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RAFAEL BARBOSA PINTO

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“*CYTOGENETIC AND TAXONOMIC STUDIES IN BRAZILIAN SPECIES OF Swartzia* Schreb. *(LEGUMINOSAE-PAPILIONOIDEAE)*”

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RAFAEL BARBOSA PINTO

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Orientadora: Profa. Dra. Eliana Regina Forni Martins

Co-orientador: Dr. Vidal de Freitas Mansano

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Dissertação de Mestrado apresentada ao Programa de Pós-Graducação em Biologia Vegetal do Instituto de Biologia da Universidade Estadual de Campinas para obtenção do título de Mestre em Biologia Vegetal.

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BANCA EXAMINADORA

Profa. Dra. Eliana Regina Forni Martins (Orientadora)

Eliana R Forni Martins

Assinatura

Profa. Dra. Ana Maria Goulart de Azevedo Tozzi

Ana M G Azevedo Tozzi

Assinatura

Prof. Dr. Itayguara Ribeiro da Costa

Itayguara Ribeiro da Costa

Assinatura

Prof. Dr. Ricardo Augusto Lombello

Assinatura

Dra. Nair Dhamer

Assinatura

Dedico este trabalho ao meu querido filho Samuel Aram que carrega em seus cromossomos parte dos meus...

“Sou eu moléculas orgânicas que ganharam vida
Milhares e milhares de cadeias peptídicas
Probabilidades de eventos reunidas.
Sou eu talvez a massa escura vista de outro planeta
Talvez seja a Terra para Vênus um cometa
A imagem transtornada por uma retina preta.
Sou eu, um denso espaço vazio ambulante
Um ser predestinado a ser um caminhante
Parte da história da evolução errante.
Sou eu encontros e desencontros do negativo e positivo
Espírito encarnado em estado sensitivo
Até onde sei, vivo.”
(Rafael B Pinto)

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SUMÁRIO

RESUMO

Swarzia é um gênero basal da subfamília Papilionoideae (Leguminosae). Apesar do seu posicionamento ter gerado debate entre muitos autores no passado, estudos sistemáticos recentes confirmam a monofilia de *Swartzia,* compondo o clado swartzióide juntamente com mais sete gêneros. A diversidade morfológica e a ampla distribuição geográfica na região neotropical tornam o gênero um interessante objeto de estudos taxonômicos e sistemáticos. Embora *Swartzia* apresente centro de diversidade amazônico, também possui alta riqueza de espécies na região extra-amazônica, apresentando complexos de espécies, com difícil delimitação morfológica de alguns táxons, necessitando de ferramentas adicionais para uma melhor compreensão da evolução no grupo. A citogenética, mediante estudos cromossômicos, fornece informações importantes na elucidação de relações supra e infra genéricas e, através de uma abordagem citotaxonômica, pode contribuir para o esclarecimento de problemas sistemáticos e taxonômicos. O presente trabalho visa ampliar os estudos do gênero, contribuindo com um inédito estudo citogenético e ampliando estudos taxonômicos das *Swartzia* na região extra-amazônica brasileira. Para o capítulo 1 foram coletadas sementes de 18 espécies distribuídas no território brasileiro para análise cromossômica e no capítulo 2 é apresentado um estudo taxonômico de *Swartzia* na região extra-amazônica brasileira, com chave de identificação. *Swartzia* apresentou número cromossômico constante entre as espécies analisadas ($2n=2x=26$). Entretanto, *S. leptopetala* demonstrou potencial de autopoliploidização ao apresentar sementes $2n=2x=26$ e $2n=4x=52$ numa mesma árvore, configurando processos de poliploidização em meristemas isolados. O tamanho dos cromossomos (tamanho relativo dos cromossomos e comprimento total de cromatina - TCL) foram medidos para todas as 18 espécies coletadas. No geral, os cromossomos são pequenos, sendo o menor cromossomo encontrado em *S. acuminata* (0.25µm), enquanto o maior foi encontrado em *S. euxylophora* (1.41µm). Os números de bandas $CMA^+/DAPI^-$ (2) e sítios de rDNA 45S (2) e 5S (2) também não apresentaram variação interespecífica. *Swartzia euxylophora*, cuja inclusão no gênero havia sido anteriormente questionada, apresentou as características citogenéticas semelhantes às demais *Swartzia* e, somadas à morfologia observada em campo, sustentam o posicionamento do táxon dentro do gênero. Os dados cariotípicos (número e tamanho cromossômicos, e número de bandas CMA/DAPI e de genes ribossomais) não permitem a diferenciação das espécies em nível de sessão. Até o momento são disponibilizadas informações cromossômicas para cerca de 10% das *Swarztia*, não sendo possível sugerir mecanismos de evolução cariotípica no gênero. Mediante a análise dos dados citogenéticos fornecidos neste trabalho e disponíveis na literatura é possível afirmar que os gêneros do clado swartzióide apresentam números cromossômicos diferentes, sendo este um caráter diagnóstico. No capítulo 2, os estudos taxonômicos para as *Swartzia* extra-amazônicas resultaram na descrição de cinco novas espécies e na elaboração de uma chave de identificação para táxons da região. Quatro delas, *S. alagoensis*, *S. arenophila*, *S. revoluta* e *S. submontana*, pertencem à seção *Acutifoliae* que se destaca por possuir alta diversidade e por ser exclusivamente brasileira. *Swartzia thomasii* pertence à seção *Glabriplantae*, anteriormente uma seção exclusivamente amazônica.

Palavras-chave: Poliploidia, Hibridização in situ fluorescente, taxonomia, Fabaceae

ABSTRACT

Swartzia is a basal genus of subfamily Papilionoideae (Leguminosae). Although the positioning of the genus has been a controversial issue among some authors in the past, recent systematic studies confirm the monophily of *Swartzia* as being part of a swartzioid clade with other seven genera. The morphological diversity and the widespread geographical distribution at the Neotropical region, make the genus an interesting object of taxonomic and systematic studies. Although *Swartzia* present an amazonian diversity center, it also has high species richness at extra-amazonian region, presenting species complex, with hard morphological delimitation of some taxa, requiring additional tools for a better comprehension of evolution within the group. Cytogenetics, by studying chromosomes, provides important informations for elucidating supra- and infrageneric relations and, by a citotaxonomic approach, it can contribute to solve systematic and taxonomic problems. The present study aims to increase the studies of the genus, contributing with an inedit cytogentic study and extending taxonomic studies of Brazilian extra-amazonian *Swartzia*. For chapter 1, there were collected 18 species distributed through Brazilian territory for chromosomal analyses and in chapter 2 we presenting a taxonomic study of *Swartzia* in extra-Amazonian region of Brazil with a description key. *Swartzia* presented a conservated chromosome number among species (2n=2x=26). However, *S. leptopetala* demonstrated an autopolyploidization potential, presenting seeds with 2n=2x=26 and 2n=4x=52 in the same tree, being a polyploidization process in isolated meristems. Chromosome length (relative chromosome length and total chromatin length - TCL) were measured for all 18 species collected. In general, *Swartzia* chromosomes are small, being the shortest chromosome found in *S. acuminata* (0.25µm) and the longest in *S. euxylophora* (1.41µm). The number of $CMA^+/DAPI^-$ bands (2) and rDNA sites 45S (2) and 5S (2) did not present interspecific variation too. *Swartzia euxylophora*, which the inclusion in the genus was questioned, presented all cytogentics characteristics similar to all other analyzed *Swartzia* and togheter with morphological features observed in the field, it supports the taxon as belonging to the genus. The karyotypic data (number and size of chromosomes, and number of CMA/DAPI and ribosomal genes) do not allow the differentiation of species at section level. Until now, there is chromosomal information for about 10% of *Swartzia* species available, not being possible suggest karyotypic evolution mechanisms in the genus. By analyzing cytogentic data provided by this study and available in the literature, it is possible to say that genera in swartzioid clade have different chromosome number, being a diagnostic character. In chapter 2, the taxonomic studies of extra-Amazonian *Swartzia* resulted in a description of five new species and the elaboration of a reginal key for the regional taxa. Four of them, *S. alagoensis*, *S. arenophila*, *S. revoluta* and *S. submontana*, belong to section *Acutifoliae*, which stands out for having high diversity and for be exclusively Brazilian. *Swartzia thomasii* belongs to section *Glabriplantae*, otherwise an exclusively Amazonianian section.

Key-words: Polyploidy, Fluorescent in situ hybridization, taxonomy, Fabaceae

INTRODUÇÃO GERAL

A família Leguminosae é composta por aproximadamente 727 gêneros e 19.400 espécies, sendo considerada a terceira mais diversificada família de Angiospermae em número de espécies (Lewis *et al.* 2005). Diversos grupos integrantes da família são amplamente utilizados na alimentação humana e de animais domésticos, na utilização da madeira, em ornamentações e obtenção de fármacos de conhecimento tradicional ou para indústrias farmacêuticas (Ducke 1981; Lewis *et al.* 2005), tornando a família popularmente reconhecida e a segunda família de vegetais superiores de maior importância econômica, ficando atrás apenas de Poaceae (Wojciechowski *et al.* 2004). A família também exerce uma importante função ecológica, uma vez que suas raízes são capazes de formar nódulos com bactérias fixadoras de nitrogênio, enriquecendo o solo e auxiliando no manejo e desenvolvimento da vegetação (Herrera *et al.* 1993; Franco & Faria 1997).

Atualmente a família é dividida em três subfamílias (Caesalpinoideae, Mimosoideae e Papilionoideae) e apresenta uma distribuição cosmopolita, comportando uma rica diversidade de espécies, hábitos e ambientes de ocorrência (Lewis 1987; Lewis *et al.* 2005). Apesar de extensa, muitos esforços têm sido feitos para uma melhor compreensão da sistemática e evolução da família e, nos últimos anos, o uso da biologia molecular tem contribuído para esclarecer e/ou confirmar hipóteses sistemáticas e evolutivas (Doyle *et al.* 2000; Wojciechowski 2003; Lavin *et al.* 2004; Wojciechowski *et al.* 2004).

Dentre as três subfamílias, Mimosoideae e Papilionoideae são monofiléticas, porém a subfamília Caesalpinoideae, que contém os grupos basais de Leguminosae, é parafilética e a sua relação com as Papilionoideae ainda é pouco compreendida (Doyle *et al.* 2000; Wojciechowski *et al.* 2004). Um exemplo desta complicada relação é o posicionamento da tribo Swartzieae dentro da família, tendo sido considerada integrante das Caesalpinoideae por alguns taxonomistas (Burkart 1943; Cowan 1967; Pettigrew & Watson 1977). Contudo, estudos moleculares indicam o posicionamento dos gêneros da tribo na base da subfamília Papilionoideae (Herendeen 1994; Wojciechowski 2003).

Polhill (1994) circunscreveu a tribo Swartzieae como sendo composta por 15 gêneros neotropicais que compartilhavam cálice inteiro no botão floral. Também apresentavam a corola não papilionácea (freqüentemente composta de uma única pétala) e geralmente estames numerosos, que em vários gêneros, como *Swartzia* e *Ateleia* (DC.) Benth., estão associados com um meristema circular durante a ontogenia dos estames. Tal estrutura está associada ao elevado número de estames (Tucker 2003).

