 Mar 1986, Sterile, *Palacios 1291* (COAH); 50 m de la pista aérea, 0° 25' 05” S, 72° 20' 05” W, 100 m.a.s.l., 11 Mar 1986, Sterile, *Palacios 1270* (COAH); 50 m de la pista aérea, 0° 25' S, 72° 20' W, 104 m.a.s.l., 11 Mar 1986, Sterile, *Palacios 1284* (COAH); cerca de la pista aérea, 0° 37' S, 72° 24' W, 100 m.a.s.l., 14 Oct 1990, FR, *Duivenvoorden 186* (COAH); Chagra de Oscar Román y los Comiyares, 0° 25' 10” S, 72° 21' W, 103 m.a.s.l., 15 Nov 1982, FL, *Midrobo 11243* (COAH, COL); rio Caqueta, Caño Paujil, 10 km NO de Araracuara, 0° 47' 30” S, 72° 22' 30” W, 225 m.a.s.l., 3 Dec 1993, FL, *Arbelaez 535* (COL, HUA); rio Caqueta, Caño Paujil, 10 km NO de Araracuara, 0° 47' 30” S, 72° 22' 30” W, 225 m.a.s.l., 3 Dec 1993, FR, *Arbelaez 544* (COL, HUA); rio Caqueta, Caño Paujil, 10 km NO de Araracuara, 0° 46' 30” S, 72° 22' 30” W, 175 m.a.s.l., 19 Feb 1993, Sterile, *Arbelaez 388* (COAH, HUA); rio Caqueta, Caño Paujil, 10 km NO de Araracuara, 0° 46' 30” S, 72° 22' 30” W, 175 m.a.s.l., 20 Feb 1993, Sterile, *Arbelaez 397* (COAH, HUA); cerca de la pista aérea, 0° 25' S, 72° 19' W, 250 m.a.s.l., 27 Jan 1989, Sterile, *Gentry 65281* (COAH); río Caquetá, balcon del diablo, cerca de la pista aérea, 0° 36' S, 72° 24' W, 100 m.a.s.l., 19 Nov 1993, FL, *Cárdenas 4126* (COAH); cerca de la pista aérea, 0° 25' 10” S, 72° 20' 10” W, 103 m.a.s.l., 15 Nov 1982, FL, *Midrobo 11441* (COAH, COL); río Caqueta, 0° 40' S, 72° 10' W, 110 m.a.s.l., 23 Aug 1986, Sterile, *Palacios 1879* (COAH, COL); rio Mesay, raudal Masaca, 00°

20' S, 72° 20' W, 400 m.a.s.l., 15 Nov 1995, FL, *Duque 5187* (COAH); Sabanas del Yari, 40 min del chorro de Gamitana, 00° 14' S, 72° 26' W, 250 m.a.s.l., 20 Mar 1998, Sterile, *Arbelaez 948* (COAH); **Guainia**. Maimachi: Serrania de Naquén, camino de Caño Grande a la Cachivera., 2° 12' 0" N, 68° 12' 0" W, 420 m.a.s.l., 7 Jul 1992, FR, *Cortés 290* (COAH); Nabuquén: 2° 43' 18" N, 68° 55' 31" W, 303 m.a.s.l., 1 Mar 1995, Sterile, *Córdoba 782* (MO); 2° 51' 12.7" N, 65° 38' 33.9" W, 500 m.a.s.l., 25 Feb 1995, FR, *Córdoba 542* (COAH, COL); Puerto Inírida: Raudal Samuro, 03° 15' 10.2" N, 72° 06' 06.5" W, 250 m.a.s.l., 21 Nov 1998, Buds, *Marin 609* (COAH); Resguardo La Ceiba, 3° 45' N, 67° 50' W, 241 m.a.s.l., 3 Nov 1997, FR, *Galeano 2319(2)* (COAH); Vía a Caño Vitina, 3° 49' 26" N, 67° 53' 25.9" W, 125 m.a.s.l., 28 Apr 2004, FR, *Cárdenas 14850* (COL); **Santa Isabel**. Sabanas de Solarte, 01° 05' S, 71° 10' W, 91 m.a.s.l., 4 Dec 1996, FL, *Arbelaez 676* (COAH, HUA); Sabanas de Solarte, 01° 05' S, 71° 10' W, 91 m.a.s.l., 4 Dec 1996, FL, *Arbelaez 630* (COAH, HUA); **Vaupés**. Cerro de Circasia, entre el río Tí y Ñamú, 1° 00' 00" N, 70° 40' W, 405 m.a.s.l., 30 Oct 1962, FR, *Barriga 15029* (COL); río Apaporis, Cachivera de Jirijirimo, 0° 8' 0" N, 70° 39' 0" W, 250 m.a.s.l., 13 Jun 1951, FR, *Schultes 12467* (COL, US); río Kubiyú, Guranjudá, 1° 20' 0" N, 70° 30' 0" W, 375 m.a.s.l., 30 Jun 1958, FL-old, *Barriga 16052* (COL, K); río Kuduyarí, Yapobodá, 1° 200' 00" N, 70° 40' W, 159 m.a.s.l., 14 Aug 1960, FR, *Schultes 22611* (COL); río Macu (Macu-Parana)., 0° 44' 0" N, 69° 30' 0" W, 94 m.a.s.l., 11 Aug 1943, FR, *Allen 3018* (COL, MO); Mitú: Carretera Mitú-Bogotá Cachivera, km 15. Cucura, 1° 15' 0" N, 70° 13' W, 161 m.a.s.l., Jul 1998, FR, *Galeano 39 (1)* (COL); rio Vaupés, comunidad de Mandi, 1° 15' 0" N, 70° 13' W, 161 m.a.s.l., 26 Oct 1993, Sterile, *MEJIA 157* (COL); rio Vaupés, Mirití, 1° 15' 0" N, 70° 13' W, 161 m.a.s.l., 24 Nov 1993, FL, *Galeano 1876 (4)* (COAH, COL); rio Vaupés, Mirití, 1° 15' 0" N, 70° 13' W, 161 m.a.s.l., 24 Nov 1993, FL, *Galeano 1993* (COAH); rio Vaupés, Mirití, 1° 15' 0" N, 70° 13' W, 161 m.a.s.l., Nov 1993, FL, *Galeano 3326 (3)* (COAH, COL); rio Vaupés, Mirití, 1° 15' 0" N, 70° 13' 0" W, 161 m.a.s.l., Nov 1993, FL-old, *Galeano 3471 (6)* (COAH, COL); Sierra de Chiribiquete: Estación Puerto Abeja, 0° 3' 57.1" N, 72° 27' 37.9" W, 320 m.a.s.l., 2 Dec 2000, Sterile, *Dávila 619* (UDBC); Estación Puerto Abeja, 0° 4' 30" N, 72° 27' 20" W, 225 m.a.s.l., 23 Mar 1999, FR, *Garcia A153PA* (COAH); Estación Puerto Abeja, 0° 4' 27" N, 72° 27' 10" W, 220 m.a.s.l., 13 Mar 1999, FR, *Garcia PA134* (COAH); parte norte, cerca del río Guaviare, 1° 5' 48" N, 72° 44' 17" W, 919 m.a.s.l., 16 Aug 1992, FR, *Barbosa 7393 (75)* (COAH); río Cuñaré, 20 min de la boca del río Amu, 0° 13' 25.6" N, 72° 26' 12.8" W, 350 m.a.s.l., 15 Feb 2001, ?, *Mendoza 10343* (FMB); cuenca media del río Cuñare, 0° 31' 45" N, 72° 37' 45" W, 350 m.a.s.l., 15 Nov 2000, ?, *Mendoza 9438* (FMB); cuenca media del río Cuñare, 0° 31' 44.7" N, 72° 37' 50.3" W, 350 m.a.s.l., 15 Nov 2000, ?, *Mendoza 9641* (FMB); cuenca media del río Cuñare, 0° 29' 55.3" N, 72° 37' 11" W, 350 m.a.s.l., 15 Nov 2000, ?, *Mendoza 9738* (FMB); rio Sararamano, 0° 11' 11" N, 72° 36' 20" W, 350 m.a.s.l., 15 Apr 2001, ?, *Mendoza 8267* (FMB); rio Sararamano, 0° 11' 11" N, 72° 36' 20" W, 350 m.a.s.l., 15 Apr 2001, ?, *Mendoza 8705* (FMB); 1° 7' 0" N, 72° 50' 0" W, 525 m.a.s.l., 7 Dec 1990, FR, *Castroviejo 11990* (COL, MO); 1° 7' N, 72° 50' W, 525 m.a.s.l., 8 Mar 1990, FL, *González 2249* (COL); mesa Norte, 1° 05' N, 72° 40' W, 580 m.a.s.l., 15 Aug 1992, Sterile, *Franco 3642* (COL); mesa Norte, 1° 5' 0" N, 72° 40' 0" W, 580 m.a.s.l., 15 Aug 1992, Sterile, *Franco 3677* (COL, MO); mesa Norte, 1° 5' 0" N, 72° 40' 0" W, 580 m.a.s.l., 15 Aug 1992, FR, *Franco 3695* (COL, MO); Parte suroriental, 0° 21' 49" N, 72° 54' 0" W, 375 m.a.s.l., 29 Nov 1995, FL, *Cárdenas 6976* (COAH, MO); rio mesay, chorro Jacameya, 0° 23' 0" N, 72° 54' 0" W, 250 m.a.s.l., 25 Nov 1995, FL, *Cárdenas 6880* (COAH, MO); Taraira: Serrania de Taraira, 10 km al N-W del Raudal de la Libertad, 0° 58' S, 69° 45' W, 250 m.a.s.l., 8 Aug 1993, FL-FR, *Cortés 816* (COL); Serrania de Taraira, 10 km al N-W del Raudal de la Libertad, 0° 58' S, 69° 45' W, 250 m.a.s.l., 15 Aug 1993, FR, *Rodriguez 58* (COL); Serrania de Taraira, 10 km al N-W del Raudal de la Libertad, 0° 58' S, 69° 45' W, 250 m.a.s.l., 17 Aug 1993, Sterile, *Rodriguez 90* (COL); Serrania de Taraira, 10 km al N-W del Raudal de la Libertad, 0° 58' S, 69° 45' W, 250 m.a.s.l., 23 Jul 1993, Sterile, *Cortés 532* (COL); **VENEZUELA**. **Amazonas**. Alto Orinoco: 3 km al N-W from La Esmeralda, 3° 10' 0" N, 65° 33' 0" W, 160 m.a.s.l., 26 Feb 1990, FL, *Aymard 8278* (MO, NY, PORT); Cerro de la Bandera, 3° 12' 0" N, 65° 30' 0" W, 234 m.a.s.l., 20 Jul 1951, FL, *Croizat 228* (MO, PORT, VEN); La Esmeralda, 3° 10' 0" N, 65° 33' 0" W, 74 m.a.s.l., Dec 1853, FL, *Spruce 3253* (P); on La Esmeralda Ridge, 3° 10' 10" N, 65° 33' 0" W, 175 m.a.s.l., 23 Mar 1953, Buds, *Maguire 34656* (NY, VEN); Atabapo: 20 km SE from San Fernando de Atabapo, 3° 50' 0" N, 67° 47' 0" W, 110 m.a.s.l., 10 Jan 1988, FR, *Aymard 6321* (MO, VEN); 20 km SE from San Fernando de Atabapo, 3° 30' 0" N, 67° 47' 0" W, 110 m.a.s.l., 10 Jan 1988, FR, *Aymard 6526* (MO, NY, PORT, VEN); Caño Yagua, 3° 31' 0" N, 66° 48' 0" W, 130 m.a.s.l., May 1990, Buds, *Marin 1291* (MO, PORT); Chipital, Caño Yagua, 3° 29' 0" N, 66° 41' 0" W, 120 m.a.s.l., 7 May 1979, FR, *Davidse 17319* (MO, VEN); Yapacana tepui, 3° 40' 0" N, 66° 52' 0" W, 180 m.a.s.l., Nov 1989, Buds, *Marin 663* (MO, NY, PORT); 12-40 km, rd San Fernando de Atabapo-Santa Barbara, 3° 56' 43” N, 67° 18' 33” W, 110 m.a.s.l., 24 Mar 1974, FR, *Gentry 10877* (MO, VEN); Autana: San Pedro, rio Sipapo, 4° 32' 44” N, 67° 38' 11” W, 95 m.a.s.l., 23 Feb 1985, FR, *Carnevali 1861* (MO, VEN); San Pedro, Santa Rosa de Ucata. ca. 3 km N of town., 4° 23' 33” N, 67° 44' 27” W, 120 m.a.s.l., 21 Jun 1992, FR, *Berry 5218* (MO, TFVA); Manapiare: Cerro Moriche, N base, 4° 44' 57” N, 66° 24' 7” W, 114 m.a.s.l., 20 Mar 2002, FR, *Aymard 12249* (INPA); Maroa: Yavita,, 2° 55' 16” N, 67° 26' 17” W, 110 m.a.s.l., 28 Nov 1995, Buds, *Berry 5715* (MO, VEN); Rio Negro: 90 km ENE from San Carlos de Rio Negro, 2° 8' 45” N, 66° 17' 30” W, 160 m.a.s.l., 12 Oct 1987, FR, *Liesner 21872A* (MO, VEN); rio Pasimoni, entre la boca y Piedra Arapacoa, 1° 50' 0” N, 66° 35' 0” W, 29 m.a.s.l., 4 Dec 1984, FL, *Stergios 7586* (MO, PORT, TFVA); ca. 500 m from from San Carlos de Rio Negro, 1° 56' 0” N, 67° 3' 0” W, 120 m.a.s.l., 25 Apr 1979, FR, *Liesner 6976* (MO, VEN); Cerro Aracumuni, 1° 24' 0” N, 65° 38' 0” W, 600 m.a.s.l., 22 Oct 1987, FL-old, *Liesner 22352* (MO, NY); rio Pasimoni, junction with Casiquiare, 1° 53' 0” N, 66° 35' 0” W, 80 m.a.s.l., 25 Jul 1984, FR, *Davidse 27858* (MO, NY, VEN); rio Pasimoni, Piedra de Arapacoa, 1° 30' 30” N, 66° 30' 0” W, 75 m.a.s.l., 24 Jul 1982, FL, *Stergios 4075* (MO, PORT, TFVA); near San Carlos de Rio Negro playing field, 1° 55' 00” N, 67° 4' 0” W, 98 m.a.s.l., 4 Apr 1981, FR, *Christenson 1409* (NA, QCNE).

20. *Pagamea igapoana* Vicentini

Specimens measured — **BRASIL**. **Amazonas**. São Gabriel da Cachoeira: rio Içana, vila de Jauacanã, 0° 33' 47” N, 67° 24' 9” W, 73 m.a.s.l., 27 Jun 2004, FR, *Vicentini 2265* (INPA, MO); rio Içana, vila de Jauacanã, 0° 33' 47” N, 67° 24' 9” W, 73 m.a.s.l., 27 Jun 2004, FR-old, *Vicentini 2267* (INPA, MO); rio Içana, vila de Jauacanã, 0° 33' 47” N, 67° 24' 9” W, 73 m.a.s.l., 27 Jun 2004, FR, *Vicentini 2268* (INPA, MO); rio Içana, vila de Jauacanã, 0° 33' 47” N, 67° 24' 9” W, 73 m.a.s.l., 27 Jun 2004, FL-old, *Vicentini 2269* (INPA, MO); rio Içana, vila de Jauacanã, 0° 33' 47” N, 67° 24' 9” W, 73 m.a.s.l., 27 Jun 2004, FR, *Vicentini 2270* (INPA, MO); rio Içana, vila de Jauacanã, 0° 33' 47” N, 67° 24' 9” W, 73 m.a.s.l., 27 Jun 2004, FR, *Vicentini 2271* (INPA, MO); rio Içana, vila de Jauacanã, 0° 33' 47” N, 67° 24' 9” W, 73 m.a.s.l., 27 Jun 2004, FL-old, *Vicentini 2272* (INPA, MO); rio Içana, vila de Jauacanã, 0° 33' 47” N, 67° 24' 9” W, 73 m.a.s.l., 27 Jun 2004, FR, *Vicentini 2277* (INPA, MO).

21. *Pagamea acrensis* Steyerm.