Estudos moleculares concluíram que apesar de estar correta a inserção da tribo na subfamília Papilionoideae, alguns genêros estariam mais proximamente relacionados com as tribos Dalbergieae, Dipterygeae e Sophoreae, tornando a tribo polifilética (Doyle *et al.* 1997; Pennington *et al.* 2001; Wojciechowski *et al.* 2004). Estes estudos encontraram consistentemente um clado swartzióide, composto por *Swartzia* e outros cinco gêneros: *Ateleia* (20 espécies), *Bobgunnia* J.H. Kirkbr. & Wiersema (2 espécies segregadas de *Swartzia,* Kirkbride & Wiersema 1997), *Bocoa* Aubl. (3 espécies), *Cyathostegia* (Benth.) Schery (1 espécie) e *Trischidium* Tul. (5 espécies segregadas de *Bocoa*, Ireland 2007). Torke & Schaal (2008), através de uma extensa análise molecular com 77 espécies de *Swartzia* e representantes de gêneros relacionados, confirmaram a monofilia do clado swartzióide (Fig.1), sugerindo a ausência de uma ordem unidirecional na ontogenia dos estamens como uma possível sinapomorfia do clado e sustentaram a segregação das espécies de *Swartzia* e *Bocoa* citadas acima. Os autores também sustentaram a elevação de *Swartzia panamensis* a um gênero monotípico, chamado de *Fairchildia*, primeiramente proposto por Britton & Rose (1930), baseado na morfologia dos frutos e na posição da inflorescência, sustentando *Swartzia* como um gênero monofilético.

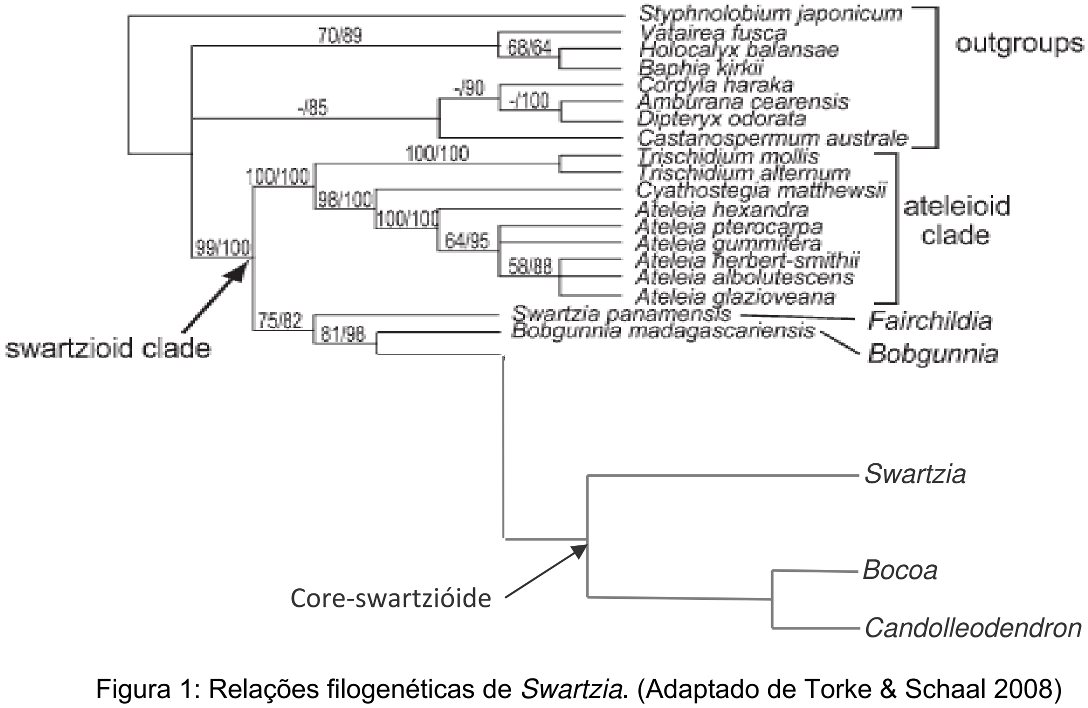

Figura 1: Relações filogenéticas de *Swartzia*. (Adaptado de Torke & Schaal 2008)

Swartzia compreende cerca de 180 espécies, sendo o maior gênero do clado swartzióide. Suas espéies estão amplamente distribuídas no neotrópico (Fig.2), principalmente em terras baixas, desde a província de Noyarit na costa do Pacífico, no México até o norte do estado do Paraná, no Brasil (Cowan 1967; Torke & Mansano 2009). As espécies de *Swartzia* estão distribuídas nos mais diversos biomas, porém são especialmente comuns e diversas nas florestas de terras baixas do norte da América do Sul (Torke & Schaal 2008; Torke & Mansano 2009), especialmente na Bacia Amazônica e Escudo das Guianas. No Brasil o gênero ocorre principalmente na Floresta Amazônica, porém possui representantes na Caatinga, Cerrado, Mata Atlântica e Pantanal (Mansano *et al.* 2012).

Figura 2: Distribuição de *Swartzia* na região neotropical. (adaptado de Torke & Mansano 2009b)

As espécies de *Swartzia* podem ser desde arbustos a grandes árvores de dossel (Fig.3: A), com folhas compostas imparipinadas, unifolioladas a plurifolioladas com margem inteira e folíolos opostos (alternos em *S. alternifoliolata* - Mansano & Tozzi 1999) . O gênero se destaca por sua morfologia peculiar para a família, especialmente devido ao cálice inteiro no botão floral, e corola monopétala ou apétala (Fig.3: B,C) , que apesar de singulares, são características aparentemente plesiomórficas, tendo se originado cedo na evolução do clado swartzióide (Torke & Schaal 2008), pois ocorre também nos gêneros *Ateleia*, *Bobgunnia*, *Bocoa* (sempre apétala), *Candolleodendron*, *Cyathostegia* e *Trischidium*. As flores também apresentam estames dimórficos (trimórfico em *S. trimorphica* - Mansano & Souza 2004) e gineceu estipitado, com algumas poucas espécies apresentando mais de um carpelo (Cowan 1967; Torke & Mansano 2009; Pinto *et al.* 2012). Uma possível sinapomorfia morfológica do gênero seria a presença de seiva aquosa nos troncos e ramos, que se torna avermelhada quando exposta (Fig.1: E). Esta característica é encontrada em diversas outras Leguminosae, porém só é encontrada em *Swartzia* dentro do clado swartzióide (Torke & Schaal 2008).

Os frutos e sementes de *Swartzia* apresentam grande diversidade morfológica entre as espécies (Cowan 1967; Torke & Mansano 2009). Estes podem ser folículos ou legumes e apresentar de uma a várias sementes (Fig.1: D,F). Também são bem variados quanto à coloração, presença de pilosidade e formatos. As sementes são geralmente ariladas (Fig.1 G), porém, o arilo está ausente em algumas espécies (Fig.1: H) como *S. arenophila*, *S. bahiensis*, *S. glazioviana*, *S. pickellii*, *S. pinheiroana* e *S. revoluta* (Pinto *et al.* 2012). A presença e ausência do arilo no gênero gerou uma interpretação equivocada na classificação de Herendeen (1994), que separou o gênero em dois ramos em sua filogenia, baseado na ocorrência do arilo. Torke & Schaal (2008) demonstraram que apenas *S. panamensis* (hoje tratada como *Fairchildia*), com ausência completa do arilo, formava um grupo a parte.

A monografia de Cowan (1967) catalogou e descreveu amplamente a diversidade do gênero no neotrópico, totalizando 127 espécies. Entretanto, com a observação de materiais adicionais é possível identificar alguns equívocos na delimitação das espécies assim como lacunas geográficas onde o gênero ainda não foi amostrado. Cowan (1967) dividiu *Swartzia* em duas seções, duas subseções e oito séries e apesar de estes grupamentos subgenéricos serem criados para facilitarem as identificações das espécies, não necessariamente delimitam grupos monofiléticos. O autor pretendia ordenar as espécies de *Swartzia* em complexos de espécies e para isso, ele assumiu que as seguintes características eram ancestrais dentro do gênero: tricomas simples, raque alada, uma única pétala, múltiplos carpelos, ovário e estilete não diferenciado, ovário alongado e estames dimórficos, com vários estames grandes. Por outro lado, ele considerou derivados os estados opostos dos mesmos caracteres: tricomas compostos, raque não alada, ausência de pétala, um único carpelo, ovário e estilete claramente diferenciados e altamente desiguais no tamanho, estilete lateral, ovário amplamente elipsóide e estames isomórficos ou com poucos estames grandes. Apesar desta hipótese de polarização dos caracteres, Cowan (1967) foi incapaz de propor uma hipótese de relação entre os principais complexos de *Swartzia*. Além disso, deixou certa quantidade de ambigüidade nos limites destes complexos em suas chaves para o gênero, colocando em alguns momentos a mesma espécie em mais de um grupo subgenérico.

Torke & Mansano (2009) apresentaram uma consistente hipótese de divisão subgenérica para *Swartzia* propondo 15 seções, sendo a seção *Possira* a mais amplamente distribuída geograficamente quase coincidindo com a distribuição de todo o gênero. A seção *Possira* também apresenta táxons com descontinuidades de ocorrência e características morfológicas associadas. Um exemplo é o que ocorre com o complexo *Swartzia simplex* var. *grandiflora* que se distribui em três regiões descontínuas: América Central, nordeste da Bolívia e Peru e no Brasil (do estado da Bahia ao estado de São Paulo). Esta espécie é suspeita de possuir origem híbrida (Mansano comm. pers.), principalmente os morfotipos do nordeste e sudeste brasileiro, devido às semelhanças morfológicas entre este possível híbrido trifoliolado e os supostos parentais: *S. simplex* var. *continentalis* com folhas unifolioladas e *S. myrtifolia* var. *elegans* com folhas de penta a enefolioladas. Destaca-se também a seção *Acutifoliae* por ser exclusivamente brasileira. A seção apresenta intrigantes casos de complexos de espécies. *Swartzia flaemingii* e *S. oblata* são reconhecidas como espécies diferentes nos herbários, entretanto, características morfológicas importantes para distinção das mesmas apresentam continuidade, necessitando de ferramentas adicionais para distinção ou união dos táxons.

Após Cowan (1967), diversos estudos vêm tentando suprir a grande demanda taxonômica que o gênero exige, justamente devido a sua grande riqueza e potencial de estabelecimento em diferentes habitats. Sinônimos e novas espécies têm sido propostos (Cowan 1973, 1981, 1985; Barneby 1991, 1992, 1996; Pipoly & Rudas 1994; Sousa & Grether 2002; Mansano & Tozzi 1999, 2001; Mansano & Souza 2004, Torke 2004, Torke 2007a,b; Torke & Zamora 2010; Pinto *et al.* 2012), assim como estudos sobre a distribuição geográfica (Cuello and Cowan 1999; Ribeiro *et al.* 1999; Barneby & Heald 2002; Mansano & Tozzi 2004; Mansano & Lima 2007).

Figura 3: A. Sapopemas de *S. polyphylla*; B. Exudato avermelhado de *S. micrantha*; C. Frutos e sementes de *S. leptopetala*; D. Flores de *S. arenophila*; E. Flores de *S. apetala*; F. Caulifloria em *S. cuspidata*; G. Semente de *S. thomasii*; H. Sementes de *S. arenophila* (Fotos A, B, D, E, F – R.B.Pinto; Fotos C, H – V.F.Mansano; Foto G – M.F.Otárola).

Uma das ferramentas biossistemáticas que vem sendo utilizada com sucesso no esclarecimento de questões taxonômicas e sistemáticas de alguns grupos é a citogenética (Guerra 1988; Stace 1989; Guerra 1990; Bernardos *et al.* 2004). Esta, através da investigação celular que compreende todo e qualquer estudo relativo ao cromossomo isolado ou em conjunto, condensado ou distendido, tanto no que diz respeito à sua morfologia, estrutura, função e comportamento (em relação à herança, organização e expressão gênica), quanto à sua variação e evolução, fornece dados que analisados à luz da taxonomia e sistemática do grupo em questão conferem às análises citológicas uma interpretação citotaxonômica (Guerra 1988; Stace 1989; Guerra 1990; Bernardos *et al.* 2004).

O número de cromossomos é o parâmetro citotaxonômico mais estudado para a maioria dos taxa e sua variação é de grande importância, uma vez que esta informação pode auxiliar na verificação da integridade de uma espécie ou na compreensão da evolução de um determinado grupo. Segundo Guerra (1988) e Stace (1989), quando as espécies apresentam números cromossômicos diferentes, estes podem vir a ser um caráter que as separe, principalmente se a diferença cromossômica acompanhar as variações morfológicas.

Em alguns grupos de Leguminosae, o número cromossômico tem se mostrado uma informação citotaxonômica valiosa e tem auxiliado os taxonomistas a tomar decisões importantes na delimitação dos táxons e na classificação sistemática dos mesmos (Seijo 1999; Mendonça-Filho *et al.* 2002; Conterato *et al.* 2007; Andrade *et al.* 2008; Dahmer *et al.* 2011). Dahmer *et al.* (2011), por exemplo, realizaram um extensivo estudo em *Mimosa* L., gênero reconhecido pela sua dificuldade taxonômica e classificação sistemática, e puderam inferir relações evolutivas e taxonômicas entre os táxons analisando as informações citológicas adiquiridas durante o trabalho e disponíveis na literatura. Poggio *et al.* (2008) fizeram um aprofundado estudo para a família no continentente americano, identificando processos citológicos que possivelmente exerceram grande influência na evolução da família, como poliploidia, disploidia descrescente, rearrajos genômicos e hibridação, encontrando um número cromossômico básico para a família de x=7.

Diante dos desafios taxonômicos e sistemáticos apresentados por *Swartzia*, esforços nas áreas de palinologia (Fergusson & Skvarla 1991) e anatomia (Gasson 1996; Angyalossy-Alfonso & Miller 2002) são encontrados na literatura, entretanto, são mais relevantes quando analisados a níveis supra-genéricos. Estudos biossistemáticos contribuem para o esclarecimento de problemas taxonômicos e evolutivos, mas são praticamente inexistentes no clado swartzióide ou para o gênero *Swartzia*.

Para o clado swartzióide, estudos relacionados à citotaxonomia do grupo ainda são incipientes. Dentre os gêneros enquadrados no clado por Torke & Schall (2008) são conhecidos números cromossômicos para as espécies: *Ateleia gummifera* (Bertero ex DC.) D. Dietr. (2n=40 – Bolkhoviskikh, *et al.* 1969), *Bobgunnia fistuloides* (Harms) J.H. Kirkbr. & Wiersema e *B. madagascariensis* (Desv.) J. H. Kirkbr. & Wiersema (2n=16 – ambos publicados por Magenot & Magenot 1957). Para *Swartzia,* há um registro impreciso apenas para *S. laevicarpa* Amshoff (2n≅28 - Goldblatt 1981), sendo necessários estudos cromossômicos adicionais.

Apesar de importantes, nem sempre o conhecimento sobre os números cromossômicos dos grupos é parâmetro suficiente para uma melhor compreensão de sua sistemática (Biondo *et al.* 2005; Trenchard *et al.* 2008). A análise da morfologia cromossômica, que está relacionada ao tamanho relativo e/ou absoluto, à posição centromérica e à presença de contrições secundárias também fornece informações importantes para uma melhor compreensão da sistemática (Ohri 1998; Ohri & Singh 2002; Ohri 2005). Estas características também estão muitas vezes relacionadas à características moleculares (Nandine & Murray 1997; Poggio *et al.* 2007; Leitch *et al.* 2009; Cires *et al.* 2010; Kim *et al.* 2012), morfológicas e ecológicas (Masterson 1994; Leitch *et al.* 2009; Treier *et al.* 2009; Cires *et al.* 2010; Lavergne *et al.* 2010; Tacuatiá *et al.* 2012).

Técnicas citogenéticas adicionais, como o bandamento cromossômico para identificação de regiões ricas em CG ou AT (CMA/DAPI) e de hibridização de DNA *in situ* (FISH), têm sido utilizadas como fonte adicional de informação citotaxonômica. Estas, têm contribuído extensamente para a solução de problemáticas taxonômicas em plantas e para a compreensão de mecanismos envolvidos na evolução dos grupos (Pedrosa-Harand & Guerra 2004; Jiang & Gill 2006).

Bandamento cromossômico e FISH podem ser úteis na identificação de pares cromossômicos, comparação de táxons e identificação de processos de poliploidização (Barros e Silva *et al.* 2010; Pellicer *et al.* 2010; Mendes *et al.* 2011; Oliveira *et al.* 2012). Em Leguminosae, estas técnicas têm sido amplamente utilizadas para estudos em espécies de interesse agronômico (Ansari *et al.* 1999; Robledo & Seijo 2008; Pedrosa-Harand *et al.* 2009; Ohmido *et al.* 2010; Almeida & Pedrosa-Harand 2011), porém há poucas as informações para espécies selvagens (Souza & Benko-Iseppon 2004; Liu *et al.* 2006). Para o clado swartzióide e o gênero *Swartzia*, nenhuma informação de bandamento (CMA/DAPI) e localização de sequências de rDNA (FISH) pôde ser encontrada na literatura.

Este trabalho tem como objetivo estudar aspectos taxonômicos e biossitemáticos de *Swartzia*, contribuindo para a evolução dos estudos taxonômicos que vem sendo feitos para o gênero, assim com fornecer informações inéditas sobre os aspectos citológicos. Os estudos citogenéticos de *Swartzia* serão apresentados no capítulo 1, revelando o número cromossômico para o maior número de espécies possível, analisar a morfologia cromossômica, identificar sítios de sequências ricas de nucleotídeos específicos e sequências de rDNA. Os dados encontrados serão confrontados com os dados existentes na literatura para uma melhor compreesão das relações infra e supra-específicas no clado swartzióide. No capítulo 2, será apresentado um estudo taxonômico sobre o gênero nas regiões extra-amazônicas do Brasil, com análises de campo, herbário e a confecção de uma chave de identificação para os táxons extra-amazônicos.

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CAPÍTULO 1

Cytogenetic studies in Brazilian species of *Swartzia* Schreb. (Leguminosae, Papilionoideae)

***Rafael Barbosa Pinto*[1]**

1. Departamento de Biologia Vegetal, Laboratório de Biossistemática, Programa de Pós-Graduação em Biologia Vegetal, Instituto de Biologia, CP 6109, Universidade Estadual de Campinas - UNICAMP, CEP 13083-970, Campinas, SP, Brasil. E-mail: rafaelbpinto@gmail.com

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ABSTRACT

We are presenting inedit cytogenetic data for *Swartzia*, a basal genus of the subfamily Papilionoideae and the largest genus of swartzioid clade. Chromosome number, chromosome length, relative chromosome length and total chromatin length (TCL) were obtained for 18 species from different sections and geographic regions of Brazil. CMA/DAPI and FISH analyzes were also carried out for 17 species. All *Swartzia* species presented 2n=2x=26, however, *S. leptopetala* presented diploid and tetraploid (2n=4x=52) seeds collected from the same tree, being a rare record of modular polyploidization in literature, never reported for Leguminosae. *Swartzia euxylophora*, which the inclusion in the genus was questioned, presented all cytogentics characteristics similar to all other analyzed *Swartzia* and together with morphological features observed in the field, this work supports the taxon as belonging to the genus. The longest chromosome was found in *S. euxylophora* (1.41μm), such as the biggest TCL (31.32μm). The shortest chromosome was found in *S. acuminata* (0.25μm), as well the smallest TCL (9.28μm). *Swartzia* presented quite small variation among chromosome length of each species, being the smallest ratio longest/shortest chromosome found in *S. dipetala* (1.23) and the biggest in *S. linharensis* (1.71). Two sites of $CMA^{+}/DAPI^{-}$ and two sites of 45S and 5S rDNA were found for all analysed species. None of these cytological features correlated with infrageneric sectional classification, morphological features or geographical distribution. Further cytological studies are needed in the clade for a better understanding of the relation between genera and evolutionary processes in the swartzioid clade, however, according to our results and data available in the literature, we suggest that genera in swartzioid clade can be distinguished by chromosome number (x=13 in *Swartzia*, x=8 in *Bobgunnia* and x=20 in *Ateleia*).

Key-words: swartzioid clade, FISH, citotaxonomy, modular polyploidization, Fabaceae

INTRODUCTION

Swartzia Schreb. belongs to Leguminosae family and is a basal genus of the subfamily Papilionoideae. Included in a swartzioid clade, *Swartzia* is closely related to seven other genera (*Ateleia* (DC.) Benth., *Bobgunnia* J.H. Kirkbr. & Wiersema, *Bocoa* Aubl., *Candolleodendron* R.S.Cowan, *Cyathostegia* (Benth.) Schery, *Fairchildia* Britton & Rose and *Trischidium* Tul.). Supported as a monophyletic genus (Torke & Schall 2008; Torke & Mansano 2009), *Swartzia* has undergone a complex diversification and today presents about 200 species in neotropical region (Pinto *et al.* 2012), being the largest and most widespread genus of the clade.

Several studies have been done about the great taxonomic complexity of the group (Cowan 1967; Mansano & Tozzi 1999a; Mansano & Tozzi 1999b; Mansano & Tozzi 2001; Mansano & Tozzi 2004; Torke 2004; Pinto *et al.* 2012) and it is clear that only the morphological observation is, in more than a few cases, not enough to distinguish taxa. Based on that, additional tools are needed to improve the understanding and the knowledge about the taxonomy and systematic of the genus and the swartzioid clade.

Cytological studies are of great importance in elucidating of taxonomic, geographic or even ecological approaches. The cytotaxonomy consists in a correlation with the studies of chromosomes morphology, function, behavior and the systematics. This approach has helped several taxonomists in solving problems and gets better understanding about the evolution and the relation among taxa (Takhtajan 1969; Guerra 1988; Stace 1989; Moraes *et al.* 2007; Yamagashi-Costa & Forni-Martins 2009; Yano *et al.* 2010).

Chromosome number is still the most commonly parameter used to compare taxa in cytotaxonomic studies and according to Guerra (1988) and Stace (1989), when the species have different chromosome number, this can be an indicative of speciation, especially if followed by morphological variations. Sometimes, the limitation between species can difficult the identification, especially when they are morphologically similar. *Lippia alba* (Mill.) N.E. Br. ex Britton & P. Wilson ($2n=30$) and *L. geminata* Kunth ($2n=32$), member of the family Verbenaceae, for example, are very similar morphologically, however, they have different chromosome number, suggesting that they are different taxa (Brandão *et al.* 2007). The chromosome number can also be added to phylogenetic studies, supporting infrageneric lineages as showed by Escudero *et al.* (2008) in a systematic study of *Carex* L. In Leguminosae, Flores *et al.* (2006) pointed that the chromosome number is a good character to draw an infrageneric classification in *Crotalaria* L. Also, Cusma-Velari & Feoli-Chiapella (2009) used the chromosome number of genera from Genisteae, a Papilionoideae tribe, to improve suprageneric evolutionary discussions.