Specimens measured — **BRASIL**. **Acre**. Cruzeiro do Sul: BR-307, 6 km to Boa Fé, ramal dos Carobas, 7° 28' 22” S, 72° 49' 17” W, 192 m.a.s.l., 16 Oct 2001, FL-old, *Maas 8974* (MO, NY); 7° 38' 0” S, 72° 36' 0” W, 80 m.a.s.l., 19 Oct 1989, FL, *Cid 10135* (INPA); km 32 rd to Benjamin Constant, 7° 24' 36” S, 72° 25' 12” W, 80 m.a.s.l., 23 Oct 1984, FL-FR, *Cid 5208* (INPA, NY); 7° 38' 0” S, 72° 36' 0” W, 80 m.a.s.l., 10 Feb 1976, FR, *Monteiro 280* (INPA); BR-307, rd near ramal Pentecoste, 7° 26' 8” S, 72° 58' 9” W, 200 m.a.s.l., 12 Dec 2000, FL-old, *Daly 10625* (MO, NY); BR-307, rd near ramal Pentecoste, 7° 24' 01.5” S, 73° 01' 16.4” W, 200 m.a.s.l., 26 Apr 2001, FL-old, *Daly 10667* (MO, NY); Mâncio Lima: 7° 43' 38” S, 73° 13' 5” W, 200 m.a.s.l., 7 Jun 1994, FR, *Silveira 795* (MO); 7° 37' 0” S, 72° 55' 0” W, 186 m.a.s.l., 24 Mar 1992, FR, *Cid 10941* (ACRE, MO, NY); ramal do Banho, 7° 36' 0” S, 72° 57' 0” W, 186 m.a.s.l., 13 May 1996, FR, *Daly 9056* (MO); 7° 54' 0” S, 72° 88' 0” W, 199 m.a.s.l., 8 Nov 1991, FL, *Cid 10621* (ACRE, MO, NY); **Amazonas**. São Gabriel da Cachoeira: Boca do rio Içana, Boa Vista, 0° 30' 0” N, 67° 21' 0” W, 89 m.a.s.l., 12 Nov 1987, FL, *Kawasaki 106* (INPA, MO, NY); Cucui, rio Xié, 0° 58' 0” N, 67° 10' 0” W, 84 m.a.s.l., 25 Oct 1987, FL, *Daly 5486* (INPA, MO, NY); 0° 8' 0” S, 67° 5' 0” W, 73 m.a.s.l., 1852, FL, *Spruce 2260* (BM, NY, P); boca do Igarapé Tuari, Lago Amaro, lado oposto à Ilha de Aparecida, 0° 20' 0” N, 67° 19' 0” W, 77 m.a.s.l., 6 Nov 1987, FL, *Rodrigues 10871* (INPA, MO); rio Cubate, afluente do Içana, 0° 26' 0” N, 67° 32' 0” W, 72 m.a.s.l., 2 Nov 1987, FL, *Farney 1867* (INPA, MO); rio Içana, vila Jandú-Cachoeira, 1° 28' 59” N, 68° 42' 59” W, 157 m.a.s.l., 23 Jun 2004, Sterile, *Vicentini 2240* (MO); rio Içana, vila Jandú-Cachoeira, 1° 28' 36” N, 68° 43' 9” W, 158 m.a.s.l., 23 Jun 2004, Sterile, *Vicentini 2241* (MO); rio Içana, vila Jandú-Cachoeira, 1° 28' 36” N, 68° 43' 9” W, 158 m.a.s.l., 23 Jun 2004, FR, *Vicentini 2243* (MO); rio Içana. vila Baniwa de Juivitera, 1° 16' 50” N, 68° 32' 20” W, 131 m.a.s.l., 21 Jun 2004, FR, *Vicentini 2223* (INPA, MO); rio Içana. vila Baniwa de Juivitera, 1° 16' 59” N, 68° 32' 23” W, 121 m.a.s.l., 21 Jun 2004, FR, *Vicentini 2224* (MO); rio Içana. vila Baniwa de Juivitera, 1° 17' 7” N, 68° 32' 22” W, 148 m.a.s.l., 21 Jun 2004, FR, *Vicentini 2227* (INPA, MO); rio Içana, vila de Jauacanã, 0° 33' 47” N, 67° 24' 9” W, 73 m.a.s.l., 27 Jun 2004, FR, *Vicentini 2274* (INPA, MO); rio Içana, vila de Jauacanã, 0° 33' 39” N, 67° 24' 38” W, 69 m.a.s.l., 27 Jun 2004, FR, *Vicentini 2263* (INPA, MO); rio Içana, vila de Jauacanã, 0° 33' 47” N, 67° 24' 9” W, 73 m.a.s.l., 27 Jun 2004, Sterile, *Vicentini 2260* (MO); Serra Tunuhy, rio Issana, 1° 26' 19” N, 68° 9' 29” W, 551 m.a.s.l., 25 Jun 2004, Sterile, *Vicentini 2249* (MO); Serra Tunuhy, rio Issana, 1° 26' 22” N, 68° 9' 37” W, 452 m.a.s.l., 25 Jun 2004, FR, *Vicentini 2253* (INPA, MO); Jucaby, rio Negro, mouth rio Curicuriary, 0° 13' 0” S, 66° 47' 59” W, 68 m.a.s.l., 28 Nov 1929, FL, *Ducke 22956* (F); rio Tauari, lago Uirauaçu, 0° 20' 0” N, 67° 0' 0” W, 115 m.a.s.l., 13 Nov 1987, FL, *Kawasaki 133* (F, INPA, MO, NY); Ipanoré, rio Vaupés, between Ipanoré and confluence with rio Negro, 0° 15' 0” N, 68° 28' 0” W, 90 m.a.s.l., 15 Nov 1947, FR, *Schultes 9108* (NY, US); **COLOMBIA**. **Caquetá**. Araracuara: Pintadillo, 0° 30' 0” S, 72° 00' W, 105 m.a.s.l., 14 Apr 1986, FR, *Torres 3174* (COAH, COL, NY); Quebrada el Engaño, 2-5 km abajo desembocadura, 0° 47' 0” S, 71° 54' 0” W, 175 m.a.s.l., 20 Nov 1991, FL, *Restrepo 522* (COAH, HUA, NY); Quebrada El Sol, 160 km from city, 0° 56' 0” S, 71° 22' 0” W, 125 m.a.s.l., 10 Apr 1994, FR, *Cárdenas 4648* (COAH, MO); **Vaupés**. Sierra de Chiribiquete: Estación Puerto Abeja, 0° 3' N, 72° 26' W, 150 m.a.s.l., 16 Feb 1999, FR, *Arbelaez 1108* (COAH, COL, HUA, MO); Taraira: Lago Caparú, 0.494° N, 69° 40' 01” W, 150 m.a.s.l., 21 Nov 1994, FL, *Cárdenas 6195* (COAH, MO).

Specimens seen but not measured — **BRASIL**. **Acre**. Cruzeiro do Sul: 7° 38' 0” S, 72° 36' W, 80 m.a.s.l., , ?, *Cid 11673A* (INPA); 7° 38' 0” S, 72° 36' 0” W, 80 m.a.s.l., 10 Feb 1976, FL, *Marinho 448* (IBGE); 7° 38' 0” S, 72° 36' 0” W, 80 m.a.s.l., 10 Feb 1976, Sterile, *Marinho 87* (IBGE); 7° 25' 07” S, 72° 53' 40” W, 204 m.a.s.l., 10 Feb 1976, FR, *Rosa 435* (IBGE); 7° 38' 0” S, 72° 36' 0” W, 80 m.a.s.l., 5 Feb 1976, Sterile, *Rosa 644* (IBGE); rio Ipixuna, 7° 4' 0” S, 72° 51' 0” W, 80 m.a.s.l., 30 Sep 1987, FL, *Araújo 451* (IBGE); 7° 30' 0” S, 72° 50' 0” W, 80 m.a.s.l., , ?, *Rosa 706* (NY); Mâncio Lima: 7.54960° S, 72.98574° W, 190 m.a.s.l., , ?, *Cid 11760* (INPA); 7.3973° S, 72.766° W, 200 m.a.s.l., , ?, *Cid 11778* (INPA); 7° 23' 50.28” S, 72.766° W, 200 m.a.s.l., , ?, *Cid 11787* (INPA); **Amazonas**. São Gabriel da Cachoeira: Alto rio Negro, rio Tuari, afluente do rio Negro, Piraiauara, 1° 0' 30” N, 68° 1' W, 100 m.a.s.l., 13 Nov 1987, FL, *Lima 3175* (MO, NY); Alto rio Negro, rio Tuari, afluente do rio Negro, Piraiauara, 1° 0' 40” N, 68° 0' W, 101 m.a.s.l., 13 Nov 1987, FL, *Lima 3177* (MO, NY); **COLOMBIA**. La Pedrera: Resguardo Indígena Curare, 1° 17' S, 69° 44' W, 100 m.a.s.l., 23 Mar 2004, FR, *Cordero-P 511* (COL); **Caquetá**. Araracuara: 0° 37' S, 72° 24' W, 100 m.a.s.l., 9 Dec 1991, Sterile, *Duivenvoorden 2575* (COAH); río Caquetá, 0° 25' S, 72° 21' W, 103 m.a.s.l., , Sterile, *Bergeron 229142* (COAH); río Caquetá, 0° 25' S, 72° 22' W, 103 m.a.s.l., , ?, *Bergeron 765142* (COAH); **Guainia**. Maimachi: Serrania de Naquén, cerca La Planada, 2° 12' 0” N, 68° 12' 0” W, 320 m.a.s.l., 6 Aug 1992, Sterile, *Cortés 281* (MO); **Vaupés**. Sierra de Chiribiquete: Estación Puerto Abeja, 0° 4' 27” N, 72° 27' 05” W, 224 m.a.s.l., 3 Dec 1999, FL, *Eusse 836* (COAH); **PERU**. **Loreto**. Requena: rio Blanco, 5° 85' 76.83” S, 73° 76' 03.33” W, 140 m.a.s.l., 30 Oct 2004, Buds, *Dávila 1094* (AMAZ, F).

22. *Pagamea sessiliflora* Spruce ex Benth.

Specimens measured — **VENEZUELA**. **Amazonas**. Rio Negro: 4 km E from San Carlos de Rio Negro, 1° 56' 0” N, 67° 4' 0” W, 120 m.a.s.l., 10 Nov 1977, FL, *Liesner 3275* (MO, VEN); margen de los conucos, 1° 55' 0” N, 67° 4' 0” W, 100 m.a.s.l., 3 Jan 1942, FR, *Williams 14547* (F, US, VEN); San Carlos de Rio Negro, caminito al Caño Marimajari, 1° 55' 37” N, 67° 03' 37” W, 120 m.a.s.l., 26 Mar 2000, FR, *Berry 7280* (MO); rio Pasimoni, Yatua, Piedra Catipan, 1° 30' 0” N, 66° 25' 0” W, 120 m.a.s.l., 20 Nov 1953, FR, *Maguire 36478* (NY, VEN); rio Pasimoni, Yatua, Piedra Catipan, 1° 30' 0” N, 66° 25' 0” W, 120 m.a.s.l., 30 Nov 1953, FL, *Maguire 36479* (NY, USM, VEN); San Carlos de Rio Negro, 1° 55' 0” N, 67° 4' 0” W, 98 m.a.s.l., Mar 1853, FR, *Spruce 3045* (BM, F, K, NY); San Carlos de Rio Negro, 1° 55' 0” N, 67° 4' 0”

W, 100 m.a.s.l., 1942, FR, *Williams 14544* (F, NY); San Carlos de Rio Negro, 1° 55' 0” N, 67° 4' 0” W, 100 m.a.s.l., 1942, FR, *Williams 14649* (F, US, VEN).

Specimens seen but not measured — **VENEZUELA**. **Amazonas**. Rio Negro: 20 km de la confluencia del rio Negro y el Brazo Casiquiare, 1° 56' N, 67° 3' 0” W, 119 m.a.s.l., 30 Mar 1981, FR, *Delascio 9442* (VEN); 4 km E from San Carlos de Rio Negro, 1° 56' 0” N, 67° 3' 0” W, 120 m.a.s.l., 15 May 1979, FR, *Liesner 7431* (MO, VEN); carretera San Carlos de Rio Negro-Solano, 1° 56' 0” N, 67° 3' 30” W, 120 m.a.s.l., 10 Jul 1969, FR, *Bunting 4135* (VEN); río Yatua, Piedra Capitán, 1° 35' N, 66° 25' W, 130 m.a.s.l., 9 Apr 1970, FR, *Steyermark 102503A* (VEN); río Baría, 1° 5' 0” N, 66° 25' 0” W, 80 m.a.s.l., 29 Jun 1984, FR, *Davidse 26837* (F, MO, NY, PORT).

23. *Pagamea peruviana* Vicentini

Specimens measured — **PERU**. **Loreto**. Iquitos: Allpahuayo. Estacion Experimental del IIAP, 4° 11' 0” S, 73° 29' 0” W, 113 m.a.s.l., Dec 1990, FL, *Vasquez 15423* (MO, MOL); Carretera Iquitos-Nauta, km 22, 3° 54' 52” S, 73° 24' 15” W, 127 m.a.s.l., 5 Mar 2004, FR, *Vicentini 2193* (AMAZ, HUT, INPA, MO, USM); Carretera Iquitos-Nauta, km 31.5, 4° 00' 09” S, 73° 26' 02” W, 149 m.a.s.l., 29 Feb 2004, Sterile, *Vicentini 2181* (AMAZ, HUT, INPA, MO, USM); Carretera Iquitos-Nauta, km 31.5, 4° 00' 09” S, 73° 26' 02” W, 149 m.a.s.l., 29 Feb 2004, FR, *Vicentini 2182* (AMAZ, HUT, INPA, MO, USM); Carretera Iquitos-Nauta, km 31.5, 4° 00' 09” S, 73° 26' 02” W, 149 m.a.s.l., 29 Feb 2004, FR, *Vicentini 2183* (AMAZ, HUT, INPA, MO, USM); Iquitos-Nauta, 3° 54' 33” S, 73° 21' 49” W, 113 m.a.s.l., 18 Apr 1977, FR, *Rimachi 2949* (AMAZ, F, MO, US, USM); Iquitos-Nauta km 21, caserio Yarana, rio Nanay., 4° 21' 55” S, 73° 29' 0” W, 130 m.a.s.l., 3 Jul 1996, FR, *Rimachi 11731* (MO, NY, USM); Iquitos-Nauta km 3 de Quisto Cocha a Nauta, 3° 54' 33” S, 73° 22' 0” W, 150 m.a.s.l., 28 Jun 1984, FL, *Rimachi 7542* (US, USM); Tamshiyacu, Estación Biológica Quebrada Blanco, 4° 23' 0” S, 73° 17' 0” W, 108 m.a.s.l., 4 Jul 1985, FR, *Castro 24* (F, MO, NY); Requena: Carretera Genero Herrera a Colonia Angamos, km 4.5, 4° 54' 00” S, 73° 37' 48” W, 102 m.a.s.l., 4 Mar 2004, FR, *Vicentini 2186* (AMAZ, HUT, INPA, MO, USM); Carretera Genero Herrera a Colonia Angamos, km 4.5, 4° 54' 00” S, 73° 37' 48” W, 102 m.a.s.l., 4 Mar 2004, FR, *Vicentini 2189* (AMAZ, HUT, INPA, MO, USM); Carretera Genero Herrera a Colonia Angamos, km 4.5, 4° 54' 00” S, 73° 37' 48” W, 102 m.a.s.l., 4 Mar 2004, FR, *Vicentini 2190* (AMAZ, HUT, INPA, MO, USM); **San Martin**. Tarapoto: Carretera Tarapoto-Yurimaguas km 75, 6° 14' 04” S, 76° 16' 31” W, 188 m.a.s.l., 26 Feb 2004, Sterile, *Vicentini 2174* (AMAZ, HUT, INPA, MO, USM); Carretera Tarapoto-Yurimaguas km 75, 6° 14' 04” S, 76° 16' 31” W, 188 m.a.s.l., 26 Feb 2004, Sterile, *Vicentini 2175* (AMAZ, HUT, INPA, MO, USM); Carretera Tarapoto-Yurimaguas km 85, 6° 11' 05” S, 76° 15' 44” W, 180 m.a.s.l., 26 Feb 2004, FR, *Vicentini 2176* (AMAZ, HUT, INPA, MO, USM); Carretera Tarapoto-Yurimaguas km 85, 6° 11' 05” S, 76° 15' 44” W, 180 m.a.s.l., 26 Feb 2004, FL-old, *Vicentini 2177* (AMAZ, HUT, INPA, MO, USM).

Specimens seen but not measured — **COLOMBIA**. **Amazonas**. rio Caquetá, frente a la Isla de Mariname, 0.767° S, 72.083° W, 99 m.a.s.l., Jul 1989, Sterile, *Urrego 750* (COAH); rio Caquetá, frente a la Isla de Mariname, 0.767° S, 72.083° W, 99 m.a.s.l., Jul 1989, Sterile, *Urrego 807* (COAH); rio Caquetá, Quebrada Aguazul, 00° 34' 02” S, 72° 07' 59” W, 500 m.a.s.l., 18 Jun 1988, FR, *Sanchez 861* (COAH); rio Caquetá, 00° 50' S, 71° 50' W, 96 m.a.s.l., 5 Dec 1993, Sterile, *Duivenvoorden 2280* (COAH); La Chorrera: cerca de la pista aérea, 4° 35' 00.0” S, 74° 04' 00.0” W, 116 m.a.s.l., 10 Jun 2000, Sterile, *Velez 079* (COAH); **Caquetá**. Araracuara: rio Caquetá, en frente a la isla Sumaeta, 0° 39' S, 72° 08' W, 250 m.a.s.l., 26 Sep 1990, Sterile, *Alvarez 65* (JAUM); Villa Azul, resguardo indigena Muinane, 00° 32' S, 72° 6' W, 285 m.a.s.l., 6 Dec 1992, Sterile, *Duque 709* (COAH); Villazul, rio Caquetá, en frente a la isla Sumaeta, 0° 34' S, 72° 08' W, 250 m.a.s.l., 22 Apr 1989, Sterile, *Londoño 245* (COAH); Villazul, rio Caquetá, en frente a la isla Sumaeta, 0° 34' S, 72° 08' W, 250 m.a.s.l., 10 Sep 1989, Sterile, *Londoño 939* (COAH); **PERU**. **Loreto**. Iquitos: Allpahuayo. Estacion Experimental del IIAP, 3° 53' 0” S, 73° 30' 0” W, 115 m.a.s.l., , ?, *Fine J262* (INPA); Allpahuayo. Estacion Experimental del IIAP, 4° 12' 0” S, 73° 31' 0” W, 114 m.a.s.l., 29 May 1990, FR, *Vasquez 13766* (MO); Allpahuayo. Estacion Experimental del IIAP, 4° 10' 0” S, 73° 30' 0” W, 160 m.a.s.l., 27 May 1991, FR, *Vasquez 16602* (MO); Allpahuayo. Estacion Experimental del IIAP, 3° 57' 12” S, 73° 25' 17” W, 180 m.a.s.l., 10 Jul 1996, ?, *Vasquez 21366* (MO); Mishana, 3° 55' 0” S, 73° 35' 0” W, 130 m.a.s.l., 21 Jul 1984, FR, *Vasquez 5293* (MO, NY); Puerto Almendras, 3° 48' 0” S, 73° 25' 0” W, 112 m.a.s.l., 17 Jan 1993, Sterile, *Grández 5258* (MO); Puerto Almendras, rio Nanay, 3° 48' 0” S, 73° 21' 0” W, 122 m.a.s.l., 24 May 1990, FR, *Vasquez 13751* (MO); Quebrada de Shushuna. Carretera de Zungaro Cocha, 3° 49' 41” S, 73° 21' 28” W, 150 m.a.s.l., 15 Aug 1981, Sterile, *McDaniel 25299* (AMAZ, MO, NY); Mishana, rio Nanay, rd Iquitos to Santa Maria de Nanay, 3° 38' 22” S, 73° 13' 41” W, 140 m.a.s.l., 24 Mar 1979, FR, *Gentry 26191* (MO); Requena: Sapuena, Genaro Herrera, 4° 50' 30” S, 73° 45' 0” W, 170 m.a.s.l., 13 Nov 1987, Buds, *Vasquez 10018* (MO, USM); Sapuena, Genaro Herrera, 4° 55' 0” S, 73° 45' 0” W, 116 m.a.s.l., 21 Feb 1987, FR, *Gentry 56248* (AMAZ, MO, NY, USM).

24. *Pagamea dudleyi* Steyerm.