By obtaining the chromosome number of the taxa, it is also possible to recognize aneuploidy processes. The polyploidy, for example, is a relevant process involved in angiosperms evolution (Rieseberg & Willis 2007; Wood *et al.* 2009; Jiao *et al.* 2011) as well in Leguminosae (Poggio *et al.* 2008).

Several papers have used chromosome number to a better understanding of legume systematics (Mendonça-Filho *et al.* 2002; Biondo *et al.* 2005; Conterato *et al.* 2007; Andrade *et al.* 2008; Dahmer *et al.* 2011). Flores *et al.* (2006), for example, by analyzing the chromosome number of South American species of *Crotalaria* L., found a correlation between cytological, morphological and geographical characteristics. Nevertheless, correlations with chromosome number are hampered by variations in the number, as demonstrated by Rodrigues *et al.* (2009) who found polysomatic meristems in *Acosmium* Schott. species (2n=18/32). Therefore, the length analyses can help in comparison among taxa and sometimes in the understanding of behavior and morphologic features or evolutionary mechanisms.

The observation of chromosomes length and total chromatin length has been often correlated with DNA content and ploidy level (Nandini & Murray 1997; Poggio *et al.* 2007; Leitch *et al.* 2009; Cires *et al.* 2010; Kim *et al.* 2012), which in turn has been correlated with morphological and ecological features (Masterson 1994; Treier *et al.* 2009; Cires *et al.* 2010; Lavergne *et al.* 2010; Tacuatiá *et al.* 2012), systematics classification (Ohri 1998; Ohri & Singh 2002; Ohri 2005) or even geographical characteristics (Nagaowaska *et al.* 2006; Kim *et al.* 2012). The ratio of longest and shortest chromosome can also be a useful data for citotaxonomy of legumes as showed by Ohri & Singh (2002), in an infrageneric and infraspecific studies of *Cajanus* Adans. which presented the same chromosome number for all analyzed taxa (2n=22), but, relevant differences in the length and symmetry of the karyotype.

Furthermore, detailed analyses such as the location of GC or AT-rich bands (known as CMA/DAPI banding) and the detection of specific sequences of rDNA on the chromosome body (known as fluorescent *in situ* hybridization - FISH) are also widely applied to refine the interpretations of cytogenetic data (Pedrosa-Harand & Guerra 2004; Jiang & Gill 2006).

Fluorochrome banding with chromomycin (CMA) reveal heterochromatin sites composed of GC-rich DNA, which can be useful in finding chromosome pairs, comparing taxa or identify polyploidization processes (Barros e Silva *et al.* 2010; Pellicer *et al.* 2010; Mendes *et al.* 2011; Oliveira *et al.* 2012). In Leguminosae this technique has been largely used, mainly correlated with FISH results. Several papers have reinforced the relation among GC-rich bands and 45S and 5S rDNA sites (Mondin *et al.* 2007; Gaeta *et al.* 2010), albeit there are exceptions (Morales *et al.* 2012).

For Leguminosae there are not much data about specific localization of rDNA bands and most of the published papers provide data about legumes of agronomic interest (Ansari *et al.* 1999; Robledo & Seijo 2008; Pedrosa-Harand *et al.* 2009; Ohmido *et al.* 2010; Almeida & Pedrosa-Harand 2011). Souza & Benko-Iseppon (2004) and Liu *et al.* (2006) stand out with their *in situ* hybridization studies in wild legume plants.

Cytogenetic related studies published for swartzioid clade are almost absent. Among the genera included in the clade by Torke & Schaall (2008) the chromosome number are known for *Ateleia gummifera* (Bertero ex DC.) D.Dietr. (2n=40 – Bolkhviskikh *et al.* 1969), *Bobgunnia fistuloides* (Harms) J.H.Kirkbr. & Wiersema and *B. madagascariensis* (Desv.) J.H.Kirkbr. & Wiersema (2n=16 – both published by Mangenot & Mangenot 1957) and for *Swartzia laevicarpa* Amshoff (2n≅28 – Goldblatt 1981). Nothing about specific nucleotide rich bands or rDNA hybridization is known for the clade. Thus, the aim of this paper is to add information about cytogenetic aspects of *Swartzia*, a basal genus of Papilionoideae subfamily and improve the understanding of inter and infrageneric relations within the swartzioid clade.

MATERIAL E METHODS

Fruits and seeds of 18 species of *Swartzia* were collected in the wild and in live collections throughout Brazil. The classification in sections followed Torke & Mansano (2009) infrageneric classification for *Swartzia*. Voucher of all specimens collected were deposited at the herbarium of Universidade Estadual de Campinas (UEC) and the herbarium of Instituto de Pesquisas do Jardim Botânico do Rio de Janeiro (RB). The vouchers are: *S. acuminata* Willd. *ex* Vog.: V.F.Mansano 737; *S. anomala* R.S.Cowan: F.N.Cabral 426; *S. apetala* Raddi var. *apetala*: R.B.Pinto 238; *S. arenophila* R.B.Pinto, Torke & Mansano: R.B.Pinto 118; *S. dipetala* Willd. *ex* Vog.: R.B.Pinto 246; *S. euxylophora* Rizzini & A.Matos: V.F.Mansano 860; *S. grandifolia* Bong. *ex* Benth.: R.B.Pinto 341; *S. jorori* Harms: R.B.Pinto 339; *S. langsdorffii* Raddi: R.B.Pinto 338; *S. leptopetala* Benth.: R.B.Pinto 346; *S. linharensis* Mansano: V.F.Mansano 226; *S. multijuga* Vog.: V.F.Mansano 558; *S. myrtifolia* var. *elegans* (Schott) R.S.Cowan: A.Lobão 1701; *S. oblata* R.S.Cowan: R.B.Pinto 337; *S. polita* (R.S.Cowan) Torke: V.F.Mansano 857; *S. polyphylla* DC.: R.B.Pinto 234; *S. simplex* var. *continentalis* Urb.: G.S.Siqueira 640; *S. simplex* var. *grandiflora* (Raddi) R.S.Cowan: L.F.G. da Silva 76.

Procedures to avoid fungal attack during seed germination were carried out. For all the species the seeds were washed in hypochlorite 2% for 15-30min. After that, the seeds were hydrated in regular water for at least 6 hours. For the arillated species, the arils were removed before the wash in hypochlorite.

The sowing was made in gerbox with vermiculite as substrate. *Swartzia* seeds responded very well to this substrate and the conditions of 25°C and 12hr/12hr of photoperiod. Root tips were pretreated with 2mM 8-hydroxyquinoline for 24hr. The root tips were subsequently fixed in Farmer solution (ethanol:acetic acid, 3:1 v/v – from Merck®) for 24hr in environment temperature and after that stored in freezer.

The root tips were prepared for enzymatic digestion by washing in distilled water, pat-dried with paper towels and then treated with a solution of 1% macerozyme, 2% cellulose and

20% pectinase in an eppendorf and stored in an incubator at 37°C for 1hr. Root tips were then squashed between a slide and a coverslip in a drop of 45% acetic acid. The coverslips were subsequently removed in liquid nitrogen.

The slides were first stained with 10µl of DAPI/glycerol for the selection of the best metaphasic cells. After selected, the slides were stored for 3 days at room temperature avoiding dust for CMA/DAPI banding techniques.

For CMA staining, 10µl of CMA solution (0,5mg/ml) was dropped on the slides and then stored in humid chamber for 1hr at room temperature in the dark and posteriorly washed with distilled water and quickly dried with an air pump. Then, for DAPI staining, 10µl of DAPI solution (2µg/ml) was dropped on the slides and then stored in humid chamber for 30min at room temperature in the dark. Same wash and dry procedures were done. The slides were then mounted with glycerol/McIlvaine solution and stored in humid chamber at room temperature for three days.

Hibridization *in situ* (FISH) was performed using probes of rDNA. The 45S rDNA probe (18S-5.8S-25S) is a fragment of 6.5-kb took from *Arabidopsis thaliana* (Wanzenböck *et al.* 1997) and the 5S rDNA probe is a fragment of 500-bp took from *Lotus japonicus* (Pedrosa *et al.* 2002). Probes were labeled by nick translation with digoxigenin-11-dUTO for 5S rDNA and biotin-14-dATP for 45S rDNA.

Before hybridization process, the slides were incubated at 60°C for 30min and stored at room temperature. Posteriorly, slides were incubated in 1% RNase solution for 1hr at 37°C in humid chamber. The slides were then washed in 2xSSC, fixed in 4% paraformaldehyde for 10min and washed again in 2xSSC. The slides were dehydrated in a 70-100% ethanol series and air-dried. Each slide was treated with labeling solution comprising 100% formamide, 50% dextran, 20xSSC, 10% SDS, probes (rDNA 45S and 5S) and distilled water. The solution was heated at 75°C for 10min and transferred to ice for at least 5min. It was dropped 15µl of hybridization solution for each slide and then, chromosomes were denatured using a thermal cycler at 70°C for 7min. After that the slides were kept at 37°C for 48hr in a humid chamber.

After hybridization, the slides were washed in 2xSSC at room temperature for at least 5min. Then, they were washed twice in 2xSSC at 42°C for 5min, 0.1xSSC at 42°C for 5min, 2xSSC at 42°C for 5min and 4xSSC/0.2% Tween 20 at room temperature for 5min. For detection, the slides were then treated with 50µl of 5% BSA and 20µl of antibody solution (0.5µl of avidin-FITC, 0.5µl of anti-dig-rhodamine and 19µl of 5%BSA) and incubated in humid chamber at 37°C for 1hr. Posteriorly, the slides washed in 4xSSC/0.2% Tween 20 for 5min, 2xSSC and mounted with 10µl of DAPI/Vectashield.

The slides were examined by microscope Leica DM2500 for epifluorescence and photomicrographs were taken via LAS 3.6 applicative.

The chromosomes measurements were made by selected photomicrographs with DAPI stained cells. The sum of the chromosome length for each species was classified as total chromatin length (TCL) according concepts of Greilhuber *et al.* (2005).

RESULTS

A conserved chromosome number (2n=2x=26) was presented by all 18 species of *Swartzia* analyzed with emphasis for the duplicated number (2n=4x=52) found in some seeds of *S. leptopetala* (Table 1). In this case, seeds from only one tree were collected, being a rare record of wild modular polyploidization process.

Swartzia chromosomes are very small as observed on table 1. Due to the small size of chromosomes it was not possible to have a detailed morphological description and a detailed karyotype.

The shortest chromosome was found in *S. acuminata* (0.25µm) and the longest in *S. euxylophora* (1.41µm). These species also presented the shortest TCL (*S. acuminata* = 9.28µm) and the longest TCL (*S. euxylophora* = 31.31µm). So, total chromatin length varies substantially among species (Table 1).

The ratio between the longest and shortest chromosome indicated the variations in relative chromosome length. Among *Swartzia* species there are no great differences among the longest and the shortest chromosomes, and the ratio varied from 1.23 in *S. dipetala* to 1.71 in *S. linharensis* (Table 1). We observed a gradual length variation among all chromosomes from each analyzed species of *Swartzia* (Fig.1, 2, 3).

In the present study, CMA/DAPI and FISH analyses also presented a conserved banding pattern, with two CMA^+/$DAPI^-$ sites (one pair), two 45S and two 5S rDNA sites in mitotic cells of all analyzed species (Table 1). It was not possible to have data from *S. arenophila* and the polyploid sample of *S. leptopetala* due to scarcity of roots.

The CG-rich sites were found at the terminal portion of the chromosomes in all species, and these sites are co-localized with 45S rDNA sites (Fig.3). 5S rDNA sites were found in different chromosomes and were also detected at terminal portion of the chromosome (Fig.3).

Table 1. Chromosome number (2n), Chromosome data for length and total chromatin length (TCL), number of CMA/DAPI and 45S/5S rDNA sites for 18 species of *Swartzia*.

Section	Species	2n	Chromosome lenght variation (μm)	Longest/shortest chromosome ratio	TCL (μm)	CMA+/DAPI-	45S	5S
Acutifoliae	*S. arenophila*	26	0,34 - 0,56	1,64	12,20	*	*	*
	S. langsdorffii	26	0,70 - 1,03	1,47	21,44	2	2	2
	S. linharensis	26	0,46 - 0,79	1,71	14,93	2	2	2
	S. multijuga	26	0,41 - 0,62	1,51	13,94	2	2	2
	S. oblata	26	0,62 - 1,01	1,62	20,88	2	2	2
	S. polita	26	0,51 - 0,70	1,37	15,71	2	2	2
Digynae	*S. dipetala*	26	0,34 - 0,42	1,23	10,10	2	2	2
Multistaminae	*S. grandifolia*	26	0,35 - 0,48	1,37	10,68	2	2	2
Orthostylae	*S. acuminata*	26	0,25 - 0,41	1,64	09,28	2	2	2
	S. polyphylla	26	0,46 - 0,74	1,60	15,05	2	2	2
Pittierianae	*S. jorori*	26	0,56 - 0,84	1,50	16,66	2	2	2
Possira	*S. myrtifolia* var. *elegans*	26	0,31 - 0,52	1,67	10,28	2	2	2
	S. simplex var. *continentalis*	26	0,51 - 0,79	1,52	15,69	2	2	2
	S. simplex var. *grandiflora*	26	0,36 - 0,55	1,52	11,14	2	2	2
Swartziae	*S. apetala* var. *apetala*	26	0,79 - 1,10	1,39	24,01	2	2	2
Terminales	*S.* cf. *leptopetala*	26/52	0,92 - 1,28	1,39	27,03	2	2	2
Unifoliolateae	*S. anomala*	26	0,35 - 0,55	1,57	10,93	2	2	2
**	*S. euxylophora*	26	1,07 - 1,41	1,31	31,32	2	2	2

*data unknown due to paucity of samples.

**This species needs further studies for section classification.

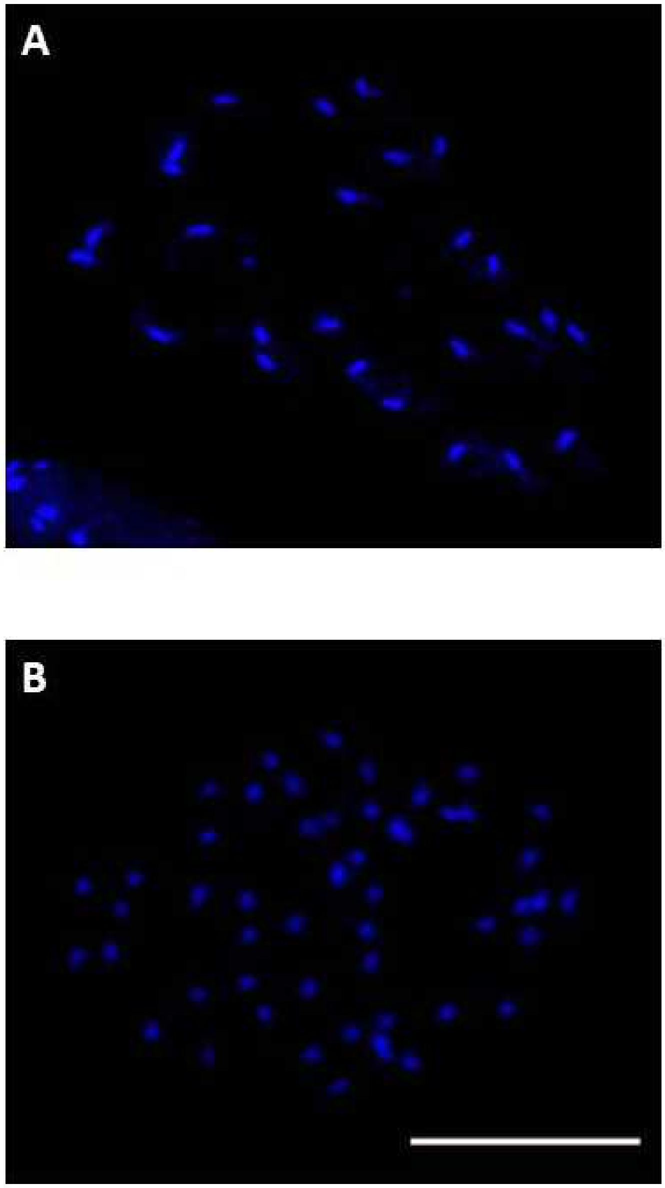

Figure 1. Mitotic metaphases chromosomes of *Swartzia leptopetala*. Both metaphases came from different seeds of the same tree. (A. Diploid metaphase – 2n=2x=26; B. Tetraploid metaphase – 2n=4x=52). Bar = 10 μm.

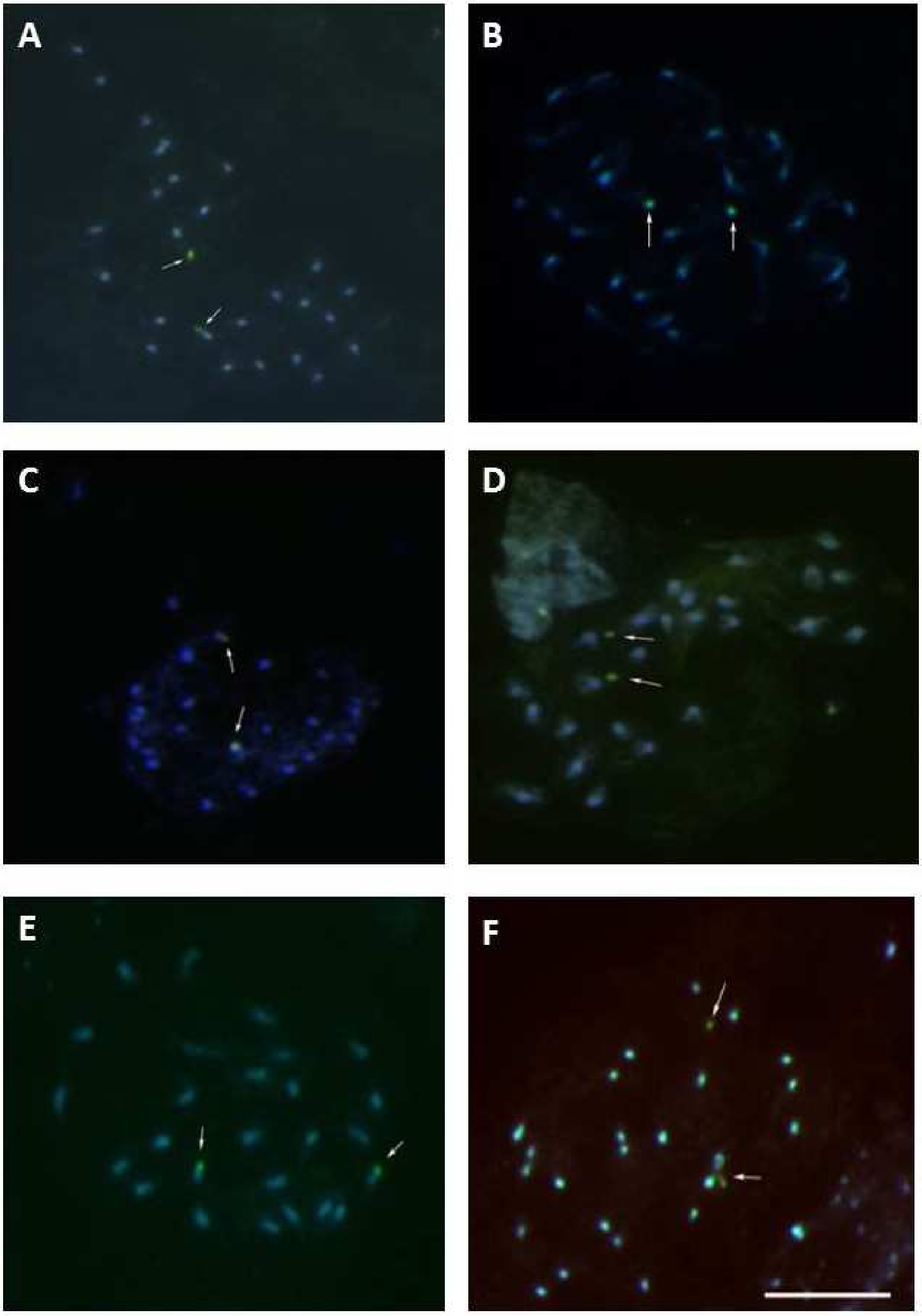

Figure 2: Mitotic metaphases chromosomes of six species of *Swartzia* showing CMA$^+$/DAPI$^-$ sites. (A. *S. apetala* var. *apetala*; B. *S. anomala*; C. *S. grandifolia*; D. *S. polyphylla*; E. *S. euxylophora*; F. *S. simplex* var. *grandiflora*). Arrows point to CMA$^+$ sites - CG rich sequences (green). Chromosomes were counterstained with DAPI (blue). Bar = 10 μm.