Specimens measured — **COLOMBIA**. **Valle del Cauca**. Buenaventura: Bajo Calima, 3° 55' 0” N, 77° 0' 0” W, 100 m.a.s.l., 21 Feb 1985, FR, *Monsalve 691* (COL, JAUM, MO); Quebrada de San Joaquím, 3° 50' 0” N, 77° 0' 0” W, 5 m.a.s.l., 20 Feb 1946, FL-old, *Cuatrecasas 19893* (F, VALLE); Bajo Calima, Juanchaco Palmeras, 3° 56' 0” N, 77° 8' 0” W, 50 m.a.s.l., 16 Apr 1987, Sterile, *Gentry 56961* (MO); **ECUADOR**. **Morona-Santiago**. Limon Indanza: Cordillera del Condor, 03° 09' 16” S, 78° 14' 50” W, 1020 m.a.s.l., 5 Oct 2002, FR, *Katan 10* (MO, QCNE); Cordillera del Condor, 03° 03' 40” S, 78° 14' 21” W, 1260 m.a.s.l., 16 Jun 2005, FR, *Morales 1263* (MO, QCNE); **Zamora-Chinchipe**. El Pangui: Cordillera del Condor, 03° 37' 48” S, 78° 26' 50” W, 1685 m.a.s.l., 9 Dec 2005, FL, *Neill 15086* (MO); Nagaritza: Cordillera del Condor, 04° 18' 23” S, 78° 41' 11” W, 1050 m.a.s.l., 25 Aug 2002, FR, *Quizhpe 207* (MO); Cordillera del Condor, 04° 12' S, 78° 40' W, 1200 m.a.s.l., 23 Feb 2003, FL, *Quizhpe 540* (MO, QCNE); **PERU**. **Amazonas**. Bagua: Imaza, Chiriaco, Cerro Tayu-Mujaji, 5° 15' 46” S, 78° 21' 52” W, 1031 m.a.s.l., 16 Feb 2004, Sterile, *Vicentini 2155* (HUT, INPA, MO, USM); Imaza, Chiriaco, Cerro Tayu-Mujaji, 5° 15' 46” S, 78° 21' 52” W, 1031 m.a.s.l., 16 Feb 2004, FR, *Vicentini 2156* (HUT, INPA, MO, USM); Imaza, Chiriaco, Cerro Tayu-Mujaji, 5° 15' 46” S, 78° 21' 52” W, 1031 m.a.s.l., 16 Feb 2004, Sterile, *Vicentini 2158* (HUT, INPA, MO, USM); Imaza, Chiriaco, Cerro Tayu-Mujaji, 5° 15' 56” S, 78° 22' 7” W, 1200 m.a.s.l., 21 Oct 1997, FL, *Rojas 362* (HUT, MO, USM); **Huánuco**. Pucallpa: SW slope of rio Llulla Pichas watershed, Cerros del Sira, 9° 26' 0” S, 74° 45' 0” W, 1000 m.a.s.l., 23 Jul 1969, FL, *Dudley 13148* (NA); SW slope of rio Llulla Pichas watershed, Cerros del Sira, 9° 27' 0” S, 74° 46' 0” W, 1000 m.a.s.l., 23 Jul 1969, FL, *Dudley 13162* (NA); SW slope of rio Llulla Pichas watershed, Cerros del Sira, 9° 25' 0” S, 74° 43' 0” W, 1950 m.a.s.l., 30 Jul 1969, FL, *Dudley 13438* (NA); SW slope of rio Llulla Pichas watershed, Cerros del Sira, 9° 25' 0” S, 74° 42' 0” W, 1850 m.a.s.l., 31 Jul 1969, FL, *Dudley 13543* (NA); **Junin**. La Merced: Hacienda Schunke, 11° 3' 0” S, 75° 19' 0” W, 1200 m.a.s.l., 1 Sep 1923, FL, *Macbride 5785* (BM, F); **Pasco**. Oxapampa: 10° 45' S, 74° 55' W, 1400 m.a.s.l., 30 Jun 2003, FL, *Monteagudo 5578* (MO); Palcazu: Palcazu, Parque Nacional Yanachaga-chemillen, El Paujil, 10° 43' S, 74° 54' W, 800 m.a.s.l., 12 May 2003, FR, *Monteagudo 5193* (MO); **Puno**. Carabaya: Cabeceras del rio Candamo, 13° 25' 0” S, 69° 55' 0” W, 400 m.a.s.l., 6 Mar 1997, FR, *Cornejo 2902* (MO); **San Martin**. Tarapoto: Carretera Tarapoto-Yurimaguas km 13, 6° 27' 49” S, 76° 18' 26” W, 884 m.a.s.l., 25 Feb 2004, Sterile, *Vicentini 2166* (HUT, INPA, MO, USM); Carretera Tarapoto-Yurimaguas km 13, 6° 27' 41” S, 76° 18' 35” W, 911 m.a.s.l., 25 Feb 2004, Sterile, *Vicentini 2170* (HUT, INPA, MO, USM); Carretera Tarapoto-Yurimaguas km 13, 6° 27' 44” S, 76° 18' 31” W, 912 m.a.s.l., 25 Feb 2004, FR, *Vicentini 2173* (HUT, INPA, MO, USM).

Specimens seen but not measured — **ECUADOR**. **Morona-Santiago**. Limon Indanza: Cordillera del Condor, 03° 03' 31” S, 78° 14' 48” W, 20 Dec 2005, FL, *Kajekai 284* (HUT, LOJA, MO, QCNE); Cordillera del Condor, 03° 06' 02” S, 78° 15' 48” W, 18 Jun 2006, FR, *Kajekai 336* (HUT, LOJA, MO, QCNE); Cordillera del Condor, 03° 03' 40” S, 78° 14' 21” W, 1250 m.a.s.l., 19 Jun 2005, FR, *Katan 314* (MO, QCNE); **Zamora-Chinchipe**. El Panqui: Cordillera del Condor, 03° 34' 44” S, 78° 26' 07” W, 5 Dec

2005, FL, *Neill 14964* (MO, QCNE); Cordillera del Condor, 03° 34' 44” S, 78° 26' 07” W, 4 Apr 2006, FR, *Neill 15124* (MO, QCNE); Miazi: Ridge top, above military base on rio Nangaritza, 04° 18' S, 78° 40' W, 1090 m.a.s.l., 30 Jul 1993, Sterile, *Gentry 80791* (QCNE); **PERU**. **Pasco**. Palcazu: Palcazu, El Paujil, 10° 20' 12” S, 75° 15' 39” W, 12 May 2005, FR, *vanderWerff 20034* (MO); **San Martin**. Tarapoto: Carretera Tarapoto-Yurimaguas km 13, 6° 27' 48” S, 76° 18' 27” W, 902 m.a.s.l., 25 Feb 2004, Sterile, *Vicentini 2167* (HUT, INPA, MO, USM).

25. *Pagamea macrocarpa* (Steyerm.) Vicentini

Specimens measured — **COLOMBIA**. **Caquetá**. Araracuara: 8 km SE of Tres Esquinas, río Caquetá below río Orteguaza, 0° 43' 0” N, 75° 16' 0” W, 200 m.a.s.l., 4 Mar 1945, FR, *Little 9533* (COL, K, NY, P, US); **PERU**. **Amazonas**. Bagua: Carretera Ceasme a Santa Maria de Nieva, 4° 38' 13” S, 77° 50' 20” W, 224 m.a.s.l., 18 Feb 2004, Sterile, *Vicentini 2164* (HUT, INPA, MO, USM); Imaza, Carretera Puente Nieva a Sarameriza, 5 km del cruce Ceasme, 4° 40' 31” S, 77° 47' 12” W, 365 m.a.s.l., 18 Feb 2004, Sterile, *Vicentini 2163* (HUT, INPA, MO, USM); Imaza, Carretera Puente Nieva a Sarameriza, 5 km del cruce Ceasme, 4° 40' 06” S, 77° 46' 50” W, 335 m.a.s.l., 18 Feb 2004, Sterile, *Vicentini 2160* (HUT, INPA, MO, USM); Imaza, Carretera Puente Nieva a Sarameriza, 5 km del cruce Ceasme, 4° 40' 06” S, 77° 46' 50” W, 335 m.a.s.l., 18 Feb 2004, Sterile, *Vicentini 2161* (HUT, INPA, MO, USM); Imaza, Carretera Puente Nieva a Sarameriza, 5 km del cruce Ceasme, 4° 40' 06” S, 77° 46' 50” W, 335 m.a.s.l., 18 Feb 2004, Sterile, *Vicentini 2162* (HUT, INPA, MO, USM); Imaza, Chiriaco, Cerro Tayu-Mujaji, 5° 15' 18” S, 78° 21' 34” W, 600 m.a.s.l., 16 Feb 2004, Sterile, *Vicentini 2151* (HUT, INPA, MO, USM); Imaza, Chiriaco, Cerro Tayu-Mujaji, 5° 15' 18” S, 78° 21' 34” W, 650 m.a.s.l., 16 Feb 2004, Sterile, *Vicentini 2152* (HUT, INPA, MO, USM); Imaza, Chiriaco, Cerro Tayu-Mujaji, 5° 15' 18” S, 78° 21' 34” W, 750 m.a.s.l., 16 Feb 2004, Sterile, *Vicentini 2153* (HUT, INPA, MO, USM); Imaza, Chiriaco, km 92 Carretera Bagua-Imacita, Cerro Chinim, 5° 0' 0” S, 78° 17' 27” W, 750 m.a.s.l., 29 Aug 1996, FR, *Diaz 8071* (HUT, MO); Zonas altas de Putuim, 5° 37' 5” S, 78° 24' 0” W, 715 m.a.s.l., 19 Jan 1996, FR, *Diaz 7695A* (MO).

26. *Pagamea resinosa* Vicentini

Specimens measured — **PERU**. **Loreto**. Iquitos: Carretera Iquitos-Nauta, km 13, 3° 52' 27” S, 73° 20' 47” W, 140 m.a.s.l., 2 Mar 2004, FR, *Vicentini 2184* (AMAZ, HUT, INPA, MO, USM); Carretera Iquitos-Nauta, km 13, 3° 52' 20” S, 73° 20' 46” W, 140 m.a.s.l., 2 Mar 2004, FR, *Vicentini 2185* (AMAZ, HUT, INPA, MO, USM); Carretera Iquitos-Nauta, km 22, 3° 54' 52” S, 73° 24' 15” W, 127 m.a.s.l., 5 Mar 2004, FR, *Vicentini 2192* (AMAZ, HUT, INPA, MO, USM); Carretera Iquitos-Nauta, km 22, 3° 54' 52” S, 73° 24' 15” W, 127 m.a.s.l., 5 Mar 2004, FR, *Vicentini 2195* (AMAZ, HUT, INPA, MO, USM); Iquitos-Nauta km 10, 4° 21' 49” S, 73° 28' 21” W, 150 m.a.s.l., 9 Sep 1987, FR, *Rimachi 8254* (F, MO, NY, USM); Iquitos-Nauta km 7 de Quisto Cocha, 4° 0' 0” S, 73° 13' 5” W, 140 m.a.s.l., 12 May 1993, FR, *Rimachi 10573* (MO, NY, USM).

27. *Pagamea spruceana* Vicentini

Specimens measured — **BRASIL**. **Amazonas**. São Gabriel da Cachoeira: Igarapé Jurupary, rio Uaupés infer, 1° 37' 0” N, 68° 53' 0” W, 94 m.a.s.l., 2 Nov 1932, FL, *Ducke 24417* (F); Igarapé Tibuiari, afluente do rio Uaupés, Monte Cristo, 0° 5' 0” N, 67° 20' 0” W, 74 m.a.s.l., 22 Nov 1987, FR, *Kawasaki 242* (NY); rio Içana, acima de Peraiauara, 1° 0' 0” N, 68° 0' 10” W, 99 m.a.s.l., 14 May 1973, FR, *Silva*

1530 (INPA, US); rio Içana, vila de Jauacanã, 0° 33' 47” N, 67° 24' 9” W, 73 m.a.s.l., 27 Jun 2004, Sterile, *Vicentini 2266* (MO); rio Içana, vila de Jauacanã, 0° 33' 47” N, 67° 24' 9” W, 73 m.a.s.l., 27 Jun 2004, Sterile, *Vicentini 2276* (MO); rio Içana, Jauacanã, 0° 23' 0” N, 67° 33' 0” W, 71 m.a.s.l., 2 Nov 1987, FL, *Farney 1859* (INPA, MO).