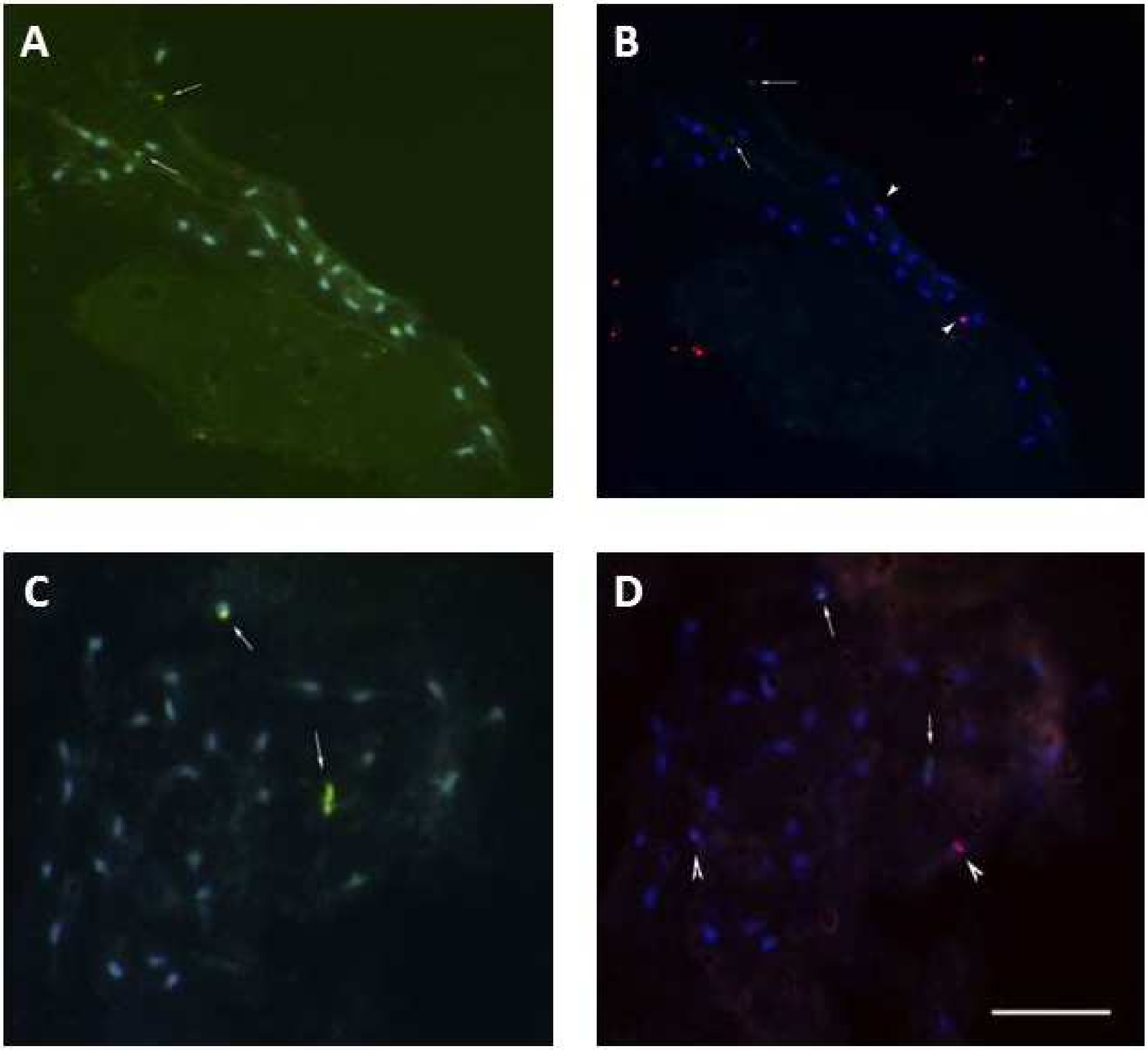

Figure 3: Mitotic metaphases chromosomes of two species of *Swartzia* showing the co-localization of CMA$^+$/DAPI$^-$ sites (A e C) and 45S/5S rDNA genes loci (B e D). (A. *S. langsdorffii*; B. *S. langsdorffii* - same cell; C. *S. oblata*; D. *S. oblate* - same cell). Arrows indicate CMA$^+$ sites (greens signal in A,C); and hybridization sites of 45S rDNA probes (green signal in B,D). Arrow heads indicate sites of 5S rDNA probes (red signal in B,D). Bar = 10 µm.

DISCUSSION AND CONCLUSION

Chromosome number, chromosome length and TCL

Swartzia presented a conservative chromosome number (2n=26) shared among all the 18 analyzed species. A single chromosome count for *Swartzia* available in the literature was published by Goldblatt (1981) who proposed 2n≅28 for the Amazonian *S. laevicarpa*. Although, this is probably a miscounted estimative, once 18 species of the genus from 9 sections, including Amazonian representatives such as *S. acuminata, S. anomala, S. leptopetala* and *S. polyphylla* presented a non-varied 2n=26. Some studies point that the chromosome number can be an important infrageneric character, as shown in *Senna* Mill. (Biondo *et al.* 2005b) and *Crotalaria* (Flores *et al.* 2006). On the other hand, *Swartzia* did not present any differences among the nine sections analyzed for the chromosome number. Even in an infraspecific approach, as in *S. simplex*, both varieties presented the same chromosome number.

Polyploidy has been related to several Leguminosae groups (Biondo *et al.* 2005a; Cusma-Velari & Feoli-Chiapella 2009; Dahmer *et al.* 2011; Santos *et al.* 2012) and has been an important undergone process in the evolutionary history of the family (Poggio *et al.* 2008; Soltis *et al.* 2009). Allopolyploidy and autopolyploidy are both mechanisms of polyploidization (Stebbins 1971; Leitch & Bennet 1997; Soltis *et al.* 2007) and have been issue of taxonomical discussions (Lewis 1980; Soltis *et al.* 2007). In nature, auto and allopolyploidy are not always clearly recognizable but, in *Swartzia leptopetala*, that presented diploid and tetraploid cells in different seeds gathered from the same tree (Fig.1), it is possible to state that this is a case of autopolyploidy. Cases like this are scarce in the literature, notwithstanding they are probably not so uncommon in plants (Soltis *et al.* 2003; Parisod *et al.* 2010). Hallé (1986) described the different forms of modular growth in angiosperms and identified the development of many trees as a repetition of meristematic modules. This unlimited growth, cell totipotency and recurrent ontogenesis in plants make the separation of somatic cells and germinative cells impossible (D'Amato 1999), which means that a mutation at the meristematic cells can be transferred to germinative cells and consequently to seeds.

By analyzing the new chromosomes counts for *Swartzia* and the data available in the literature about the swartzioid clade, we suggest that genera in this clade can be determined by chromosome number. According to recent phylogeny of the swartzioid clade (Torke & Schall 2008), *Swartzia* (2n=26) is closed related to a small clade consisted by *Candolleandendron* R.S.Cowan and *Bocoa* Aubl., which do not have chromosome number record. These three genera comprise the core-swartzioid clade, sister to *Bobgunnia* (2n=16 – Magenot & Magenot 1957) and *Fairchildia*. The other three genera *Trischidium*, *Cyathostegia* and *Ateleia* (*Ateleia gummifera* (Bertero ex DC.) D. Dietr.– 2n=40 – Bolkhviskikh *et al.* 1969) are less related to *Swartzia* but also share molecular and morphological synapomorphies with the cited genera, supporting all of them as the swartzioid clade (Torke & Schall 2008).

Thus, we corroborate the combination done by Kirkbride & Wiersema (1997) who proposed the genus *Bobgunnia* (2n=16 – Magenot & Magenot 1957) for two African species treated otherwise as *Swartzia* (2n=26), supported by fruit anatomy, geographic distribution, leaf morphology and chromosome number. Also, assuming the differences in the chromosome number among genera of swartzioid clade, the number found for *S. euxylophora* is significant to confirm its inclusion in the genus, once Lewis (1987), by analyzing incomplete herbarium sheet, suggested that it could not be a *Swartzia* or not even be a legume. Our cytological results (uniformity of chromosome number) and the observation of the morphology of fruits and seeds in the field corroborate that this species belongs to *Swartzia*.

Swartzia chromosomes range from 0.25µm in *S. acuminata* and 1.41µm in *S. euxylophora* and are relatively small when compared with other legumes (e.g. 2.12-6.99µm in *Sesbania* species – Forni-Martins *et al.* 1994; 4.37-8.86µm in *Lathyrus* species – Seijo & Fernández 2003). Chromosome length correlates positively with TCL, although, the chromosomes length and TCL do not correlated with the ratio of longest and shortest chromosomes. The smallest variation on chromosome relative length was found in *S. dipetala* (1.23) while, the biggest were found in *S. linharensis* (1.71), followed by *S. myrtifolia* var. *elegans* (1.67). It was also not possible to correlate chromosome length or TCL with sectional classification, despite the variation in length analysis among species (Table 1). This feature is also variable intraspecificaly, as observed in *S. simplex* varieties. Longest and shortest chromosome ratio also presented a randomly variation among species and sections, not supporting a systematic approach. Still, more species of this big genus need to be analysed to improve the cytological information allowing a more precise evolutionary and systematic discussion.

Moscone *et al.* (2007) and Leitch *et al.* (2009) correlated the TCL with DNA content, finding a positive correlation among these characteristics. Different ecological correlations with DNA content exists in the literature (Dolezel & Göhde 1995; Knigth *et al.* 2005; Treier 2009; Tacuatiá *et al.* 2012) and the observations suggest that genome size can have a great influence on establishment and ecological strategies adopted. Knight & Ackerly (2002) and Leitch *et al.* (2009) correlated DNA C-values with life habits, life cycles and ecological distribution.

S. euxylophora, the species of *Swartzia* with the longest total chromatin length (31.32µm), and probably with the biggest DNA content, occurs in a very specific Atlantic Forest vegetation on south of Bahia state. Its distribution is restricted to a small area of occurrence as observed in field and herbarium records. The smallest TCL was found in *S. acuminata* (9.28µm), followed by *S. dipetala* (10.1 µm) and *S. myrtifolia* var. *elegans* (10.28 µm). These are widely distributed species. *S. acuminata* occurs in a very wide east-west range in Brazilian Amazon Forest, occupying different habitats. *S. dipetala* occurs only in Bahia state, nevertheless this species is found along a great extension of its coast. *S. myrtifolia* var. *elegans* can be found in very distinct habitats of Atlantic Forest in four Brazilian states (Mansano *et al.* 2012).

On the other hand, in *Swartzia* species, total chromatin length is not correlated with life habits. The smallest TCL were found in *S. acuminata* (9.28µm) and *S. dipetala* (10.1µm) which are emergent trees of the Amazonian Forest and medium size trees from Bahia state restingas respectively and the biggest TCL were found in *S. euxylophora* (31.32µm) and *S. leptopetala* (27.03µm), both emergent trees from the Bahian Atlantic Forest and Amazonian Forest respectively.

According to Knigth *et al.* (2005) and Hodgson *et al.* (2010), there is probably a correlation between small genomes and big seeds; although in *Swartzia* there is no correlation between TCL and morphological features. Despite *S. acuminata* presents one of the biggest legume seeds in nature and the smallest TCL for *Swartzia* (9.28 µm), this correlation is not true to other analyzed species. *Swartzia acuminata* is found in along some Amazonian river margins and one of the dispersion strategies adopted by this plant is hydrochory due to the possibility of fluctuation of the big seed as observed in field.

Hodgson *et al.* (2010) emphasized that there is a more consistent correlation between genome size and stomata length as found in different groups of plants (Joachimiak & Grabowska-Joachimiak 2000; Oliveira *et al.* 2004) and Knight & Beaulieu (2008) found a positive correlation between genome size and stomatal density in angiosperms. Accepting the hypothesis that increase of DNA content can be a result of polyploidization process, the observation of guard-cells size can be an important ploidy level indicative and in cases similar to *S. leptopetala*, which present different ploidy level in the same tree, it could be useful to identify polyploid branches. Gigantism has been related as a possible consequence of polyploidy. Muller (1979) showed that there is an association between high ploidy levels and larger pollen grains. Keeler & Davis (1999) observed that different cytotypes of *Andropogon gerardii* Vitman (Poaceae) presented an increasing in the development of floral and vegetative organs when detected polyploidy. Nevertheless, further studies are necessary to verify if polyploidy seeds from *S. leptopetala* can establish in the environment and if it presents an increase in the development of organs.

CMA/DAPI and Fluorescent in situ hybridization

The CMA/DAPI and FISH data obtained showed the same conserved pattern as the chromosome number among species (Table 1). Of the 18 species presented in this work, it was possible to gather CMA/DAPI and FISH data for 17 species. All the results presented are unpublished for *Swartzia*.

Analyzes of localization and number of GC/AT-rich bands and FISH using 45S and 5S rDNA probes have also been used in Leguminosae as an additional cytological tool for evolutionary and cytotaxonomic approaches (Souza & Benko-Iseppon 2004; Almeida & Pedrosa-Harand 2011; Mondin & Aguiar-Perecin 2011).

A pair of GC-rich bands is present in the mitotic cells and is CMA^+/$DAPI^-$ in S*wartzia*. This pattern has been found in other legumes (Galasso *et al.* 1996; Forni-Martins & Guerra 1999; Souza & Benko-Iseppon 2004; Gaeta *et al.* 2010). However, $DAPI^+$ heterocromatin bands were found in the Papilionoideae *Arachis* L. (Robledo & Seijo 2008) and *Crotalaria* L. (Mondin & Aguiar-Perecin 2011). Souza & Benko-Iseppon (2004) have described CMA^- /$DAPI^+$ pattern in few Caesalpinioideae from Amazon Forest and a CMA/$DAPI^+$ pattern was reported to *Cicer* L. (Galasso *et al.* 1996).

The GC-rich bands are co-localized with 45S rDNA site (Fig. 3) at the terminal portion of the chromosome for all 17 species analyzed. This co-localization is a recurrent characteristic in Leguminosae (Galasso *et al.* 1996; Mondin *et al.* 2007; Morales *et al.* 2012), but, studies with species from a related tribe showed locations of 45S rDNA sites at the centromeric region as provided by Liu *et al.* (2010) with *Sophora*, *Robinia* and *Amorpha*. This co-localization between 45S rDNA sites and CMA^+ bands can also be found in other groups of plants (Marques *et al.* 2010; Pellicer *et al.* 2010).

Fluorescent *in situ* hybridization has been useful to identify polyploidization processes, hybridization among species and comparison of taxa (Ran *et al.* 2001; Brandão *et al.* 2007; Silva *et al.* 2010). Although, in *Swartzia*, due to the conserved occurrence of the rDNA genes among the analyzed species, FISH analyses could not be used to discriminate sections and species in a systematic approach and also not correlated with ecological or geographical features.

We conclude that *Swartzia* has quite strongly conserved karyotype patterns (chromosome number, CMA/DAPI bands, FISH for 45S/5S rDNA genes). Therefore, it is not secure to state any evolutionary process relating chromosomal features and the diversity reached by the genus. These karyotype features were analyzed for 18 species from 9 out of 15 sections recognized for *Swartzia* and there is no correlation between cytological data and sectional classification.

Before this study, *Swartzia* only had an unprecise cytogenetic data available at the literature. However, with this study, 10% of the species have their cytological data known. Being a big genus of trees and having a widespread distribution of the species on the neotropics, including a center of diversity at Amazonian Rain Forest, studies that requires living material are difficult to perform.

Further studies are needed to a better understand of the swartzioid clade and the cytological processes involved in the evolution of genera. Nevertheless, chromosome number was relevant for distinction of genera within the clade as observed for *Swartzia* (x=13), *Bobgunnia* (x=8) and *Ateleia* (x=20).

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CAPÍTULO 2

Updates to the taxonomy of *Swartzia* (Leguminosae) in extra-Amazonian Brazil, with descriptions of five new species and a regional key to the genus

Rafael Barbosa Pinto[1]

1. Departamento de Biologia Vegetal, Laboratório de Biossistemática, Programa de Pós-Graduação em Biologia Vegetal, Instituto de Biologia, CP 6109, Universidade Estadual de Campinas - UNICAMP, CEP 13083-970, Campinas, SP, Brasil. E-mail: rafaelbpinto@gmail.com

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Updates to the taxonomy of *Swartzia* (Leguminosae) in extra-Amazonian Brazil, with descriptions of five new species and a regional key to the genus

RAFAEL BARBOSA PINTO[1], BENJAMIN M. TORKE[2] AND VIDAL DE FREITAS MANSANO[3]

[1]Instituto de Biologia, Departamento de Botânica, Universidade Estadual de Campinas, CP 6109, CEP 13083-970, Campinas, SP, Brazil; email: rafaelbpinto@gmail.com

[2]Institute of Systematic Botany, The New York Botanical Garden, Bronx, NY, 10458-5126, USA; e-mail: btorke@nybg.org

[3]Instituto de Pesquisas, Jardim Botânico do Rio de Janeiro, DIPEQ, Rua Pacheco Leão, 915, CEP 22460-030, Rio de Janeiro, RJ, Brazil; email: vidalmansano@gmail.com

Abstract. In advance of an updated monographic revision of *Swartzia* (Leguminosae), we discuss the taxonomy of the genus in extra-Amazonian Brazil and present descriptions of five new species. All of the new species are narrowly distributed in eastern Brazil in threatened Atlantic wet forest and coastal scrub habitats. Four of them – *S. alagoensis, S. arenophila, S. revoluta*, and *S. submontana*– belong to the diverse and taxonomically challenging section *Acutifoliae*, which has undergone extensive evolutionary radiation in the region. The fifth, *S. thomasii*, is a member of the otherwise Amazonian section *Glabriplantae* and is only subtly distinct from the Amazonian species *S. reticulata.* The new species and other recent additions to the genus are incorporated in a key to the species of *Swartzia* of extra-Amazonian Brazil.

Key Words. Eastern Brazil, extra-Amazonian Brazil, Fabaceae, Leguminosae, new species, *Swartzia*, taxonomy.

Resumo. Como parte do estudo de atualização da monografia de *Swartzia* (Leguminosae), são apresentados dados sobre os táxons do Brasil extra-amazônico com a descrição de cinco espécies novas. Todas as novas espécies propostas neste trabalho apresentam distribuição restrita em habitats potencialmente ameaçados na floresta atlântica brasileira e vegetação arbustiva costeira. Quatro novos táxons – *S. alagoensis, S. arenophila, S. revoluta* e *S. submontana*– pertencem a seção *Acutifoliae*, um grupo diverso e taxonomicamente complexo que teve alta radiação evolutiva na região. A quinta espécie, *S. thomasii*, pertence a seção *Glabriplantae*, um grupo mais comum na amazônia, e é apenas sutilmente distinta de *S. reticulata,* uma espécie amazônica. Devido ao fato da inclusão destes novos táxons e outras alterações recentes na taxonomia de *Swartzia* no Brasil extra-amazônico, é apresentada uma chave para distinguir as espécies de *Swartzia* desta área.

INTRODUCTION

Although strongly Amazonian-centered, the neotropical genus *Swartzia* (Leguminosae) has undergone nontrivial levels of speciation in extra-Amazonian Brazil, in the cerrado and other dry-land formations of the Brazilian interior and especially in the narrow zone of tropical wet forest and stunted vegetation on marine sands (i.e., “restinga”) that parallels the east coast of the country. Within this region, numerous, mostly narrowly restricted species are finely differentiated, often incompletely so, along abrupt habitat transitions and across porous geographical barriers. The wet coastal area was one of the earliest and most intensively botanized parts of the neotropics, and many of the species of *Swartzia* that occur there, were well known to the 19th century botanical explorers of the region. Nevertheless and despite the fact that much of extra-Amazonian Brazil has been severely impacted by deforestation and wholesale landscape conversion for development and agriculture, new species and new infraspecific taxa of *Swartzia* continue to be discovered from both coastal and interior habitat fragments throughout the region (Cowan, 1968, 1973, 1981, 1985; Mansano and Tozzi, 1999, 2001; the current contribution).

Of the 15 mutually exclusive subclades of *Swartzia* recovered in the phylogenetic study of Torke and Schaal (2008) and subsequently treated as sections of the genus by Torke and Mansano (2009), eight are lacking in extra-Amazonian Brazil and four have only a single species in the region: Section *Pittierianae* (R. S. Cowan) Torke & Mansano is represented by *S. jorori* Harms, a widespread species in southwestern Amazonia and the "Chiquitano" forest of Bolivia whose distribution extends also into the Brazilian Pantanal. The primarily Amazonian distributed section *Recurvae* (R. S. Cowan) Torke & Mansano is represented by the distinctive and narrowly endemic species *S. alternifoliolata* Mansano of coastal Bahia and Espírito Santo. Two other sections, *Digynae* Torke & Mansano and *Glabriplantae* Torke & Mansano, have single species restricted to the coastal forest of Bahia, *S. dipetala* Willd. ex Vogel and a new species described herein, respectively. Cowan's (1968) synonymization of *S. microstylis* Benth. under *S. dipetala* is at odds with consistent morphological differences that mirror a large geographical disjunction. The former name should be applied to a species confined to the Guayana Shield; the later to an exclusively Bahian species, which has a white (versus yellow in *S. microstylis*) petal, relatively long pedicels (3–20 mm versus 1–7 mm), and bracteoles inserted on the lower half of the pedicel (versus on the upper half of pedicel or at the base of flower bud).

The vast majority of the species of *Swartzia* in extra-Amazonian Brazil belong to three sections: *Acutifoliae* (R. S. Cowan) Torke, *Possira* (Aubl.) DC., and *Swartzia*. Cowan's (1968) taxonomy of section *Swartzia* in eastern Brazil was revisited by Mansano and Tozzi (1999) and by Torke (2007), with the cumulative effect of subsuming the name *S. peremarginata* R. S. Cowan within *S. riedelii* R. S. Cowan, reducing the number of varieties of *S. apetala* from four to two, and describing a new species, *S. capixabensis* Mansano. Extensive herbarium and field studies generally support Cowan's treatment of section *Possira* as being regionally represented by two imperfectly separated species, *S. simplex* (Sw.) Spreng. and *S. myrtifolia* Sm. The integrity of the several varieties that Cowan recognized within these two species, both of which are broadly distributed in the neotropics, is currently under analysis.

Section *Acutifoliae*, one of the few sizeable clades of *Swartzia* to have radiated largely outside of Amazonia, has most of its diversity concentrated in extra-Amazonian Brazil, where it is by far the most speciose section. Although many of the ca. 25 species of section *Acutifoliae* are closely related and difficult to distinguish, Cowan's (1968, 1973, 1985) circumscriptions of the species *S. acutifolia* Vogel, *S. flaemingii* Raddi, and *S. macrostachya* Benth, each containing several varieties, are overly broad, since many of the varieties are individually diagnosable and geographically and ecologically distinct. Moreover, the character that Cowan relied on most to unite varieties within species, leaflet shape, is inconsistent and correlates poorly with other potentially diagnostic characters. The dismemberment of these complexes began with publications by Mansano and Tozzi (1999, 2001) and by Torke (2007), in which several of the varieties of *S. acutifolia* and *S. flaemingii* were recognized as distinct species. In keeping with the trend, the name *S. psilonema* Harms is reinstated, thereby reducing *S. flaemingii* var. *psilonema* (Harms) R. S. Cowan to synonymy. The differences between *S. psilonema* and *S. flaemingii* are embodied in the key that follows.

In the course of ongoing herbarium and field-based revisionary studies of *Swartzia*, we have come across five species from extra-Amazonian Brazil heretofore undocumented in the literature. To facilitate their identification, a key is provided that includes all species and varieties of *Swartzia* that occur in the portion of Brazil south of the Amazon River Basin. We conclude that the genus is regionally represented by 31 species and 9 varieties.