28. *Pagamea occulta* Vicentini

Specimens measured — **BOLIVIA**. **La Paz**. Iturralde: Siete Cielos, rio Manupar, 12° 27' 0” S, 67° 37' 0” W, 180 m.a.s.l., 6 Jun 1987, FR, *Solomon 16933* (MO, P); **Santa Cruz**. Velasco: 150 km de Florida a Bella Vista, 13° 42' 9” S, 61° 31' 59” W, 210 m.a.s.l., 4 Nov 1994, Buds, *Guillen 2537* (F, MO, NY); Laguna Guarasug'we, 13° 37' 27” S, 61° 30' 21” W, 210 m.a.s.l., 13 Aug 1995, FR, *Halloy 4412* (NY); Parque Nacional Noel Kempff M., 13° 33' 0” S, 61° 0' 0” W, 200 m.a.s.l., 23 May 1991, FL-FR, *Pena 173* (MO, NY); Parque Nacional Noel Kempff M., 13° 39' 0” S, 60° 49' 0” W, 200 m.a.s.l., 18 May 1994, FR, *Quevedo 2597* (MO, NY); Parque Nacional Noel Kempff M., 13° 39' 20” S, 60° 49' 8” W, 200 m.a.s.l., 27 Nov 1993, FL, *Arroyo 604* (NY); Parque Nacional Noel Kempff M., 13° 36' 0” S, 60° 54' 0” W, 530 m.a.s.l., 12 Aug 1992, FR, *Toledo 44* (F, MO, UZQ); **BRASIL**. **Amazonas**. Barcelos: 0° 21' 54” N, 63° 14' W, 74 m.a.s.l., , ?, *Carneiro 24* (INPA, MO); Serra do Aracá, surrounding lowlands, 0° 12' 15” S, 63° 9' 23” W, 66 m.a.s.l., 23 Aug 2001, Sterile, *Vicentini 1790* (INPA, MO); rio Uniusi [Unini], afluente do rio Negro, 1° 41' 0” S, 61° 31' 0” W, 35 m.a.s.l., 23 Jun 1976, FL-old, *Coelho 512* (INPA); Humaitá: Plateau between rio Livramento and rio Ipixuna, 7° 32' 44” S, 63° 0' 0” W, 62 m.a.s.l., 8 Nov 1934, Buds, *Krukoff 7083* (BM, F, MO, NY, US); Manaus: rio Cuieiras, 2° 39' 16” S, 60° 21' 20” W, 57 m.a.s.l., 5 Apr 1974, FR, *Campbell 21854P* (INPA, MO, NY, US); rio Cuieras, Igarapé da Cachoeira, 2° 49' 39” S, 60° 30' 33” W, 37 m.a.s.l., 25 Jun 1962, FL, *Rodrigues 4877* (INPA, US); rio Cuieras just below mouth of rio Branquinho, 2° 29' 1” S, 60° 20' 38” W, 71 m.a.s.l., 26 Sep 1971, FL, *Prance 14895* (INPA); Nova Japurá: Vila Bittencourt, rio Apapóris, igarapé Preguiça, 1° 14' 0” S, 69° 25' 0” W, 80 m.a.s.l., 21 Nov 1982, FL, *Cid 3763* (INPA, NY); Santa Isabel do Rio Negro: rio Ayuana, margem direita do rio Negro, 0° 34' 41” S, 64° 55' 36” W, 41 m.a.s.l., 3 Dec 2003, FL-old, *Vicentini 2131* (INPA); rio Ayuana, margem direita do rio Negro, 0° 34' 42” S, 64° 55' 33” W, 29 m.a.s.l., 3 Dec 2003, FL-old, *Vicentini 2133* (INPA); Campina do Dodono, rio Uneiuxi, 35 km above mouth, 0° 39' 16” S, 65° 26' 11” W, 49 m.a.s.l., 20 Oct 1971, FL, *Prance 15443* (F, INPA, MO, NY, US); São Gabriel da Cachoeira: rio Negro, Macubeta on rio Marié, 0° 27' 0” S, 66° 25' 0” W, 65 m.a.s.l., 31 Jan 1942, FR, *Froes 12440/184* (F, NY); rio Curicuriari, 2-10 km above the mouth, 0° 13' 0” S, 67° 0' 0” W, 70 m.a.s.l., 25 Oct 1978, FL, *Madison 6627* (F, K, US); rio Içana, próximo à Serra do Grilo, 0° 30' 0” N, 67° 22' 0” W, 88 m.a.s.l., 5 Nov 1987, FL, *Farney 1901* (INPA); rio Negro, upstream from mouth of rio Xié, 0° 57' 0” N, 67° 11' 0” W, 83 m.a.s.l., 25 Oct 1987, FL, *Maas 6861* (INPA, MO); rio Negro, near mouth of rio Marié, 0° 27' 0” S, 66° 25' 0” W, 65 m.a.s.l., 12 Oct 1987, FL, *Maas 6730* (INPA, MO); São Paulo de Olivença: 3° 27' 0” S, 68° 48' 0” W, 72 m.a.s.l., Apr 1945, FR, *Froes 20722* (NY); Estrada Bomfim, trail beyond rd, 6 km S of town center, 3° 30' 0” S, 68° 57' 0” W, 60 m.a.s.l., 26 Nov 1986, FL, *Daly 4446* (NY); Tonantins: Vila Velha, rio Tonantins, 2° 53' 0” S, 67° 50' 0” W, 65 m.a.s.l., 18 Nov 1986, FL, *Daly 4362* (MO, NY); **Rondônia**. Km 216-219 Madeira-Mamoré railroad near Abunã, 9° 42' 0” S, 65° 23' 0” W, 112 m.a.s.l., 10 Jul 1968, FR, *Prance 5831* (COL, F, INPA, NY, P); Costa Marques: BR-429; 123 km de Costa Marques, 12° 5' 0” S, 63° 35' 0” W, 206 m.a.s.l., 24 Mar 1987, FR, *Cid 8667* (INPA, MO); **COLOMBIA**. **Amazonas**. Leticia: Quebrada El Sol, 160 km from city, 0° 56' 0” S, 71° 22' 0” W, 125 m.a.s.l., 10 Apr 1994, FR, *Cárdenas 4644* (COAH, MO); **Caquetá**. Araracuara: rio Yavillaré, 5 km arriba de la desembocadura al Yavilla, 0° 17' 20” S, 72° 24' 0” W, 250 m.a.s.l., 20 Nov 1995, FL, *Cárdenas 6814* (COAH, MO); **Vaupés**. Sierra de Chiribiquete: río Cuñare, raudal del tubo, 0° 30' 0” N, 72° 30' 0” W, 290 m.a.s.l., 4 Feb 1992, FR, *Fund CHI87* (NY); **PERU**. **Loreto**. Requena: Carretera Genero Herrera a Colonia Angamos, km 4.5, 4° 54' 00” S, 73° 37' 48” W, 102 m.a.s.l., 4 Mar 2004, FR, *Vicentini 2187* (AMAZ, HUT, INPA, MO, USM); Carretera Genero Herrera a Colonia Angamos, km 4.5, 4° 54' 00” S, 73° 37' 48” W, 102 m.a.s.l., 4 Mar 2004, FR, *Vicentini 2188* (AMAZ, HUT, INPA, MO, USM); Carretera Genero Herrera a Colonia Angamos, km 4.5, 4° 54' 00” S, 73° 37' 48” W, 102 m.a.s.l., 4 Mar 2004, FR, *Vicentini 2191* (AMAZ, HUT, INPA, MO, USM); Reserva Nacional Pacaya Samiria, río Yanacacu, El Cocal, 4° 51' 48” S, 74° 1' 0” W, 90 m.a.s.l., 21 Nov 1992, FL, *Del 1808* (MO, USM); Reserva Nacional Pacaya Samiria, río Yanacacu, El Cocal, 4° 51' 48” S, 74° 1' 0” W, 93 m.a.s.l., 21 Nov 1992, FL, *Del 1798* (MO, USM); Sapuena, Genaro Herrera, 4° 50' 0” S, 73° 45' 30” W, 170 m.a.s.l., 13 Nov 1987, FR, *Vasquez 10019* (F, MO, NY, USM); Sapuena, Genaro Herrera, 4° 50' 0” S, 73° 45' 0” W, 170 m.a.s.l., 15 Sep 1987, FL, *Vasquez 9604* (MO, USM); Carretera Genero Herrera a Colonia Angamos, km 4.5, 4° 51' 0” S, 73° 46' 0” W, 200 m.a.s.l., 17 Apr 1987, FR, *Acevedo-Rdgz 1594* (F, MO, NY); Sapuena, Genaro Herrera, 4° 55' 0” S, 73° 45' 0” W, 116 m.a.s.l., 21 Feb 1987, FR, *Gentry 56236* (AMAZ, F, MO, NY, USM); **Madre de Dios**. Tambopata: Parque Nacional Bahuaja-Sonone, 12° 57' 11” S, 68° 54' 48” W, 210 m.a.s.l., 11 Oct 1997, Buds, *Diaz 9458* (MO); Santuario Nacional Pampas del Heath, quebrada Patuyacu, 12° 57' 11” S, 68° 54' 48” W, 210 m.a.s.l., 5 Apr 1996, FR, *Aguilar 522* (MO, USM); **Puno**. Carabaya: Cabeceras del rio Candamo, 13° 18' 0” S, 70° 7' 0” W, 825 m.a.s.l., 15 Nov 1996, Sterile, *Cornejo 2723* (MO); **VENEZUELA**. **Amazonas**. Atabapo: Caño Perro de Agua, 30 km SE mouth of Ventuari river, 3° 34' 17” N, 66° 42' 51” W, 100 m.a.s.l., 30 Nov 1978, FR, *Huber 2750* (COL, NY, VEN); Yapacana tepui, 3° 40' 0” N, 66° 52' 0” W, 180 m.a.s.l., Nov 1989, FL, *Marin 644* (MO, PORT); alto rio Atacaví, 3° 15' 10” N, 67° 20' 15” W, 115 m.a.s.l., 7 Sep 1960, Buds, *Foldats 3763* (VEN); bajo río Ventuari, 10 km NE boca Caño Marueta, 4° 18' 0” N, 66° 16' 0” W, 110 m.a.s.l., 18 Feb 1981, FL, *Huber 6120* (NY, VEN); río Caname, 1 km confl. rio Atabapo., 3° 41' 0” N, 66° 27' 0” W, 95 m.a.s.l., Nov 1989, FL, *Yanez 103* (MO, NY, PORT); rio Ventuari, ca. 5 km por sendero en frente a la Isla Caymán, 4° 4' 46” N, 66° 38' 34” W, 120 m.a.s.l., 16 Mar 2002, FR, *Aymard 12235* (MO, PORT); Caño Yagua al N del Cerro Cucurito, 3° 37' 0” N, 66° 34' 0” W, 120 m.a.s.l., 18 Jan 1979, FR, *Huber 3127* (K, NY, VEN); San Antonio de Orinoco, 3° 36' 0” N, 66° 34' 0” W, 120 m.a.s.l., 8 May 1979, FR, *Davidse 17390* (MO, US, VEN); Autana: San Pedro, rio Autana, 4° 44' 77” N, 67° 41' 57” W, 370 m.a.s.l., Nov 1948, FL, *Delgado 73* (VEN); San Pedro, rio Autana, 4° 44' 78” N, 67° 41' 59” W, 260 m.a.s.l., 16 Oct 1999, FL, *Castillo 6852* (MO); San Pedro, rio Autana, 4° 44' 77” N, 67° 41' 57” W, 262 m.a.s.l., 16 Feb 2001, Buds, *Castillo 7321* (MO); San Pedro, rio Autana, 4° 44' 77” N, 67° 41' 57” W, 262 m.a.s.l., 16 Feb 2001, Buds, *Castillo 7380* (VEN); Maroa: Yavita, río Temi, 2° 52' 36” N, 67° 19' 5” W, 115 m.a.s.l., 17 Nov 1996, FL, *Berry 6360* (MO, TFVA, VEN); Yavita, río Temi, 2° 55' 0” N, 67° 25' 0” W, 125 m.a.s.l., 22 Apr 1970, FL, *Steyermark 102959* (NY, VEN); Yavita, río Temi, 2° 52' 15” N, 67° 18' 30” W, 110 m.a.s.l., 25 Nov 1995, FR, *Berry 5657* (MO, TFVA, VEN); Yavita, río Temi, above Budare, 2° 53' 53” N, 67° 17' 19” W, 110 m.a.s.l., 24 Nov 1995, FR, *Berry 5617* (MO, PORT, VEN); Yavita, río Temi, below Sejal, 3° 2' 56” N, 67° 25' 59” W, 110 m.a.s.l., 19 Nov 1996, FR, *Berry 6417* (MO, TFVA); Yavita,, 2° 55' 19” N, 67° 26' 7” W, 128 m.a.s.l., 30 Jan 1942, FL-old, *Williams 14079* (F, US, VEN); Yavita, caño Colorado, 2° 55' 19” N, 67° 26' 7” W, 128 m.a.s.l., 28 Jan 1942, FR, *Williams 14042* (F, VEN); Yavita, río Temi, 2° 56' 44” N, 67° 21' 49” W, 128 m.a.s.l., 28 Jan 1942, FR, *Williams 14031* (F, MO, NY, US, VEN); rio Guainía, 2° 44' 11” N, 67° 33' 45” W, 127 m.a.s.l., 11 Feb 1942, FR, *Williams 14293* (F, US, VEN); Rio Negro: rio Pasimoni, Mamurividi, 1° 32' 0” N, 66° 32' 0” W, 125 m.a.s.l., 3 Apr 1984, FR, *Liesner 17172* (F, MO, NY, TFVA, VEN); rio Pasimoni, Piedra de Arapacoa, 1° 31' 30” N, 66° 30' 0” W, 73 m.a.s.l., 24 Jul 1982, FR, *Stergios 4102* (MO, PORT, TFVA, VEN); Río Baría, entre la boca de la Laguna Yuruvi y la Laguna-laja Bajáiö, 1° 28' 56” N, 66° 31' 56” W, 62 m.a.s.l., 7 Nov 1994, FL, *Stergios 16302* (MO, NY, US); río Baría, 1° 25' 0” N, 66° 24' 0” W, 90 m.a.s.l., May 1991, FL, *Velazco 1885* (MO, PORT); rio Pasimoni, 1° 36' 0” N, 66° 30' 0” W, 64 m.a.s.l., 3 Feb 1992, FR, *Stergios 15535* (MO, NY, PORT, US, VEN); **Apure**. Puerto Carreño: 6° 44' 0” N, 67° 20' 0” W, 85 m.a.s.l., 28 Feb 1978, FR, *Davidse 14686* (MO, NY, VEN); 6° 42' 0” N, 67° 48' 0” W, 70 m.a.s.l., 2 Mar 1979, FR, *Davidse 15965A* (MO, NY, VEN); 6° 39' 0” N, 67° 16' 0” W, 60 m.a.s.l., 18 Jan 1989, FR, *Gómez 338* (MO); banks of río Meta, 6° 19' 0” N, 67° 50' 0” W, 60 m.a.s.l., 11 Feb 1978, FR, *Davidse 13846* (MO, NY, VEN); Caño El Caballlo, 6° 19' 0” N, 68° 19' 0” W, 75 m.a.s.l., 27 Feb 1979, FR, *Davidse 15843* (MO, VEN); Laguna la Guacharaca, 6° 42' 0” N, 67° 27' 0” W, 70 m.a.s.l., 24 Feb 1979, FR, *Davidse 15663* (MO, NY, VEN); PN Santos Luzardo, río Capanaparo-Cinaruco, 6° 42' 0” N, 67° 27' 30” W, 40 m.a.s.l., 31 Mar 1989, FL-FR, *Thirza 4411* (MO, VEN); banks of río Capanaparo, 6° 58' 0” N, 67° 49' 0” W, 55 m.a.s.l., 10 May 1977, FR, *Davidse 12991* (MO, VEN); bank of río Juriepe, 6° 2' 0” N, 68° 23' 0” W, 70 m.a.s.l., 27 Feb 1979, FR, *Davidse 15781* (MO, VEN); río Capanaparo, caño La Macariella, 7° 00' 00” N, 68° 00' 00” W, 53 m.a.s.l., 17 Jan 1982, FR, *Rodrigues 1447* (VEN).

Specimens seen but not measured — BOLIVIA. **Santa Cruz**. Velasco: Parque Nacional Noel Kempff M., 13° 33' 6” S, 61° 0' 29” W, 210 m.a.s.l., 6 Jun 1994, ?, *Quevedo 2683* (MO); Parque Nacional Noel Kempff M., 13° 39' 20” S, 60° 49' 8” W, 200 m.a.s.l., 27 Nov 1993, FR, *Arroyo 604A* (F, MO, NY);

Parque Nacional Noel Kempff M., 13° 38' 22” S, 60° 53' 44” W, 500 m.a.s.l., 15 Jan 1997, ?, *Fuentes 1665* (MO); Serrania de Huanchaca, 14° 22' S, 60° 57' W, 245 m.a.s.l., 10 Nov 91, Buds, *Foster 13889* (F, MO, USZ); **BRASIL**. **Amazonas**. Barcelos: Serra do Aracá, surrounding lowlands, 00° 18' 16” N, 63° 01' 35” W, 75 m.a.s.l., , ?, *Cid P1R10* (INPA); Serra do Aracá, surrounding lowlands, 00° 18' 18” N, 63° 01' 38” W, 69 m.a.s.l., , ?, *Cid P22* (INPA); Manaus: rio Cuieras, 2° 45' 48” S, 60° 26' 40” W, 13 m.a.s.l., 2001, Sterile, *Oliveira 3719* (INPA); Santa Isabel do Rio Negro: 0° 21' 59” S, 64° 59' 48” W, 60 m.a.s.l., , ?, *Amaral 01* (INPA); rio Ayuana, margem direita do rio Negro, 0° 34' 42” S, 64° 55' 33” W, 29 m.a.s.l., 3 Dec 2003, FR, *Vicentini 2132* (INPA); **Mato Grosso**. Agrochapada Paramatinga: Córrego Santiago, 13.45° S, 54.28° W, 400 m.a.s.l., 28 Oct 1990, Buds, *Macedo 2979* (INPA); Cataqui-iamain: Entre Cataqui-iamain e o 1o. de Terr. M. Grosso., 11° 16' 41” S, 63° 15' 18.04” W, 227 m.a.s.l., Jan 1919, FL, *Kuhlmann 2361* (SP); **Rondônia**. Furnas P-13, , ?, *Cohn-Haft 04* (MO); Furnas P-13, 9° 35' 08.15” S, 64° 59' 54.74” W, 98 m.a.s.l., , ?, *Cohn-Haft 05* (MO); Porto Velho: 8° 46' 0” S, 63° 54' 0” W, 75 m.a.s.l., 19 Sep 1975, Buds, *Mota 185* (INPA); **COLOMBIA**. **Amazonas**. rio caquetá, 1.2 km abajo de la boca del Quebradón del Metá, 0° 55' 54” S, 71° 36' 01” W, 94 m.a.s.l., 28 Oct 1997, Sterile, *Sanchez 6902* (COAH); rio Caquetá, 2.5 km abajo boca quebrada El Engaño, 0.783° S, 71.9° W, 94 m.a.s.l., 13 May 1988, Sterile, *Sanchez 392* (COAH); río Igará-Paraná, 2° 08' 39.44” S, 71° 47' 12” W, 98 m.a.s.l., 13 Mar 1974, FR, *Midrobo 6950* (COL); La Pedrera: río Puré en límite con Brasil, 02° 05' 00” S, 69° 37' 23” W, 200 m.a.s.l., 24 Jul 1997, Sterile, *Cárdenas 8110* (COAH); Miraña: 10.8 km de la boca del rio Cahuinarí, 1° 21' 10” S, 70° 44' W, 85 m.a.s.l., 31 Jan 1988, FL, *Duivenvoorden 66* (COAH); 10.8 km de la boca del rio Cahuinarí, 1° 21' S, 70° 44' W, 88 m.a.s.l., 31 Jan 1988, FR, *Sanchez 38* (COAH); rio Cahuinari, 1° 21' 05” S, 70° 45' W, 88 m.a.s.l., 12 Sep 1988, Sterile, *Sanchez 1158* (COAH); **Caquetá**. 0° 04' 16” N, 72° 26' 48” W, 150 m.a.s.l., 3 Mar 1993, FR, *Hernández CHI216* (COAH); Araracuara: Puerto Santander, sitio Ciudad Perdida, 0° 50' 0” S, 72° 20' 0” W, 250 m.a.s.l., Feb 1997, FR, *Arbelaez 766* (COAH, MO); 0° 25' S, 72° 23' W, 103 m.a.s.l., , Sterile, *Bergeron 526662* (COAH); rio Caqueta, Caño Paujil, 10 km NO de Araracuara, 0° 46' 30” S, 72° 22' 30” W, 175 m.a.s.l., 28 Oct 1992, FL-old, *Arbelaez 293* (COAH, COL, HUA); rio Quinché, upstream of Saladode Quinche, 00° 55' 00” S, 72° 00' W, 180 m.a.s.l., 12 1990, FL-old, *Wijninga 678* (COAH); **Guainia**. Maimachi: Serrania de Naquén, 2° 6' 0” N, 68° 10' 0” W, 100 m.a.s.l., 1 Apr 1993, Sterile, *Madriñan 814* (COL, MO); Nabuquén: 2° 47' 24” N, 68° 45' 49” W, 24 m.a.s.l., 4 Mar 1995, FR, *Córdoba 864* (COAH, COL, MO); **Vaupés**. Sierra de Chiribiquete: Estación Puerto Abeja, 0° 3' 57.1” N, 72° 27' 37.9” W, 320 m.a.s.l., 30 Oct 2000, FR, *Dávila 102* (COAH, UDBC); río Cuñaré, 20 min de la boca del río Amu, 0° 13' 39.4” N, 72° 26' 38.2” W, 350 m.a.s.l., 15 Feb 2001, ?, *Mendoza 10211* (FMB); río Cuñaré, 20 min de la boca del río Amu, 0° 13' 34” N, 72° 25' 22.7” W, 350 m.a.s.l., 15 Feb 2001, ?, *Mendoza 10287* (FMB); río Cuñaré, 20 min de la boca del río Amu, 0° 13' 3.4” N, 72° 25' 22.7” W, 350 m.a.s.l., 15 Feb 2001, ?, *Mendoza 12354* (FMB); río Cuñaré, 20 min de la boca del río Amu, 0° 13' 39.4” N, 72° 26' 38.2” W, 350 m.a.s.l., 15 Feb 2001, ?, *Mendoza 13045* (FMB); cuenca alta del río mesay, 0° 16' 13” N, 72° 55' 22” W, 350 m.a.s.l., 20 Jan 2000, ?, *Mendoza 8017* (FMB); cuenca alta del río mesay, 0° 14' 24” N, 72° 56' 2” W, 350 m.a.s.l., 20 Jan 2000, ?, *Mendoza 8117* (FMB); cuenca alta del río mesay, 0° 14' 54” N, 72° 56' 5” W, 350 m.a.s.l., 20 Jan 2000, ?, *Mendoza 8179* (FMB); cuenca media del río Cuñare, 0° 31' 44.7” N, 72° 37' 50.3” W, 350 m.a.s.l., 15 Nov 2000, ?, *Mendoza 9909* (FMB); **Vichada**. Maipures: PNN El Tuparro, río Tomo, 24 km de la confluencia con el río Orinoco, 5° 18' 27” N, 67° 57' 0” W, 200 m.a.s.l., 1 Feb 2004, ?, *Mendoza 15692* (FMB); **PERU**. **Madre de Dios**. Tambopata: Santuario Nacional de las Pampas del Heath, 12° 57' 0” S, 68° 53' 0” W, 200 m.a.s.l., 17 Jun 1992, FL, *Castillo 7050* (USM); Santuario Nacional Pampas del Heath, refugio Juliaca, 12° 57' S, 68° 53' W, 200 m.a.s.l., 23 Jun 1996, FR, *Beltrán 2403* (UMS); Santuario Nacional Pampas del Heath, quebrada Patuyacu, 12° 57' 11” S, 68° 54' 48” W, 210 m.a.s.l., 5 Apr 1996, Sterile, *Aguilar 515* (MO, USM); **VENEZUELA**. **Amazonas**. Alto Orinoco: río Chicaramoni, 3° 6' 0” N, 66° 23' 0” W, 192 m.a.s.l., 15 Jan 1989, FR, *Stergios 13273* (NY, PORT); Atabapo: Yapacana tepui, 3° 41' 27” N, 66° 51' 16” W, 150 m.a.s.l., 31 Dec 1950, FR, *Maguire 30508* (COL, MO, NY, VEN); Yapacana tepui, 3° 41' 27” N, 66° 51' 16” W, 130 m.a.s.l., 1 Jan 1951, FL-old, *Maguire 30597* (MO, NY, VEN); Piedra Sapo. rio Atacavi, 3° 5' 0” N, 67° 2' 0” W, 140 m.a.s.l., Nov 1989, FL-old, *Velazco 973* (MO, NY, PORT); rio Ventuari, ca. 5 km por sendero en frente a la Isla Caymán, 4° 7' 41” N, 66° 40' 38” W, 126 m.a.s.l., 13 Mar 2002, Sterile, *Aymard 12191* (MO, PORT); rio Ventuari, ca. 5 km por sendero en frente a la Isla Caymán, 4° 7' 41” N, 66° 40' 38” W, 126 m.a.s.l., 14 Mar 2002, Sterile, *Aymard 12209* (INPA); San Fernando de Atabapo, 4° 2' 55” N, 67° 42' 8” W, 61 m.a.s.l., 3 Jul 1887, FL, *Gaillard 163* (P); Autana: San Pedro, rio Autana, 3° 44' 0” N, 65° 44' 0” W, 250 m.a.s.l., 10 Nov 1984, FL, *Guanchez 3477* (MO, TFVA, VEN); Maroa: Yavita,, 2° 48' 0” N, 67° 42' 33” W, 100 m.a.s.l., 14 Apr 1953, FR, *Maguire 35661* (COL, MO, NY, VEN); Yavita,, 2° 51' 16” N, 67° 42' 33” W, 100 m.a.s.l., 24 Oct 1998, FL, *Campbell 632* (MO, TFVA); **Apure**. Puerto Carreño: río Capanaparo-Cinaruco, 6° 58' 0” N, 67° 49' 0” W, 55 m.a.s.l., , ?, *Aymard 12106* (INPA).

29. *Pagamea plicatiformis* Steyerm.

Specimens measured — **BRASIL**. **Amazonas**. Barcelos: Parque Nacional do Jaú, campina do Patauá, 1° 48' 45” S, 61° 45' 30” W, 50 m.a.s.l., 29 Jun 1997, FL, *Ferreira 02PNJ* (INPA, MO); Parque Nacional do Jaú, campina do Patauá, 1° 48' 48” S, 61° 45' 46” W, 55 m.a.s.l., 23 Jul 2001, FR, *Vicentini 1764* (INPA, MO); Parque Nacional do Jaú, campina do Patauá, 1° 48' 56” S, 61° 45' 51” W, 49 m.a.s.l., 23 Jul 2001, Sterile, *Vicentini 1766* (INPA, MO); Parque Nacional do Jaú, campina do Patauá, 1° 49' 2” S, 61° 45' 58” W, 53 m.a.s.l., 23 Jul 2001, Sterile, *Vicentini 1767* (INPA, MO); Manaus: igarapé Tarumã-mirin, 2° 46' 10” S, 60° 15' 44” W, 50 m.a.s.l., 14 Aug 2003, FL-old, *Vicentini 2065* (MO); igarapé Tarumã-mirin, 2° 47' 27” S, 60° 15' 33” W, 52 m.a.s.l., 14 Aug 2003, FL-FR, *Vicentini 2072* (INPA, MO); Presidente Figueiredo: Manaus-Caracaraí rd, km 125, 1° 55' 0” S, 60° 1' 20” W, 110 m.a.s.l., 22 Sep 1977, FR, *Rodrigues 9774* (INPA); Manaus-Caracaraí rd, km 125, 1° 55' 0” S, 60° 1' 20” W, 110 m.a.s.l., 19 Feb 1979, FR, *Coelho 878* (INPA); Manaus-Caracaraí rd, km 140, 1° 39' 16” S, 60° 8' 44” W, 93 m.a.s.l., 21 Feb 1974, FR, *Steward 20399P* (INPA, MO, NY, US); Cachoeira da Iracema, trilha entre Iracema e Araras, 1° 56' 15” S, 60° 05' 00” W, 130 m.a.s.l., 28 Jul 2003, Sterile, *Vicentini 2051* (INPA, MO); Cachoeira da Iracema, trilha entre Iracema e Araras, 1° 56' 40” S, 60° 04' 35” W, 135 m.a.s.l., 28 Jul 2003, Sterile, *Vicentini 2053* (INPA, MO); Cachoeira da Iracema, trilha entre Iracema e Araras, 1° 57' 14” S, 60° 04' 25” W, 133 m.a.s.l., 28 Jul 2003, Sterile, *Vicentini 2055* (MO); margem direita do rio Uatumã, acima da barragem, 1° 59' 39” S, 59° 33' 43” W, 126 m.a.s.l., 31 Oct 1983, FL, *Lima 598* (INPA); **VENEZUELA**. Atabapo: 44 km al SE from Santa Barbara del Orinoco, 3° 50' 0” N, 66° 44' 0” W, 130 m.a.s.l., May 1990, FR, *Marin 1187* (MO, PORT); Maroa: 2° 44' 11” N, 67° 33' 45” W, 127 m.a.s.l., 9 Feb 1942, Sterile, *Williams 14190* (F, US, VEN); Yavita, río Temi, rd to Pimichín, 2° 52' N, 67° 26' W, 130 m.a.s.l., 11 Jul 1969, FL, *Bunting 3690* (VEN); Rio Negro: ca. 20 km S of confluence of rio Negro and Brazo Casiquiare, 1° 56' 0” N, 67° 3' 0” W, 119 m.a.s.l., 25 Nov 1981, FL, *Clark 8257* (MO, NY); Caño San Miguel, Casiquiare, Las Tinajas y el caño Iqueven, 2° 39' 0” N, 66° 45' 0” W, 160 m.a.s.l., 25 Apr 1991, FR, *Aymard 9150* (MO, NY, PORT); rio Baria, Mucuriapi, 1° 20' 0” N, 66° 26' 0” W, 80 m.a.s.l., 28 Jun 1984, FR, *Davidse 26755* (F, MO, NY, PORT, VEN).

Specimens seen but not measured — **BRASIL**. **Amazonas**. Barcelos: Parque Nacional do Jaú, campina do Patauá, 1° 48' 45” S, 61° 45' 30” W, 50 m.a.s.l., 4 Sep 1998, FR, *Vicentini 1385* (INPA); Parque Nacional do Jaú, campina do Patauá, 1° 48' 47” S, 61° 45' 39” W, 51 m.a.s.l., 23 Jul 2001, FR, *Vicentini 1763* (INPA); Parque Nacional do Jaú, campina do Patauá, 1° 48' 51” S, 61° 45' 46” W, 51 m.a.s.l., 23 Jul 2001, Sterile, *Vicentini 1765* (INPA); Manaus: igarapé Tarumã-mirin, 2° 47' 00” S, 60° 15' 20” W, 50 m.a.s.l., 14 Aug 2003, FL-FR, *Vicentini 2068* (INPA); **COLOMBIA**. **Guainia**. Puerto Inírida: Resguardo indígena Almidón-La Ceiba, Caño Agujõn, 03° 32' N, 67° 51' W, 80 m.a.s.l., 22 Mar 1998, Sterile, *Rudas 7224* (COAH).

30. *Pagamea guianensis* Aublet

Specimens measured — **BRASIL**. **Amapá**. Calçoene: BR156, 12 km W of Calçoene, 2° 28' 0” N, 51° 0' 0” W, 5 m.a.s.l., 8 Dec 1984, FL, *Mori 17271* (F, NY); BR156, 17 km NW of Calçoene, 2° 28' 0” N, 51° 1' 0” W, 7 m.a.s.l., 8 Dec 1984, FL, *Rabelo 2929* (NY); BR156, km 30 Calçoene-Rio Amapá Grande, 2° 15' 0” N, 50° 55' 0” W, 15 m.a.s.l., 12 Dec 1984, FL, *Mori 17379* (MO, NY); road to gold mines, km 12, 2° 30' 0” N, 50° 55' 0” W, 2 m.a.s.l., 20 Aug 1962, FR, *Pires 52523* (NY); Macapá: Igarapé do Lago, 0° 4' 0” N, 50° 55' 0” W, 1 m.a.s.l., 20 Oct 1980, FL, *Rabelo 739* (NY); rio Araguari, along railroad track, between Porto Platon and Macapá, 0° 4' 0” N, 50° 55' W, 1 m.a.s.l., 18 Sep 1961, FR, *Pires 51092* (F, NY); road to Amapá, km 48, 0° 0' 42” N, 51° 24' 0” W, 28 m.a.s.l., 10 Jul 1962, FR, *Pires 52060* (NY); São Joaquim de Pacui-Macapá, 0° 4' 0” N, 50° 55' 0” W, 30 m.a.s.l., 17 Jul 1980, FR, *Rabelo 545* (NY); Mazagão: 0° 7' 0” S, 51° 17' 0” W, 60 m.a.s.l., 2 Apr 1982, FL, *Rosa 4131* (IBGE, INPA, NY); região do Ariramba, 00° 07' 00” S, 51° 16' 00” W, 60 m.a.s.l., 17 Jun 1982, FR, *Rosa 4348* (IBGE, INPA); Oiapoque: S of airfield, 2 km NE of Oiapoque, 3° 50' 0” N, 51° 50' 0” W, 10 m.a.s.l., 30 Jul 1960, FR, *Irwin 47262* (F, NY, USM); Porto Grande: road to Amapá, km 108, Rio Pedreira, 0° 1' 10” N, 50° 47' 0” W, 1 m.a.s.l., 18 Jul 1962, FR, *Pires 52190* (F, NY); **Amazonas**. Apuí: Transamazon hwy, rio dos Pombos, waterfall 3 km upstream, 0° 7' 15” S, 60° 10' 0” W, 187 m.a.s.l., 20 Jun 1979, FR, *Calderon 2620* (US); Barcelos: Serra do Aracá, surrounding lowlands, 0° 48' 0” N, 63° 8' 0” W, 157 m.a.s.l., 4 Mar 1984, FL, *Pipoly 6800* (F, INPA, MO, NY); Serra do Aracá, surrounding lowlands, 0° 49' 0” N, 63° 20' 0” W, 191 m.a.s.l., 26 Feb 1977, FR, *Rosa 1675* (F, MO, NY); Serra do Aracá, surrounding lowlands, 0° 49' 0” N, 63° 20' 0” W, 191 m.a.s.l., 12 Jul 1985, FL, *Prance 29490* (F, INPA, MO, NY, SP); Serra do Aracá, surrounding lowlands, 0° 30' 0” N, 63° 30' 0” W, 83 m.a.s.l., 2 Jul 1985, Buds, *Cordeiro 134* (NY); Serra do Aracá, surrounding lowlands, 0° 42' 0” N, 63° 22' 0” W, 98 m.a.s.l., 2 Jul 1985, FL, *Silva 213* (INPA, MO, NY, SP); Serra do Aracá, surrounding lowlands, 0° 42' 0” N, 63° 22' 0” W, 98 m.a.s.l., 30 Jun 1985, FL, *Cordeiro 106* (NY); Serra do Aracá, surrounding lowlands, 0° 50' 0” N, 63° 21' 0” W, 50 m.a.s.l., 23 Jul 1985, FL, *Prance 29725* (INPA, NY); Borba: campina do rio Surubím, afluente do rio Abacaxis, 4° 29' 0” S, 58° 33' 0” W, 73 m.a.s.l., 4 Jul 1983, FR, *Cid 4046* (INPA, MO, NY); Manaus-Porto Velho hwy, km 160, 5° 21' 49” S, 61° 0' 0” W, 58 m.a.s.l., 23 Mar 1974, FR, *Campbell 20850P* (COL, INPA, MO, NY, P, US); Humaitá: BR230, Reserva Indígena dos Tenharim, 7° 55' 0” S, 62° 15' 0” W, 99 m.a.s.l., 13 Apr 1985, FR, *Cid 5464* (F, INPA, MO, NY, UNB); Iranduba: 5 km from Cacau Pirêra, 3° 5' 0” S, 60° 5' 0” W, 40 m.a.s.l., 18 Jun 1975, FL, *Prance 23509* (INPA, NY, US); Cacau Pirêra, km 2, 3° 8' 44” S, 60° 8' 44” W, 25 m.a.s.l., 18 Jun 1975, FR, *Prance 23488* (INPA, MO, NY, P, US); Manaus: 3° 6' 48” S, 60° 1' 31” W, 50 m.a.s.l., Dec 1900, FL, *Ule 5122* (F, K); Ponta Negra, 3° 2' 30” S, 60° 5' 57” W, 38 m.a.s.l., 8 Aug 2000, FL-FR, *Vicentini 1750* (INPA, MO); Ponta Negra, 3° 2' 30” S, 60° 5' 58” W, 35 m.a.s.l., 8 Aug 2000, FR, *Vicentini 1751* (INPA, MO); Ponta Negra, 3° 2' 29” S, 60° 5' 59” W, 36 m.a.s.l., 8 Aug 2000, FR, *Vicentini 1753* (INPA, MO); Cachoeira do Mindú, 3° 6' 48” S, 60° 1' 31” W, 60 m.a.s.l., 28 Jan 1936, FL, *Ducke 137* (F, K, NY, US); Estrada antiga do São Raimundo, 3° 6' 48” S, 60° 1' 31” W, 60 m.a.s.l., 1 Feb 1956, FL, *Chagas 3405INPA* (INPA); Ponta Negra, 3° 6' 48” S, 60° 1' 31” W, 35 m.a.s.l., Jan 1850, FL, *Spruce H20010176731K* (BM, K); igarapé do Parque 10, 3° 6' 48” S, 60° 1' 31” W, 50 m.a.s.l., 23 Dec 1955, FL, *Chagas 3169INPA* (INPA); Ponta Negra, 3° 2' 0” S, 60° 6' 0” W, 34 m.a.s.l., 22 May 1968, FR, *Prance 4840* (COL, F, INPA, MO, NY); Ponta Negra, 3° 2' 0” S, 60° 6' 0” W, 34 m.a.s.l., 22 May 1968, FL, *Prance 4849* (F, INPA, NY, P); Ponta Negra, 3° 2' 0” S, 60° 6' 0” W, 34 m.a.s.l., 12 May 1961, FR, *Rodrigues 2579* (US); Ponta Negra, 3° 2' 0” S, 60° 6' 0” W, 34 m.a.s.l., 18 Dec 1968, FL, *Prance 9095* (F, INPA, NY); Manicoré: Manaus-Porto Velho hwy, km 250, 5° 45' 49” S, 62° 21' 49” W, 85 m.a.s.l., 5 Jan 1974, FL, *Steward 20154P* (INPA, MO, NY, P, US); Santa Isabel do Rio Negro: próximo a foz do rio Ayuana, 0° 31' 21” S, 64° 56' 04” W, 51 m.a.s.l., 3 Dec 2003, FL, *Vicentini 2144* (INPA, MO); próximo a foz do rio Ayuana, 0° 31' 21” S, 64° 56' 04” W, 51 m.a.s.l., 3 Dec 2003, FL, *Vicentini 2145* (INPA); próximo a foz do rio Ayuana, 0° 31' 21” S, 64° 56' 04” W, 51 m.a.s.l., 3 Dec 2003, FL-FR, *Vicentini 2146* (INPA, MO); Campina do Dodono, rio Uneiuxi, 35 km above mouth, 0° 39' 16” S, 65° 26' 0” W, 48 m.a.s.l., 20 Oct 1971, FR, *Prance 15444* (F, INPA, MO, NY); Temendauí, rio Negro, 2 hours below Tapuruquara, 0° 29' 10.17” S, 64° 45' 33.50” W, 56 m.a.s.l., 4 Sep 1979, FL, *Kubitzki 79108* (NY, US); São Gabriel da Cachoeira: Temendui Lagoon, rio Negro, 0° 35' 0” S, 64° 40' 0” W, 49 m.a.s.l., 30 Jun 1979, FL, *Alencar 262* (NY); Temendui Lagoon, rio Negro, 0° 35' 0” S, 64° 40' 0” W, 49 m.a.s.l., 29 Jun 1979, FR, *Poole 1775* (INPA, MO, NY, UNB); **Bahia**. Berlinque: Estrada para Catú, 13° 6' 0” S, 38° 47' 0” W, 1 m.a.s.l., 25 Apr 1997, FR, *Silva 57* (HUEFS, US); Cairu: Ilha de Tinharé, Morro de São Paulo, caminho teatro, 13° 23' 2” S, 38° 54' 58” W, 68 m.a.s.l., 26 Jun 2000, FL-FR, *Vicentini 1539* (INPA, MO); Ilha de Tinharé, Morro de São Paulo, caminho teatro, 13° 23' 4” S, 38° 54' 56” W, 55 m.a.s.l., 26 Jun 2000, FL, *Vicentini 1540* (INPA, MO); Ilha de Tinharé, Morro de São Paulo, caminho teatro, 13° 23' 5” S, 38° 54' 51” W, 68 m.a.s.l., 26 Jun 2000, FL-FR, *Vicentini 1541* (INPA, MO); Ilha de Tinharé, Morro de São Paulo, caminho teatro, 13° 23' 31” S, 38° 55' 11” W, 73 m.a.s.l., 26 Jun 2000, FL, *Vicentini 1542* (INPA, MO); Ilha de Tinharé, Morro de São Paulo, caminho teatro, 13° 23' 49” S, 38° 55' 10” W, 35 m.a.s.l., 26 Jun 2000, FL-FR, *Vicentini 1543* (INPA, MO); Ilha de Tinharé, Morro de São Paulo, caminho do teatro, 13° 23' 53” S, 38° 55' 4” W, 34 m.a.s.l., 26 Jun

2000, FL, *Vicentini 1544* (INPA, MO); Ilha de Tinharé, Morro de São Paulo, caminho teatro, 13° 24' 8” S, 38° 55' 7” W, 53 m.a.s.l., 26 Jun 2000, FL-FR, *Vicentini 1545* (INPA, MO); Cairú: Rodovia Nilo Peçanha/ Cairú, km 4, 13° 37' 0” S, 39° 6' 0” W, 52 m.a.s.l., 9 Dec 1981, FR, *Carvalho 384* (F); Camaçari: Jardim das Mangabeiras, 2.5 km W da estrada do Côco, 12° 43' 40” S, 38° 11' 6” W, 33 m.a.s.l., 23 Jun 2000, FL-FR, *Vicentini 1520* (INPA, MO); Jardim das Mangabeiras, 2.5 km W da estrada do Côco, 12° 43' 25” S, 38° 11' 12” W, 44 m.a.s.l., 24 Jun 2000, FR, *Vicentini 1528* (INPA, MO); Jardim das Mangabeiras, 2.5 km W da estrada do Côco, 12° 43' 28” S, 38° 11' 12” W, 30 m.a.s.l., 24 Jun 2000, Sterile, *Vicentini 1530* (INPA, MO); Jardim das Mangabeiras, 2.5 km W da estrada do Côco, 12° 43' 30” S, 38° 11' 11” W, 29 m.a.s.l., 24 Jun 2000, FL-FR, *Vicentini 1531* (INPA, MO); Ilha de Cal: 12° 59' 0” S, 38° 45' 0” W, 2 m.a.s.l., 4 May 1918, FL, *Curran 115* (F, NY, US); Maraú: 14° 6' 0” S, 39° 0' 0” W, 2 m.a.s.l., 6 Oct 1965, FL-old, *Belem 1861* (CEPEC, NY); 14° 6' 0” S, 39° 0' 0” W, 2 m.a.s.l., 12 Jan 1967, FL, *Belem 3046* (CEPEC, NY); 14° 6' 0” S, 39° 0' 0” W, 2 m.a.s.l., 25 Apr 1965, FR, *Belem 906* (CEPEC, NY); 14° 6' 0” S, 39° 0' 0” W, 2 m.a.s.l., 25 Apr 1965, FL-FR, *Belem 925* (CEPEC); 5 km SE of Maraú, junction with rd to Campinho, 14° 8' 0” S, 38° 59' 0” W, 25 m.a.s.l., 14 May 1980, FL-old, *Harley 22029* (CEPEC, NY, US); 5 km SE of Maraú, junction with rd to Campinho, 14° 8' 0” S, 39° 0' 0” W, 25 m.a.s.l., 14 May 1980, FR, *Harley 22037* (CEPEC, NY, US); 5 km SE of Maraú, junction with rd Ponta do Mutá, 14° 8' 0” S, 39° 0' 0” W, 25 m.a.s.l., 2 Feb 1977, FL, *Harleyi 18477* (CEPEC, NY, P, US); BR030, a 45 km a E de Ubaitaba, 14° 9' 0” S, 39° 0' 0” W, 40 m.a.s.l., 27 Aug 1979, Sterile, *Mori 12785* (CEPEC); BR030, a 45 km a E de Ubaitaba, 14° 9' 0” S, 39° 0' 0” W, 37 m.a.s.l., 27 Aug 1979, FR, *Mori 12810* (NY); BR030, a 5 km ao S de Maraú, 14° 8' 0” S, 39° 0' 0” W, 4 m.a.s.l., 13 Jun 1979, FR, *Mori 11993* (NY); BR030, a 5 km ao S de Maraú, 14° 8' 0” S, 39° 0' 0” W, 4 m.a.s.l., 27 Feb 1980, FL-FR, *Santos 3520* (CEPEC, F); ca. 2 km do porto de Campinho, 13° 55' 2” S, 38° 58' 24” W, 1 m.a.s.l., 3 Jul 2000, FL, *Vicentini 1624* (HUEFS, INPA, MO); ca. 2 km do porto de Campinho, 13° 55' 1” S, 38° 58' 25” W, 2 m.a.s.l., 3 Jul 2000, FL, *Vicentini 1625* (HUEFS, INPA, MO); ca. 2 km do porto de Campinho, 13° 55' 2” S, 38° 58' 26” W, 10 m.a.s.l., 3 Jul 2000, FL-FR, *Vicentini 1626* (HUEFS, INPA, MO); ca. 2 km do porto de Campinho, 13° 55' 2” S, 38° 58' 27” W, 9 m.a.s.l., 3 Jul 2000, FL-FR, *Vicentini 1627* (HUEFS, INPA, MO); ca. 2 km do porto de Campinho, 13° 55' 1” S, 38° 58' 29” W, 10 m.a.s.l., 3 Jul 2000, FL, *Vicentini 1629* (HUEFS, INPA, MO); Fazenda Virgem Del Mar, 14° 5' 57” S, 38° 57' 68” W, 1 m.a.s.l., 14 Aug 1999, FL-old, *Jardim 2198* (MO); Nazaré: Estrada Nazaré-Ilha de Itaparica, 5 km antes da ponte para a ilha, 13° 1' 48” S, 38° 49' 26” W, 16 m.a.s.l., 26 Jun 2000, FL, *Vicentini 1533* (INPA, MO); Estrada Nazaré-Ilha de Itaparica, 5 km antes da ponte para a ilha, 13° 1' 49” S, 38° 49' 23” W, 17 m.a.s.l., 26 Jun 2000, FL, *Vicentini 1534* (INPA, MO); Estrada Nazaré-Ilha de Itaparica, 5 km antes da ponte para a ilha, 13° 1' 52” S, 38° 49' 28” W, 12 m.a.s.l., 26 Jun 2000, FL, *Vicentini 1536* (INPA, MO); Estrada Nazaré-Ilha de Itaparica, 5 km antes da ponte para a ilha, 13° 1' 54” S, 38° 49' 28” W, 22 m.a.s.l., 26 Jun 2000, FL, *Vicentini 1538* (INPA, MO); Ponta do Santo: Ambar, enseada de Camamu, ca. 5 km NE da sede do município, 13° 55' 0” S, 39° 0' 0” W, 1 m.a.s.l., 24 Jul 1981, FR, *Carvalho 772* (CEPEC, HUEFS, UNB); Ambar, enseada de Camamu, ca. 5 km NE da sede do município, 13° 55' 0” S, 39° 0' 0” W, 1 m.a.s.l., 24 Jul 1981, FL, *Carvalho 776* (CEPEC, HUEFS, UNB); Valença: 3 km de para Guaibim, 13° 21' 0” S, 39° 3' 0” W, 40 m.a.s.l., 8 Jun 1973, FL, *Santos 2624* (CEPEC, US); 9 km de la route de Valença à Guaibim, 14° 55' 51” S, 39° 2' 30” W, 1 m.a.s.l., 4 Dec 1986, FL, *Chautems 313* (CEPEC); 3 km de la rodovia Valença-Nazaré, 13° 21' 0” S, 39° 3' 0” W, 100 m.a.s.l., 13 Jan 1997, FL, *Arbo 7144* (CEPEC, MBM, NY); ramal km 9 estrada Valença-Guaibim, 14° 55' 51” S, 39° 2' 30” W, 10 m.a.s.l., 12 Aug 1980, FR, *Mattos 1027* (F); **Goiás**. Chapada dos Veadeiros: 1 km N of Araguaína, 7° 12' 0” S, 48° 12' 0” W, 300 m.a.s.l., 16 Mar 1968, FR, *Irwin 21289* (F, NY); **Maranhão**. Carolina: Pedra Caida, 35 km N of Carolina, 7° 8' 0” S, 47° 25' 0” W, 316 m.a.s.l., 16 Apr 1983, FR, *Taylor 1279* (F, MO, NY); São Luiz: Rozario, São Simão, 2° 31' 0” S, 44° 16' 0” W, 2 m.a.s.l., 1940, FL-old, *Krukoff 11820* (NY); **Mato Grosso**. rio dos Peixes, 11° 21' 0” S, 57° 57' 0” W, 362 m.a.s.l., 18 Mar 1980, FR, *Plowman 9747* (IBGE); Campo Novo Parecis: Aldeia Utiauty [prob. Utiariti], 13° 02' S, 58° 14' W, 400 m.a.s.l., 15 Feb 1994, FL, *Macedo 3616* (INPA); Comodoro: rio 12 de Outubro, ca. 80 km N de Comodoro, 12° 58' 47” S, 60° 0' 44” W, 530 m.a.s.l., 25 Jul 2000, FR, *Vicentini 1651* (INPA, MO); rio 12 de Outubro, ca. 80 km N de Comodoro, 12° 58' 44” S, 60° 0' 47” W, 578 m.a.s.l., 25 Jul 2000, FR, *Vicentini 1652* (INPA, MO); rio 12 de Outubro, ca. 80 km N de Comodoro, 12° 58' 45” S, 60° 0' 49” W, 539 m.a.s.l., 25 Jul 2000, Buds-FR, *Vicentini 1653* (INPA, MO); Chapada dos Parecis, BR-364, ca. 1-2 km N de Comodoro, 13° 38' 28” S, 59° 47' 58” W, 624 m.a.s.l., 24 Jul 2000, FR, *Vicentini 1643* (INPA, MO); Chapada dos Parecis, BR-364, ca. 1-2 km N de Comodoro, 13° 38' 25” S, 59° 47' 59” W, 620 m.a.s.l., 24 Jul 2000, FR, *Vicentini 1645* (INPA, MO); Chapada dos Parecis, BR-

364, ca. 1-2 km N de Comodoro, 13° 38' 26” S, 59° 48' 0” W, 630 m.a.s.l., 24 Jul 2000, FR, *Vicentini 1647* (INPA, MO); Chapada dos Parecis, BR-364, ca. 1-2 km N de Comodoro, 13° 38' 27” S, 59° 48' 1” W, 627 m.a.s.l., 24 Jul 2000, FR, *Vicentini 1648* (INPA, MO); Chapada dos Parecis, BR-364, ca. 1-2 km N de Comodoro, 13° 38' 28” S, 59° 48' 0” W, 626 m.a.s.l., 24 Jul 2000, FR, *Vicentini 1649* (INPA, MO); Chapada dos Parecis, BR-364, ca. 1-2 km N de Comodoro, 13° 38' 29” S, 59° 48' 0” W, 628 m.a.s.l., 24 Jul 2000, FR, *Vicentini 1650* (INPA, MO); Chapada dos Parecis, BR-364, ca. 1-2 km N de Comodoro, 13° 53' 30” S, 59° 45' 48” W, 589 m.a.s.l., 24 Jul 2000, Sterile, *Vicentini 1641* (INPA, MO); Fontanilhas: rio Juruena, 10° 21' 49” S, 58° 21' 49” W, 171 m.a.s.l., 22 May 1977, FR, *Rosa 1971* (MO, NY); Nova Mutuni: rio Arinos, 13° 57' 0” S, 56° 15' 0” W, 382 m.a.s.l., 28 May 1995, FR, *Macedo 4176* (INPA); Sararé: 13° 50' 0” S, 58° 55' 0” W, 590 m.a.s.l., 4 Aug 1978, Buds, *Pires 16449* (F, NY); **Pará**. Alto Tapajós, Village of Pratatí, 8° 0' 0” S, 57° 5' 0” W, 350 m.a.s.l., 11 Feb 1974, FL, *Anderson 10769* (MO, NY, US); Acará: Boa Vista. Campina do Guajará, 2° 00' S, 48° 15' 00” W, 67 m.a.s.l., 29 Jul 1980, FR, *Rosario 85* (INPA, NY); Alenquer: Estrada Lauro Sodré, 28 km de Alenquer, 1° 43' 0” S, 54° 40' 0” W, 166 m.a.s.l., 2 Nov 1987, FL, *Cid 9395* (INPA, MO); Almeirim: Monte Dourado, área da Água Azul, 1° 5' 0” S, 52° 70' 0” W, 71 m.a.s.l., 26 Mar 1986, FL, *Pires 836* (INPA); Belém: 10 km inland from Boa Vista, rio Guamá, 1° 34' 0” S, 48° 23' 0” W, 8 m.a.s.l., 1 Nov 1980, FL, *Daly D799* (F, IBGE, INPA, MO, NY); 3 km NW of Instituto Agronômico do Norte, near São Joaquim, 1° 27' 30” S, 48° 29' 30” W, 1 m.a.s.l., 30 Aug 1942, FL, *Silva 24* (NY, US); Bairro da Sacramenta, 1° 27' 0” S, 48° 29' 0” W, 1 m.a.s.l., 22 Oct 1897, FL-FR, *Guedes MG1255* (INPA, NY); Estrada Belém-Mosqueiro, 1° 8' 0” S, 48° 23' 30” W, 1 m.a.s.l., 16 Mar 1965, FL, *Silva 59707* (COL, F, NY); Ilha do Mosqueiro, 1° 7' 0” S, 48° 24' 0” W, 1 m.a.s.l., 3 Nov 1929, FL, *Killip 30504* (F, NY, US); Bragança: 7 km E of Bragança along rd Augusto Correa, 1° 3' 0” S, 46° 40' 0” W, 25 m.a.s.l., 7 Apr 1980, FL, *Davidse 17979* (INPA, MO, NY, UNB); Curuçã: Abade, 0° 42' 0” S, 47° 53' 0” W, 1 m.a.s.l., 14 Oct 1978, FL, *Silva 4043* (NY); Iririteus, margem da estrada, 0° 43' 1” S, 47° 50' W, 2 m.a.s.l., 15 Dec 1978, FL, *Nascimento 847* (NY); Gurupá: Campina do Jacopi, 1° 26' 11” S, 51° 39' 16” W, 6 m.a.s.l., 7 Feb 1979, FL, *Silva 5048* (F, MO, NY); Serraria Xingú, 1° 25' 0” S, 51° 39' 0” W, 9 m.a.s.l., 6 Feb 1979, FR, *Silva 5030* (F, NY); Ilha do Marajó: 2 km from river Pracuuba-mirim, upstream from São Sebastião da Boa Vista, 1° 21' 30” S, 49° 43' 38” W, 4 m.a.s.l., 15 Oct 1984, FL, *Sobel 4581* (F, MO, NY); 2 km from river Pracuuba-mirim, upstream from São Sebastião da Boa Vista, 1° 21' 49” S, 49° 43' 38” W, 3 m.a.s.l., 19 Oct 1984, FL, *Sobel 4713* (F, MO, NY); Itaituba: Serra do Cachimbo, aeroporto, 8° 30' 0” S, 55° 0' 0” W, 390 m.a.s.l., 19 Sep 1977, FR, *Benson 92150INPA* (INPA); Serra do Cachimbo, aeroporto, 8° 57' 0” S, 54° 54' 0” W, 424 m.a.s.l., 23 Jun 1974, FR, *Rodrigues 9419* (INPA, US); Serra do Cachimbo, BR-163, km 831, 9° 5' 30” S, 54° 54' 0” W, 590 m.a.s.l., 16 Feb 1977, FL, *Kirkbride 2834* (F, MO, NY, US); Serra do Cachimbo, BR-163, km 842 a 850, 9° 0' 0” S, 54° 58' 0” W, 475 m.a.s.l., 5 May 1983, FR, *Silva 240* (F, INPA, MO, NY); Jacarecanga: Missão Cururú, 7° 37' 0” S, 57° 35' 0” W, 96 m.a.s.l., 9 May 1977, FR, *Rosa 1873* (INPA, MO, NY, SPF, US); rio Cururú. 10-15 km downstream from Missão Cururú, 7° 35' 0” S, 57° 35' 0” W, 130 m.a.s.l., 16 Feb 1974, FR, *Anderson 11021* (NY, US); rio Cururú, Lago da Cigana, 7° 35' 0” S, 57° 31' 0” W, 140 m.a.s.l., 6 Feb 1974, FL, *Anderson 10548* (MO, NY, US); rio Cururú, Missão Cururú, 7° 35' 0” S, 57° 31' 0” W, 140 m.a.s.l., 8 Feb 1974, FL, *Anderson 10638* (NY, US); rio Cururú, village of Mouro, downstream from Missão Cururú, 7° 15' 0” S, 57° 55' 0” W, 150 m.a.s.l., 18 Feb 1974, FR, *Anderson 11046* (NY, US); Jarí: Água Branca, 1° 00' 15” S, 52° 23' 00” W, 87 m.a.s.l., 28 Jul 1969, FR, *Silva 2505* (NY); 1° 00' 10” S, 52° 27' 00” W, 95 m.a.s.l., 27 Jun 1969, FR, *Silva 2254* (NY); 1° 00' 00” S, 52° 25' 00” W, 88 m.a.s.l., 10 Apr 1969, FL-FR, *Silva 1839* (NY); Marapanim: Camara, 11 km NW of Marudá, 0° 37' 0” S, 47° 41' 0” W, 9 m.a.s.l., 3 Apr 1980, FR, *Davidse 17860* (NY); Oriximiná: Campos de Ariramba, entre os rio Jaramacaru e Igarapé Mutum, 1° 10' 0” S, 55° 35' 0” W, 269 m.a.s.l., 4 Dec 1987, FL, *Cid 9767* (INPA, NY); rio Mapuera, 10 km upriver from Cachoeira Porteira, campina das onças, 1° 5' 27” S, 57° 10' 54” W, 100 m.a.s.l., 30 Jun 1980, FR, *Davidson 10628* (INPA, MO, NY, UNB); Pinhel: 3° 8' 0” S, 55° 15' 0” W, 65 m.a.s.l., 5 Jun 1990, FR, *TMS 118* (INPA); Salinas: 0° 37' 0” S, 47° 20' 0” W, 1 m.a.s.l., 15 Dec 1944, FL, *Ducke 1670* (F, MO?, US); Tucuruí: 25 km S of Tucurui on old BR422, 3° 58' 0” S, 49° 38' 0” W, 22 m.a.s.l., 30 Oct 1981, FL, *Daly 1078* (F, IBGE, INPA, MO, NY); 25 km south of damp, BR422 to Breu Branco, 3° 52' 0” S, 49° 44' 0” W, 90 m.a.s.l., 15 Mar 1980, FR, *Plowman 9603* (F, INPA, MO, NY, UNB); rio Tocantins, BR-263, km 16, 4° 25' 0” S, 49° 32' 0” W, 27 m.a.s.l., 30 Jan 1980, FL-old, *Lisboa 1273* (NY); Vigia do Nazareth: 0° 48' 0” S, 48° 8' 0” W, 1 m.a.s.l., 11 Jun 1966, FR, *Duarte 9773* (NY); 9 km SE of Vigia, along highway to Belém, Campinas de Palha, 0° 55' 0” S, 48° 4' 0” W, 50 m.a.s.l., 31 Mar 1980, FR, *Davidse 17702* (NY); BR018, ca. 6 km S of Vigia, 0° 52' 22” S, 48° 6' 33” W, 2 m.a.s.l., 13 Nov 1980, FL, *Daly 927* (F, IBGE, INPA, MO, NY); Campina do Palha, 0° 48' 0” S, 48° 8' 0” W, 1 m.a.s.l., 4 Apr 1961, FL, *Egler 1599* (INPA); Campina do Palha, 0° 48' 0” S, 48° 8' 0” W, 1 m.a.s.l., 19 Jul 1959, FR, *Rodrigues 1225* (INPA); **Rondônia**. Vilhena: BR Vilhena-Porto Velho, ca. 30 km de Vilhena., 12° 23' 30” S, 60° 37' 11” W, 483 m.a.s.l., 26 Jul 2000, Sterile, *Vicentini 1674* (MO); BR Vilhena-Porto Velho, ca. 30 km de Vilhena., 12° 23' 26” S, 60° 37' 13” W, 367 m.a.s.l., 26 Jul 2000, Sterile, *Vicentini 1675* (MO); Fundos da cidade, 12° 43' 0” S, 60° 7' 0” W, 600 m.a.s.l., 7 Jan 1979, FL, *Silva 4193* (NY); km 3-4 da BR Vilhena-Porto Velho, 12° 43' 43” S, 60° 11' 27” W, 539 m.a.s.l., 26 Jul 2000, Sterile, *Vicentini 1668* (MO); km 3-4 da BR Vilhena-Porto Velho, 12° 43' 46” S, 60° 11' 26” W, 513 m.a.s.l., 26 Jul 2000, Sterile, *Vicentini 1670* (MO); **Roraima**. Boa Vista: Estrada da Serra Grande, 2° 50' 0” N, 60° 40' 0” W, 76 m.a.s.l., 2 Aug 1986, FL, *Silva 581* (INPA, MO, UNB); Caracaraí: 1° 21' 58” S, 61° 04' 10” W, 46 m.a.s.l., 1839, FL, *Schomburgk 985* (BM, NY, P); BR-174, km 17 from Mucajaí to Caracaraí, 2° 20' 0” N, 61° 0' 0” W, 66 m.a.s.l., 8 Nov 1977, FR, *Coradin 1011* (NY, US); estrada da Perdida, 2 km da BR-174, 1° 28' 49” N, 60° 58' 9” W, 78 m.a.s.l., 7 Aug 2000, Sterile, *Vicentini 1746* (INPA); **GUYANA**. 6° 01' 57” N, 58° 22' 26” W, 68 m.a.s.l., 1839, FL, *Schomburgk 510* (BM, NY, P); Warrewarrema, 6° 28' 57” N, 57° 54' 19” W, 3 m.a.s.l., 1837, FL, *Schomburgk 467* (BM, F, P); **Cuyuni-Mazaruni**. Pakaraima Mts: Ayanganna Plateau, 3 km N of Koatse river, 5° 38' 0” N, 60° 4' 0” W, 660 m.a.s.l., 27 Feb 1987, FL, *Pipoly 10721* (US); **Demerara-Mahaica**. 3-4 km S of Loo Creek along Linden Hwy, 6° 12' 0” N, 59° 15' 0” W, 5 m.a.s.l., 2 Mar 1989, FR, *Gillespie 775* (NY, US); Soesdyke-Linden hwy, from Timehri aiport to Kuru-Kuru Creek., 6° 25' 0” N, 58° 15' 0” W, 20 m.a.s.l., 18 Mar 1988, FL, *Hahn 3927* (NY, US); 5 mi E of Atkison field., 6° 30' N, 58° 17' 50” W, 2 m.a.s.l., 30 Dec 1953, FL, *Irwin 104* (US); Atkinson-Mackenzie hwy., 6° 30' 00” N, 58° 17' 00” W, 2 m.a.s.l., Jan 1968, FR, *Davis 0619* (NY); CEIBA center, Soesdyke-Linden hwy., 6° 18' N, 60° 35' W, 4 m.a.s.l., 14 Jan 1996, FL, *Clarke 780* (MO); East Coast Water Conservancy, SE of Georgetown, 6° 48' 0” N, 58° 10' 0” W, 1 m.a.s.l., 26 Nov 1919, FL, *Hitchcock 16925* (NY, US); Linden hwy, 6 km S of Kuru-Kuru Creek., 6° 23' 0” N, 58° 14' 0” W, 15 m.a.s.l., 3 Jan 1992, FR, *Hoffman 715* (MO); Linden hwy, near St. Cuthbert’s, 6° 28' 0” N, 58° 16' 0” W, 15 m.a.s.l., 24 Feb 1989, FR, *Gillespie 724* (MO, NY); Linden-Soesdyke hwy, ca. 16 mi S of Georgetown, 6° 20' 0” N, 58° 15' 0” W, 25 m.a.s.l., 19 Jan 1987, FL, *Pipoly 9160* (MO, NY, P); Linden-Soesdyke hwy, between Dora and Maibia creeks, 6° 18' 0” N, 58° 14' 0” W, 30 m.a.s.l., 21 Jan 1987, FR, *Pipoly 9685* (MO, NY, P, US); Mabura Hill, 180 km SSE of Georgetown, 5° 20' 0” N, 58° 40' 0” W, 25 m.a.s.l., 6 Sep 1988, FR, *Steege 510* (MO); **East Berbice-Corentyne**. Corentyne river, near Orealla Amerindian village., 5° 20' 0” N, 57° 22' 0” W, 35 m.a.s.l., 26 Apr 1990, FR, *McDowell 2507* (COL, MO, NY); Canje river, 0.75 km N of Ekwarum river, 5° 20' 0” N, 57° 38' 0” W, 10 m.a.s.l., 10 Apr 1987, FR, *Pipoly 11385* (BM, NY, US); Canje river, SW Digitima creek mouth, 5° 36' 0” N, 57° 35' 0” W, 15 m.a.s.l., 13 Apr 1987, FL, *Pipoly 11529* (COL, F, HUA, INPA, MO, NY); **Essequibo Islands-West**. Santa Mission, along main trail SW of the village, 6° 30' N, 58° 23' W, 100 m.a.s.l., 30 Nov 92, FL, *Goerts 464* (MO); **Essequibo Islands-West Demerara**. Coverden, 6° 34' 0” N, 58° 13' 0” W, 1 m.a.s.l., Sep 1924, FR, *Persuad 137* (F, NY); **Potaro-Siparuni**. Upper Rupununi river, near Dadanawa, 2° 45' 0” N, 59° 39' 16” W, 150 m.a.s.l., 24 Jul 1922, FR, *De 1774* (F, MO, NY); Rupununi: Parabaru Savanna, between Rupununi and Kuyuwini rivers, 2° 10' 0” N, 59° 21' 49” W, 408 m.a.s.l., 16 Feb 1938, FL, *Smith 3070* (F, MO, NY, P, US); **Upper Demerara-Berbice**. Malali, Demerara river, 5° 35' 0” N, 58° 28' 0” W, 138 m.a.s.l., 1 Nov 1922, FL, *De 2647* (F, MO, NY); 15 km E of Rockstone, on Linden-Tockstone rd, 5° 58' 0” N, 58° 30' 0” W, 25 m.a.s.l., 1 Jan 1987, FL, *Pipoly 9565* (MO, NY, P); 15 km E of Rockstone, on Linden-Tockstone rd, 5° 58' 0” N, 58° 35' 0” W, 60 m.a.s.l., 19 Jan 1987, Sterile, *Pipoly 9622* (MO, NY, P, US); 5 km E of Rockstone, on Linden-Tockstone rd, 5° 58' 0” N, 58° 35' 0” W, 60 m.a.s.l., 19 Jan 1987, FL, *Pipoly 9653* (MO, NY, US); lower Kajarau Creek, 1 km above Macouria river, 6° 28' 0” N, 58° 32' 0” W, 5 m.a.s.l., 29 Apr 1993, FR, *Henkel 1993* (COL, MO, NY); Warunana, Berbice river, 5° 33' 0” N, 58° 2' 0” W, 48 m.a.s.l., 7 Jun 1958, FR, *Hansou 1055* (NY); **GUYANE FRANCAISE**.4° 34' 38” N, 51° 49' 15” W, 4 m.a.s.l., , FL-old, *Aublet snTYPE* (BM); **GUYANE FRANÇAISE**. 5° 41' 39” N, 53° 54' 49” W, 1 m.a.s.l., 1876, FL, *Melinon 307* (F, P, US); **GUYANE FRANCAISE**. Cayenne, 4° 56' 0” N, 52° 20' 0” W, 9 m.a.s.l., , FL, *Unknown KH20010176734* (K); **GUYANE FRANÇAISE**. Cyapock, montagne des Trois Pitons., 4° 13' 0” N, 51° 51' 0” W, 114 m.a.s.l., 8 Oct 1969, FR, *Oldeman 453* (US); **GUYANE FRANCAISE**. Kouron, 8 km NW, 5° 08' N, 52° 37' W, 1 m.a.s.l., 19 Dec 1976, FL, *Roubik 73* (MO); **GUYANE FRANÇAISE**. Route de L’Est, km 8, sur butte de micashiste., 4° 45' 0” N, 52° 26' 0” W, 100 m.a.s.l., 22 Oct 1986, FL, *Sastre 8020* (US); Route de Mana, 400 m aprés les Melgaches à 100 m coté EST de la chapelle, 5° 40' 0” N, 53° 47' 0” W, 4 m.a.s.l., 1 Mar 1956, FR, *Lindeman 7324* (NY, P); **GUYANE FRANCAISE**. Savane de Organabo, 5° 32'

0” N, 53° 25' 0” W, 1 m.a.s.l., 20 Mar 1994, FR, *Andersson 2015* (MO, NY); Savane Maititi, ca. 10 km SE of Kourou, 5° 3' 0” N, 52° 36' 0” W, 1 m.a.s.l., 11 Mar 1994, FR, *Andersson 1956* (MO, NY); **PERU**. 1832, FL, *Poeppig 2984* (F); **SURINAME**. 5° 33' 35” N, 54° 35' 13” W, 12 m.a.s.l., 1841, FL, *Berthoud-Coulon 163* (BM); 5° 19' 10” N, 55° 16' 10” W, 65 m.a.s.l., 16 Jul 1919, FL, *Herb 4502* (BM, MO); Tibiti savanne, km 3.2, 5° 23' 0” N, 55° 56' 0” W, 17 m.a.s.l., 14 Jan 1949, FL-FR, *Lanjouw 1821* (NY); **Brokopondo**. Brownsberg, 4° 53' 0” N, 55° 13' 0” W, 332 m.a.s.l., 1 Dec 1924, FL, *Herb 6735* (F, K); Brownsberg, 4° 53' 0” N, 55° 13' 0” W, 332 m.a.s.l., 24 Mar 1925, FR, *Herb 6813* (NY, US); **Para**. Jodensavanne-Mapane, near Blakawatra, 5° 25' 0” N, 54° 59' 0” W, 20 m.a.s.l., 17 Dec 1954, FL, *Lindeman 6878* (F); Zanderij, 5° 27' 0” N, 55° 12' 0” W, 23 m.a.s.l., 19 Dec 1950, FL, *Florschutz 643* (NY); Zanderij I., 5° 27' 0” N, 55° 12' 0” W, 23 m.a.s.l., 4 Jun 1944, FR, *Maguire 23736a* (F, NY); **Saramaca**. Wayombo river, Donder creek., 5° 22' 0” N, 56° 20' 0” W, 17 m.a.s.l., 29 Aug 1920, FR, *Pulle 366HB* (BM, MO); **Suhosa**. Upper Suriname river, 5° 35' 47” N, 54° 56' 22” W, 5 m.a.s.l., 14 Apr 1949, FR, *Lanjouw 3370* (NY).

Specimens seen but not measured — . , ?, *BM 4_2* (BM); , ?, *unknown 243* (BM); **BRASIL**. , FL, *Newman SN* (F); **Amapá**. Calçoene: Cunani, 2° 52' 0” N, 51° 6' 0” W, 9 m.a.s.l., 17 Oct 1895, FL-old, *Huber 12389INPA* (INPA); Macapá: rio Massocari-Macapá, 0° 4' 0” N, 50° 55' 0” W, 1 m.a.s.l., 27 Apr 1981, FL, *Rabelo 1225* (NY); Porto Palton, na estrada de Porto Santana-Porto Platon, km 106, 0° 4' 0” N, 50° 55' 0” W, 1 m.a.s.l., 11 Feb 1962, FL, *Mattos 10019* (SP, UNB); Mazagão: 0° 7' 0” S, 51° 17' 0” W, 60 m.a.s.l., 20 Oct 1981, FL, *Araújo 338* (IBGE, INPA); Porto Grande: 00° 43' 00” N, 51° 23' 00” W, 44 m.a.s.l., , ?, *Cid 11679* (INPA); 00° 43' 30” N, 51° 23' 30” W, 45 m.a.s.l., , ?, *Cid P314* (INPA); 00° 43' 45” N, 51° 23' 15” W, 44 m.a.s.l., , ?, *Cid 11648* (INPA); **Amazonas**. Iranduba: Cacau Pirêra, km 2, 3° 8' 44” S, 60° 8' 44” W, 25 m.a.s.l., 2 Jul 1975, FR, *Macedo 51* (US); Cacau Pirêra, km 5, 3° 8' 44” S, 60° 8' 44” W, 25 m.a.s.l., 18 Jun 1975, FR, *Lisboa 109* (US); Manaus: 3° 6' 48” S, 60° 1' 31” W, 50 m.a.s.l., 16 Nov 1910, FL-old, *Ducke 11084* (F); Ponta Negra, 3° 07' 40” S, 59° 59' 55” W, 30 m.a.s.l., Jun 1851, FR, *Spruce 1200* (BM, NY, P); Ponta Negra, 3° 2' 29” S, 60° 6' 0” W, 45 m.a.s.l., 8 Aug 2000, Sterile, *Vicentini 1752* (INPA); Ponta Negra, 3° 2' 30” S, 60° 6' 1” W, 31 m.a.s.l., 8 Aug 2000, Sterile, *Vicentini 1754* (INPA); Ponta Negra, 3° 2' 31” S, 60° 6' 1” W, 31 m.a.s.l., 8 Aug 2000, FR, *Vicentini 1755* (INPA); Ponta Negra, 3° 2' 31” S, 60° 6' 0” W, 33 m.a.s.l., 8 Aug 2000, FL-FR, *Vicentini 1756* (INPA); Ponta Negra, 3° 2' 31” S, 60° 5' 59” W, 30 m.a.s.l., 8 Aug 2000, Sterile, *Vicentini 1757* (INPA); Ponta Negra, 3° 2' 30” S, 60° 5' 58” W, 38 m.a.s.l., 8 Aug 2000, Sterile, *Vicentini 1758* (INPA); Ponta Negra, 3° 2' 29” S, 60° 5' 59” W, 38 m.a.s.l., 8 Aug 2000, Sterile, *Vicentini 1759* (INPA); rio Negro, campina do Jauacoeara, 3° 03' 47” S, 60° 05' 48” W, 35 m.a.s.l., 20 Oct 1912, FR, *Ducke 12199* (F); Cachoeira do Mindú, 3° 6' 48” S, 60° 1' 31” W, 60 m.a.s.l., 28 Jan 1936, FL, *Ducke 35059* (F); Chapada, 3° 6' 48” S, 60° 1' 31” W, 60 m.a.s.l., 21 Mar 1958, FL, *Pessoal 6235INPA* (F, INPA); Estrada da Praia Dourada, Tarumazinho, 3° 2' 30” S, 60° 4' 0” W, 40 m.a.s.l., 29 Jun 1976, FR, *Monteiro 1240* (INPA); igarapé de Santa Maria, 3° 6' 48” S, 60° 1' 31” W, 50 m.a.s.l., 14 Dec 1954, FL, *Chagas 386INPA* (F, US); Ponta Negra, 3° 2' 0” S, 60° 6' 0” W, 34 m.a.s.l., 17 Dec 1974, FL, *Gentry 13385* (MO); Ponta Negra, 3° 2' 0” S, 60° 6' 0” W, 34 m.a.s.l., 2 Dec 1960, FL, *Rodrigues 1987* (INPA); rio Negro, 3° 6' 48” S, 60° 1' 31” W, 50 m.a.s.l., Jan 1902, FL, *Ule 5999* (F); Santa Isabel do Rio Negro: 0° 21' 59” S, 64° 59' 48” W, 60 m.a.s.l., , ?, *Amaral 04* (INPA); **Bahia**. 1834, FL, *Blanchet 2188* (F); , ?, *Blanchet 684 (1062)* (BM, F); Barreiras: Cachoeira Acaba Vida, 12° 9' 10” S, 44° 59' 24” W, 452 m.a.s.l., 14 Jul 1983, FL, *Guedes 759* (HALCB); Cairu: 13° 22' 0” S, 38° 54' 0” W, 2 m.a.s.l., 28 Oct 1996, FR, *Guedes 4741* (HALCB); 13° 30' 0” S, 39° 3' 0” W, 1 m.a.s.l., 14 Aug 1993, FR, *Guedes snB* (HALCB); Fazenda Maramdiba, 13° 30' 0” S, 38° 3' 0” W, 2 m.a.s.l., 12 Aug 1993, Sterile, *Guedes snA* (HALCB); Ilha de Tinharé, Morro de São Paulo, caminho teatro, 13° 23' 0” S, 38° 54' 0” W, 2 m.a.s.l., 13 Sep 1987, FR, *Guedes 1354* (HALCB); Ilha de Tinharé, Morro de São Paulo, 13° 23' 0” S, 38° 54' 0” W, 2 m.a.s.l., 20 Apr 1980, FR, *Gusmão 133* (HALCB); Ilha de Tinharé, Morro de São Paulo, 13° 23' 0” S, 38° 54' 0” W, 2 m.a.s.l., 20 Apr 1980, FL, *Gusmão 463* (HALCB); Ilha de Tinharé, Morro de São Paulo, entre Mangabeira e Gamboa, 13° 23' 0” S, 38° 54' 0” W, 2 m.a.s.l., 4 Oct 1996, FR, *Harley 28420* (HUEFS, MBM); Ilha de Tinharé, Morro de São Paulo, lagoa da fonte grande, 13° 23' 0” S, 38° 54' 0” W, 2 m.a.s.l., 9 Apr 1982, FL, *Gusmão 514* (CEPEC, HALCB, HUEFS, IBGE, INPA); Cairú: Praia da Mangabeira, 13° 23' 0” S, 38° 55' 0” W, 1 m.a.s.l., 7 Jul 1986, FL, *Guedes 1066* (HALCB); Praia da Mangabeira, 13° 23' 0” S, 38° 55' 0” W, 1 m.a.s.l., 10 Jul 1987, FL, *Guedes 1303* (HALCB); Camaçari: Jardim das Mangabeiras, 2.5 km W da estrada do Côco, 12° 43' 32” S, 38° 11' 12” W, 50 m.a.s.l., 24 Jun 2000, Buds-FR, *Vicentini 1521* (INPA); Jardim das Mangabeiras, 2.5 km W da estrada do Côco, 12° 43' 33” S, 38° 11' 11” W, 43 m.a.s.l., 24 Jun 2000, FL, *Vicentini 1526* (INPA, MO); Jardim das Mangabeiras, 2.5 km W da estrada do Côco, 12° 43' 27” S, 38° 11' 14” W, 42 m.a.s.l., 24 Jun 2000, Buds, *Vicentini 1527* (INPA, MO); Jardim das Mangabeiras, 2.5 km W da estrada do Côco, 12° 43' 26” S, 38° 11' 12” W, 44 m.a.s.l., 24 Jun 2000, Sterile, *Vicentini 1529* (INPA, MO); Rodovia que liga a BA-099 à Vila Parafuso, 12° 48' 0” S, 38° 21' 0” W, 6 m.a.s.l., 14 Jul 1983, FL, *Bautista 835* (IBGE); Entre Rios: Praia de Subaúma, 12° 13' 0” S, 37° 48' 0” W, 6 m.a.s.l., 8 Dec 1982, FL, *Araújo 372* (CEPEC, HALCB, HUEFS, IBGE); Ilhéus: 14° 49' 0” S, 39° 2' 0” W, 1 m.a.s.l., , Sterile, *Blanchet F776679* (F); Itanagra: Fazenda Brejo Verde, 12° 16' 0” S, 38° 3' 0” W, 65 m.a.s.l., 8 Dec 1979, FL-FR, *Gusmão 133b* (HALCB); Fazenda Brejo Verde, 12° 16' 0” S, 38° 3' 0” W, 65 m.a.s.l., 22 Jun 1975, FL-FR, *Gusmão 133c* (HALCB); Fazenda Brejo Verde, 12° 16' 0” S, 38° 3' 0” W, 65 m.a.s.l., 9 Aug 1975, FL-FR, *Gusmão 149* (IBGE, UNB); Fazenda Brejo Verde, 12° 16' 0” S, 38° 3' 0” W, 65 m.a.s.l., 8 Dec 1974, FL, *Gusmão sn* (HALCB); Jaguaribe: Fábrica da ODESA, 13° 7' 0” S, 38° 54' 0” W, 68 m.a.s.l., 8 Jul 1997, FL, *Guedes 5059* (HALCB); Lençóis: rio Ribeirão, 12° 34' 0” S, 41° 23' 0” W, 427 m.a.s.l., 16 May 1991, FR, *Cabral sn* (SPF); Maraú: 4 km do município, 14° 7' 0” S, 39° 0' 0” W, 3 m.a.s.l., 12 Mar 1977, FL, *Shepherd 4528* (SP); ca. 2 km do porto de Campinho, 13° 55' 1” S, 38° 58' 28” W, 9 m.a.s.l., 3 Jul 2000, FL-FR, *Vicentini 1628* (HUEFS, INPA, MO); Maraú/BR-0300, ca. 3 km ao N da cidade., 14° 6' 21” S, 39° 0' 25” W, 3 m.a.s.l., 5 Sep 1999, FR, *Carvalho 6761* (MO); Nazaré: Estrada Nazaré-Ilha de Itaparica, 5 km antes da ponte para a ilha, 13° 1' 49” S, 38° 49' 22” W, 19 m.a.s.l., 26 Jun 2000, FL, *Vicentini 1535* (INPA, MO); Estrada Nazaré-Ilha de Itaparica, 5 km antes da ponte para a ilha, 13° 1' 53” S, 38° 49' 29” W, 22 m.a.s.l., 26 Jun 2000, Buds-FR, *Vicentini 1537* (INPA, MO); Salvador: Ilha dos Frades, 12° 47' 0” S, 38° 39' 0” W, 1 m.a.s.l., 18 Oct 1995, FL-old, *Ribeiro SN* (HALCB); Vera Cruz, Aratuba, 12° 57' 0” S, 38° 36' 0” W, 1 m.a.s.l., 12 Nov 1996, FR, *Guedes 6616* (HALCB); São Sebastião do Passé: ao lado da Caraiba Metais., 12° 30' 45” S, 38° 29' 43” W, 37 m.a.s.l., 20 Oct 1998, FL, *Nascimento 179* (CEPEC, HALCB); Valença: estrada de Valença para Guaibim, ca. 2 km, 13° 19' 44” S, 39° 5' 25” W, 94 m.a.s.l., 26 Jun 2004, FR, *Fiaschi 2344* (CEPEC, MO); **Mato Grosso**. 10° 18' 0” S, 52° 34' 0” W, 305 m.a.s.l., 10 Nov 1977, FL, *Mileshi 1187* (IBGE); rio dos Peixes, 11° 21' 0” S, 57° 57' 0” W, 362 m.a.s.l., 29 Jul 1977, FR, *Silva 03* (IBGE); Comodoro: Chapada dos Parecis, BR-364, ca. 1-2 km N de Comodoro, 13° 38' 30” S, 59° 47' 58” W, 626 m.a.s.l., 24 Jul 2000, FR, *Vicentini 1642* (INPA, MO); Chapada dos Parecis, BR-364, ca. 1-2 km N de Comodoro, 13° 38' 27” S, 59° 47' 58” W, 622 m.a.s.l., 24 Jul 2000, FR, *Vicentini 1644* (INPA, MO); Chapada dos Parecis, BR-364, ca. 1-2 km N de Comodoro, 13° 38' 26” S, 59° 48' 0” W, 617 m.a.s.l., 24 Jul 2000, FR, *Vicentini 1646* (INPA, MO); Chapada dos Parecis, BR-364, ca. 1-2 km N de Comodoro, 13° 53' 20” S, 59° 45' 48” W, 615 m.a.s.l., 24 Jul 2000, FL, *Vicentini 1640* (INPA); Chapada dos Parecis, BR-364, ca. 1-2 km N de Comodoro, 13° 53' 30” S, 59° 45' 48” W, 589 m.a.s.l., 24 Jul 2000, Sterile, *Vicentini 1654* (MO); rio 12 de Outubro, ca. 80 km N de Comodoro, 12° 50' 0” S, 59° 45' 0” W, 487 m.a.s.l., 24 Apr 1977, FR, *Oliveira 188* (IBGE); Nova Mutuni: rio Arinos, 13° 57' 0” S, 56° 15' 0” W, 382 m.a.s.l., 21 Sep 1978, FL, *Amaral 148* (IBGE); Vale do Guaporé: 13° 55' 0” S, 59° 37' 0” W, 513 m.a.s.l., 10 Apr 1978, FR, *Amaral 43* (IBGE); **Pará**. 1° 38' 05” S, 48° 16' 13” W, 47 m.a.s.l., Mar 1944, FR, *Kappler 1416* (MO, P); 0° 52' 23” S, 47° 59' 48” W, 23 m.a.s.l., 1929, FL, *Miles 32* (F, US); , FL, *Miles SN1* (BM); 1919, FL, *Miles SN2* (BM); 1750, FL, *Sellow sn* (US); Estrada de Pinheiros, Suyana, 27 Feb 1902, FR, *Ducke 2601* (F); Belém: 1° 27' 0” S, 48° 29' 0” W, 1 m.a.s.l., Apr 1929, FR, *Dahlgren 429* (F); 1° 27' 0” S, 48° 29' 0” W, 1 m.a.s.l., Apr 1929, FR, *Dahlgren 741* (F); Belém-Tocantins, , ?, *Cid sn1* (INPA); Belém-Tocantins, , ?, *Cid sn2* (INPA); Guamá, 01° 30' 61” S, 48° 22.8' 24” W, 1 m.a.s.l., , ?, *Cid 12140* (INPA); Guamá, 1 m.a.s.l., , ?, *Cid sn6* (INPA); Colares: 00° 56' 00” S, 48° 17' 00” W, 1 m.a.s.l., 1832, FR, *Poeppig 2934* (F); Itaituba: Serra do Cachimbo, aeroporto, 8° 30' 0” S, 55° 0' 0” W, 390 m.a.s.l., 19 Jul 1977, FR, *Benson 92137INPA* (INPA); Jacarecanga: rio Cururú, Lago da Cigana, 7° 12' 0” S, 58° 3' 0” W, 140 m.a.s.l., 29 Jan 1960, FL, *Egler 1198* (MAC); Oueiras: 2° 7' 56” S, 49° 57' 57” W, 1 m.a.s.l., , ?, *Cid 11995* (INPA); 2° 7' 56” S, 49° 57' 57” W, 1 m.a.s.l., , ?, *Cid 12026* (INPA); Tucuruí: 16 km E of Represa Tucuruí, rio Tocantins, 3° 45' 0” S, 49° 39' 0” W, 70 m.a.s.l., 18 Mar 1980, FR, *Plowman 9747A* (F, IBGE, INPA, MO, NY, UNB); rio Tocantins, 4° 25' 0” S, 49° 32' 0” W, 27 m.a.s.l., 10 Dec 1979, FL, *Silva 207* (IBGE, INPA); Vigia do Nazareth: 00° 50' S, 48° 07' W, 1 m.a.s.l., , ?, *Cid 11815* (INPA); 36 km SE of Vigia along PA-140 to Belém, 1° 3' 0” S, 48° 7' 0” W, 50 m.a.s.l., 29 Mar 1980, FR, *Davidse 17529* (INPA, MO, NY, UNB); Ilha de Colares, 0° 55' 0” S, 48° 13' 0” W, 1 m.a.s.l., 30 Sep 1954, ?, *Black 5416949* (P); Perto da Campina de São Benedito, 0° 48' 0” S, 48° 8' 0” W, 1 m.a.s.l., 15 Oct 1978, Buds, *Teixeira 46* (INPA); Route de Belém á Viguié, 0° 48' 0” S, 48° 8' 0” W, 1 m.a.s.l., 6 Apr 1961, ?, *Aubreville 196* (P); **Rondônia**. Vilhena: km 3-4 da BR Vilhena-Porto Velho, 12° 43' 43” S, 60° 11' 26” W, 582 m.a.s.l., 26 Jul 2000, FR, *Vicentini 1667* (INPA);

km 3-4 da BR Vilhena-Porto Velho, 12° 43' 44” S, 60° 11' 26” W, 537 m.a.s.l., 26 Jul 2000, FL-FR, *Vicentini 1669* (INPA); km 3-4 da BR Vilhena-Porto Velho, 12° 43' 49” S, 60° 11' 26” W, 528 m.a.s.l., 26 Jul 2000, Sterile, *Vicentini 1671* (MO); km 3-4 da BR Vilhena-Porto Velho, 12° 43' 50” S, 60° 11' 26” W, 515 m.a.s.l., 26 Jul 2000, FR, *Vicentini 1672* (INPA); **Roraima**. Boa Vista: estrada para Colônia Apiaui, 02° 50' N, 60° 40' W, 76 m.a.s.l., 7 Aug 1986, FR, *Silva 657* (MO, NY); Cantá: , ?, *Cid sn3* (INPA); , ?, *Cid sn4* (INPA); Bonfim, margem da estrada para o Cantá, 02° 50' N, 60° 35' W, 83 m.a.s.l., 1 Aug 1986, FL, *Sette 630* (MO, NY); Caracaraí: estrada da Perdida, 4 km da BR-174, 1° 28' 42” N, 60° 58' 8” W, 86 m.a.s.l., 7 Aug 2000, Sterile, *Vicentini 1743* (INPA); estrada da Perdida, 4 km da BR-174, 1° 28' 43” N, 60° 58' 9” W, 69 m.a.s.l., 7 Aug 2000, Sterile, *Vicentini 1744* (INPA); estrada da Perdida, 4 km da BR-174, 1° 28' 50” N, 60° 58' 8” W, 74 m.a.s.l., 7 Aug 2000, Sterile, *Vicentini 1745* (INPA); estrada da Perdida, 4 km da BR-174, 1° 28' 47” N, 60° 58' 8” W, 70 m.a.s.l., 7 Aug 2000, Sterile, *Vicentini 1747* (INPA); estrada da Perdida, 2 km da BR-174, 1° 28' 45” N, 60° 58' 8” W, 78 m.a.s.l., 7 Aug 2000, Sterile, *Vicentini 1748* (INPA); Rodovia Perimetral Norte, 53 km de Caracaraí para Amapá, Caatinga do Anauá, 0° 1' 27” N, 60° 42' 0” W, 96 m.a.s.l., 29 Jun 1974, Sterile, *Pires 14810* (INPA); Roranópolis: margem da BR-174, alguns km ao N da linha do Equador, 0° 19' 46” N, 60° 31' 18” W, 84 m.a.s.l., 6 Aug 2000, Sterile, *Vicentini 1720* (INPA); margem da BR-174, alguns km ao N da linha do Equador, 0° 19' 49” N, 60° 31' 15” W, 85 m.a.s.l., 6 Aug 2000, Sterile, *Vicentini 1721* (INPA); margem da BR-174, alguns km ao N da linha do Equador, 0° 19' 47” N, 60° 31' 15” W, 93 m.a.s.l., 6 Aug 2000, Sterile, *Vicentini 1722* (INPA); margem da BR-174, alguns km ao N da linha do Equador, 0° 19' 46” N, 60° 31' 17” W, 82 m.a.s.l., 6 Aug 2000, Sterile, *Vicentini 1723* (INPA); margem da BR-174, alguns km ao N da linha do Equador, 0° 19' 44” N, 60° 31' 17” W, 86 m.a.s.l., 6 Aug 2000, Sterile, *Vicentini 1725* (INPA); margem da BR-174, alguns km ao N da linha do Equador, 0° 19' 52” N, 60° 31' 16” W, 83 m.a.s.l., 6 Aug 2000, Sterile, *Vicentini 1727* (INPA); margem da BR-174, alguns km ao N da linha do Equador, 0° 19' 51” N, 60° 31' 17” W, 83 m.a.s.l., 6 Aug 2000, FL-old, *Vicentini 1728* (INPA); **Sergipe**. Pirambu: 10° 44' 30” S, 36° 51' 0” W, 1 m.a.s.l., 9 Jan 1977, FL, *Fonseca sn* (IPA); 2 km após a entrada para S. José, 10° 44' 30” S, 36° 51' 0” W, 1 m.a.s.l., 10 Dec 1981, FL, *Viana 303* (IPA); São Cristovão: 11° 10' 0” S, 37° 10' 0” W, 47 m.a.s.l., 13 Nov 1981, FR, *Carneiro 175* (IPA); 11° 10' 0” S, 37° 10' 0” W, 47 m.a.s.l., 2 Dec 1981, FL, *Viana 267* (IPA); **COLOMBIA**. **Amazonas**. Vichada: Estero El Retorno, 20 km E de El Tigre, 150 m.a.s.l., 14 Mar 1971, FR, *Pinto 1255* (COL); **GUYANA**. 1821, FL, *Perrittez SN* (P); **Potaro-Siparuni**. Kaieteur plateau, 5° 9' 30” N, 59° 27' 0” W, 712 m.a.s.l., 2 May 1944, FR, *Maguire 1944* (MO); **Upper Demerara-Berbice**. 60 km N on Mabura Hill-Linden hwy., 5° 50' 0” N, 58° 30' 0” W, 60 m.a.s.l., 4 Jan 1996, FL, *Clarke 772* (MO); Demerara river, 6° 48' 0” N, 58° 10' 0” W, 1 m.a.s.l., Jan 1896, FL, *Jenman 6859* (NY); Rockstone, 5° 59' 0” N, 58° 33' 0” W, 6 m.a.s.l., 20 Jul 1921, FR, *Gleason 540* (NY); **West Demerara**. 6° 29' 55” N, 58° 13' 9” W, 5 m.a.s.l., 20 May 1997, ?, *Taylor 12079* (MO); **GUYANE FRANÇAISE**.4° 35' 12” N, 52° 18' 24” W, 13 m.a.s.l., 20 Nov 1914, ?, *Benoist 1308* (P); 4° 38' 50” N, 52° 12' 20” W, 3 m.a.s.l., 10 Jan 1914, ?, *Benoist 559* (P); 4° 40' N, 52° 13' W, 3 m.a.s.l., 19 Oct 1913, ?, *Benoist 64* (P); 4° 38' 49.08” N, 52° 12' 24” W, 3 m.a.s.l., 14 Jun 1921, ?, *Godebert 309* (P); 4° 36' 58” N, 51° 14' 42” W, 7 m.a.s.l., ?, *Herb 383* (F); 4° 51' 39” N, 52° 28' W, 6 m.a.s.l., 1792, ?, *Leblond SN* (P); 4° 52' 06” N, 52° 28' 05” W, 5 m.a.s.l., 1839, FL, *Leprieur F776442* (F); 4° 50' 32” N, 52° 28' 23” W, 4 m.a.s.l., 1838, FL, *Leprieur sn* (P); 4° 49' 50” N, 52° 29' W, 3 m.a.s.l., 1840, FL, *Leprieur snA* (P); 5° 41' 23” N, 53° 52' 24” W, 1 m.a.s.l., 1842, ?, *Melinon 127* (P); 4° 43' 49” N, 52° 34' 16” W, 30 m.a.s.l., Jun 1824, FR, *Poiteau H20010176735K* (K); Cayenne, 4° 53' 0” N, 52° 25' 0” W, 5 m.a.s.l., 1835, ?, *Leprieur snB* (F, P); Cayenne, 4° 53' 0” N, 52° 25' 0” W, 5 m.a.s.l., , ?, *Lheritier SN* (F); montagne des Trois Pitons., 4° 13' 0” N, 51° 51' 0” W, 114 m.a.s.l., 9 Jun 1980, FR, *Moretti 1161* (P); Iracoubo, Village Bellevue, 5° 28' 0” N, 53° 16' 0” W, 1 m.a.s.l., 3 Dec 1978, FL, *Sastre 6395* (P); Maroni, 5° 30' 0” N, 54° 2' 0” W, 6 m.a.s.l., 1862, FR, *Melinon 337* (BM, P); Montagnes de la Trinité, 4° 21' 49” N, 53° 21' 49” W, 500 m.a.s.l., 17 Jan 1984, Sterile, *Granville 6091* (MO); R.N. 19 km de Kourou vers Sinnamary., 5° 12' 0” N, 52° 46' 0” W, 16 m.a.s.l., 20 Sep 1977, FR, *Sastre 5993* (US); Saint Laurent-du-Maroni, 5° 30' 0” N, 54° 2' 0” W, 6 m.a.s.l., 26 Nov 1950, FL, *Service 5124* (P); Saint Laurent-du-Maroni, Malgaaber, 5° 30' 0” N, 54° 2' 0” W, 6 m.a.s.l., 16 Jan 1950, FR, *Service 5051* (P); Savane de Kouron, 5° 12' 0” N, 52° 46' 0” W, 16 m.a.s.l., 24 Jul 1962, ?, *Hallé 461* (P); **PERU**. , FL, *Poeppig F612177* (F); **SURINAME**. 5° 19' 0” N, 55° 16' 00” W, 65 m.a.s.l., 10 Jan 1917, FL, *Herb 2610* (NY, US); **Brokopondo**. Brownsweg, 4° 53' 0” N, 55° 13' 0” W, 332 m.a.s.l., 7 Dec 1926, FR, *Zaandam 6957HERB* (K); along rd from Afobakka to Brownsweg, 5° 25' 54” N, 55° 05' 38” W, 22 m.a.s.l., 19 Feb 1965, Sterile, *Lems 5232* (NA); **Para**. Zanderij, 5° 27' 55” N, 55° 10' 46” W, 16 m.a.s.l., 10 Apr 2002, FR, *Vicentini 2040* (INPA); Zanderij, 5° 28' 6” N, 55° 10' 48” W, 15 m.a.s.l., 10 Apr 2002, FR, *Vicentini 2041* (INPA); Zanderij, 5° 27' 26” N, 55° 10' 34” W, 22 m.a.s.l., 10 Apr 2002, FR, *Vicentini 2042* (INPA); **Saramaca**. Wayombo river, 5° 26' 0” N, 56° 2' 0” W, 10 m.a.s.l., Sep 1945, ?, *Stahel 355* (MO, NY).

31. *Pagamea diceras* Steyerm.

Specimens measured — **VENEZUELA**. **Amazonas**. Manapiare: Serrania Parú, río Parú, Caño Asisa, 4° 30' 32” N, 65° 48' 0” W, 2000 m.a.s.l., 4 Feb 1951, Buds, *Cowan 31241* (K, NY, US, VEN); Serrania Parú, río Parú, Caño Asisa, 4° 30' 32” N, 65° 48' 0” W, 2000 m.a.s.l., 31 Jan 1951, FL, *Cowan 31088* (NY).

32. *Pagamea puberula* Steyerm.

Specimens measured — **BRASIL**. **Amazonas**. Manaus: PDBFF, 0.5 km S of SE border of Reserva 3402, 2° 25' 0” S, 59° 54' 0” W, 100 m.a.s.l., 25 Feb 1992, FR, *Nee 42631* (MO, NY); Presidente Figueiredo: Manaus-Caracaraí rd, km 183, 3° 7' 12” S, 60° 1' 12” W, 34 m.a.s.l., 4 Apr 1975, FR, *Loureiro 48420INPA* (INPA, US); Rio Preto da Eva: Manaus-Itacoatiara, km 138, 3° 1' 12” S, 60° 1' 12” W, 53 m.a.s.l., 10 Jun 1972, FR, *Monteiro 84* (INPA, US); **Pará**. Faro: Campos a E de Faro, 2° 8' 0” S, 56° 43' 59” W, 29 m.a.s.l., 21 Aug 1907, FL-old, *Ducke 8462* (F, US); Região dos campos a E de Faro, 2° 8' 0” S, 56° 43' 59” W, 29 m.a.s.l., 6 Feb 1910, FL-old, *Ducke 10654* (F); Oriximiná: Campos de Ariramba, entre os rio Jaramacaru e Igarapé Mutum, 1° 10' 0” S, 55° 35' 0” W, 269 m.a.s.l., 4 Dec 1987, FR, *Cid 9735* (INPA, MO, NY); Campos de Ariramba, rio Jaramacarú., 1° 13' 5” S, 55° 11' 0” W, 100 m.a.s.l., 8 Jun 1980, FR, *Martinelli 6867* (INPA, MO, NY, UNB); Campos de Ariramba, rio Jaramacarú, cachoeira do Jaramacarú, 1° 13' 5” S, 55° 10' 30” W, 195 m.a.s.l., 7 Dec 1987, FL, *Martinelli 12331* (F, INPA, MO, NY); Região do Alto Ariramba, campina da cachoeira Jerminus, 1° 10' 0” S, 55° 35' 30” W, 274 m.a.s.l., 9 Dec 1910, FL, *Ducke 11401* (F); Região do Alto Ariramba, campina do Jaramacarú, 1° 10' 20” S, 55° 35' 10” W, 272 m.a.s.l., 2 Dec 1910, FL, *Ducke 11284* (F); Região do Alto Ariramba, perto do Jaramacarú, 1° 10' 0” S, 55° 35' 0” W, 269 m.a.s.l., 4 Dec 1910, FR, *Ducke 11338* (F).