New Species

Swartzia alagoensis R. B. Pinto, Torke & Mansano, **sp. nov.** Type: Brazil. Alagoas: Mun. Barra de São Miguel, na rodovia AL-101, próximo ao mirante a cerca de 10 km da sede do municipio á esquerda (sentido Piaçabuçu), ao longo estrada secundária para fazenda de cana-de-açúcar, 9°53’14”S, 35°55’58”W, 50–100 m, 17 Jun 2000 (fl), *M. Alves et al. 2074* (holotype: RB; isotypes: CEPEC, NY). (Fig. 1 F–K)

Rachidibus stipellatis et marginatis ad alatis, bracteis estipulatis, pedicellis bracteolatis, petalo albo, stipito minus quam 1.5-plo longiore quam ovario, stylo obliquo et minus quam 0.3-plo longiore quam ovario, stigmate punctiformi, fructibus aliquot-seminatis, ellipticis in cicumscriptio, loculo haud diviso, et inter semines pericarpio haud vel leviter constricto ad sectionem *Acutifoliae* (R.S.Cowan) Torke & Mansano referenda; sed indumento adpresso, trichomatibus plerumque 0.05–0.2 mm longis, stipulis 0.5–2.3 mm longis, foliolis lateralibus (4-) 5–7-jugatis et ellipticis ad oblongo-ellipticis, laminis abaxialibus inflorescentiis et calycibus extus strigulosis, bracteolis 0.6–1 mm longis, calycibus intus glabris, staminibus maioribus 3 vel 4, ovario piloso-sericeo et loculo glabro singularis.

Tree or shrub, to ca. 15 m tall; pubescence mostly of appressed, fairly straight, unbranched hairs, 0.05–0.2 mm long; leaf-bearing branchlets 1.2–4.5 mm thick, minute-strigulose, soon glabescent. Stipules triangular, 0.5–2.3 mm long, 0.2–0.4 mm wide at base, minute-strigulose abaxially, glabrescent. Leaves imparipinnate, with (4–) 5–7 pairs of opposite lateral leaflets; petioles marginate, basally pulvinate, 1–3.3 cm long, 0.7 –1.4 mm thick at middle, minute-strigulose, glabrescent, the pulvinus 1.5–4.1 X 1–2 mm; rachis stipellate, marginate to narrowly winged, caniculate between wing lobes adaxially, subterete abaxially, 6.5–13.5 cm long, 0.7–1.4

mm thick at middle of segments, minute-strigulose, glabrescent, the wings 0.9–2.2 mm wide measured across the rachis, the stipels subulate or narrowly triangular, 0.5–2 X 0.2–0.4 mm; petiolules pulvinate, adaxially caniculate, 0.5–1.3 X 0.6–1.1 mm, minutely pilosulose-strigulose, glabrescent; leaflet blades chartaceous, discolorous, narrowly elliptic to oblong-elliptic, the lowermost ovate, mostly 1.7–3.3 X longer than wide, those of the terminal leaflet 2.9–6.1 X 1.1–1.9 cm, those of the lower lateral leaflets 1.7–3.4 X 0.8–1.6 cm, those of the distal lateral leaflets 3.1–5.5 X 1.2–2 cm, the base obtuse-rounded to broadly acute, the apex rounded to bluntly acute, the adaxial surface glabrous, the abaxial surface thinly minute-strigulose, the midrib immersed adaxially, cariniform abaxially, other venation prominulous-reticulate on both surfaces, the secondary veins ca. 20, initially fairly straight and ascending at 25°–35°, forming submarginal loops distally, the highest-gauge tertiary veins more or less parallel to the secondaries. Inflorescences simple or compound racemes with a single order of branching, arising from leaf axils or from defoliate nodes of annotinous or somewhat older branchlets, to ca. 20-flowered, the flowers spirally arranged; axes ca. 6–15 (–24) cm long, 1–2.5 mm thick, densely and minutely ferruginous-strigulose; bracts triangular, 0.6–2 X 0.6–1 mm, glabrous adaxially, densely minute-strigulose abaxially, caducous; pedicels dorso-ventrally compressed, somewhat dilated apically, 8.5–13 mm long, 1.5–2.4 mm thick at middle, densely and minutely ferruginous-strigulose; bracteoles opposite to subopposite, inserted near or somewhat above the center of the pedicel, triangular, 0.6–1 X 0.3–0.8 mm, caducous; flower buds globose or ovoid, 8–10.2 X 7.2–9.7 mm, densely and minutely ferruginous-strigulose. Calyx entire in bud, splitting irregularly to reveal light green, glabrous interior, the segments 4–5, subequal, more or less elliptic, apically acute, 6–12 X 4–8 mm. Corolla monopetalous; petal adaxial, white, membranous, adaxially glabrous, abaxially strigose, somewhat densely so at base, the claw basally truncate, apically dilated, 5–5.7

mm long, ca. 1.5–2.2 mm wide at base and 2.6–3 mm wide at apex, the limb broadly ovate to oblate, 1.1–1.7 X 1.5–2 cm, the base rounded to truncate, the margin undulate, the venation semi-palmate, with ca. 10 primary veins, the central vein more robust than the others. Androecium strongly zygomorphic, the stamens dimorphic; larger stamens 3–4, abaxial in a single row, the filaments white, somewhat dorso-ventrally compressed, apically tapering, 13–13.3 mm long, 0.8–0.9 mm thick at middle, glabrous or with a few trichomes, the anthers glabrous, yellow, oblong-elliptic in outline, 2.5–2.8 X 1–1.3 mm, the smaller stamens ca. 100, adaxial to central on the floral axis, glabrous, the filaments white, 9.1–13.7 X 0.1–0.3 mm, the anthers yellow, elliptic to oblate in outline, 1.2–1.4 X 0.9–1.2 mm. Gynoecium monopistillate, curving abaxially, the stipe terete or somewhat dorso-ventrally compressed, dilated at base and apex 5.3–7.6 long, 0.7–1.2 mm thick at middle, densely silvery-pilose or sericeous, except for the nearly glabrous base, the ovary inequallaterally arcuate-elliptic, laterally compressed, 5.7–8.7 X 3.2–4.5 mm, densely silvery-sericeous, the locule glabrous, the ovules ca. 10–13, the style obliquely terminal, more or less terete, 1.5–2.1 X 0.4–0.7 mm, mostly glabrous, the stigma punctiform. Pods apparently dehiscing along both sutures, the stipe terete, apically dilated, 1.1–1.2 cm long, 5–8 mm thick at middle, sparsely strigulose, glabrescent, the body more or less flattened-ellipsoid, with a single seed chamber, 6–10 X 4.5–7 cm, fairly smooth, sparsely minute-strigulose, glabrescent. Seeds several per fruit, filling the seed chamber, cream-colored, irregularly elliptic to semi-circular in outline, 2.2–2.7 X 1.9–2.6 cm, the funicle ca. 8.4 mm long, the aril pale yellow, more or less oblong, 5.8–6.8 X 1.2–1.8 cm, rounding the seed and covering ca. two thirds of its surface.

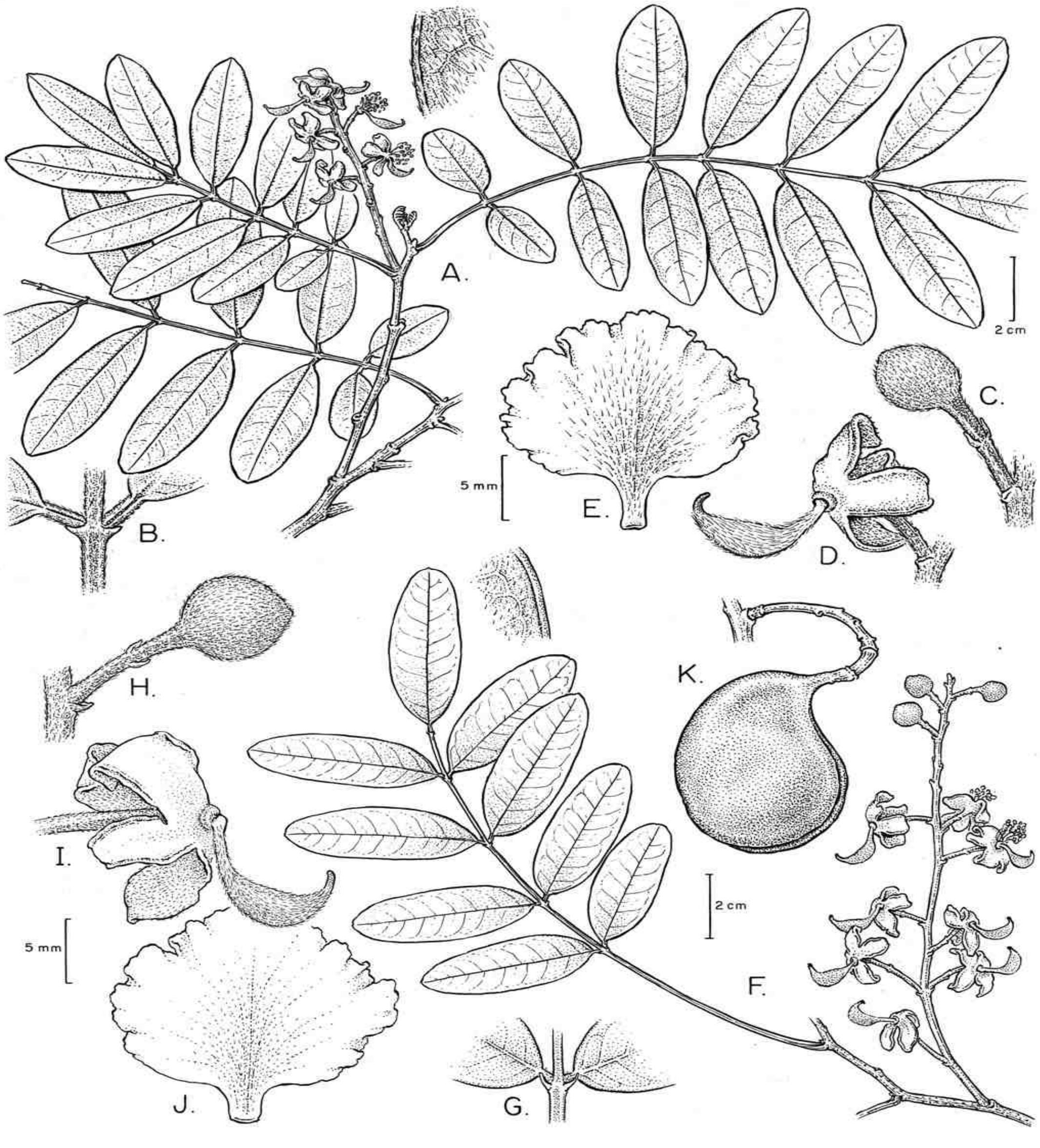

FIG.1. **A-E**. *Swartzia submontana.* **A.** Flowering branchlet bearing post-anthesis inflorescence, with detail of leaflet undersurface. **B**. Detail of rachis and leaflet bases, adaxial view. **C**. Flower bud. **D**. Post-anthesis flower. **E**. Petal, abaxial view. **F-K.** *Swartzia alagownsis.* **F**. Flowering branchlet, with detail of leaflet undersurface. **G.** Detail of rachis and leaflet bases, adaxial view. **H.** Flower bud. **I.** Post-anthesis flower. **J.** Petal, adaxial view. **K.** Fruit. (A, B, D from *Plowman & Sucre* 2892, NY; C, E from *Sucre & Plowman* 5192, K; F-J from *Alves et al.* 2074, NY; K, from *Thomas et al.* 13289, NY)

Distribution, habitat and conservation status. —The new species is known only from the coastal region of northeastern Brazil in the states of Alagoas and Sergipe (Fig. 2). It has been collected in rainforest (mata de tabuleiro) and in scrub vegetation on coastal sand dunes (restinga). Data are insufficient to make a concrete assessment of the conservation status of the species, but given the ongoing destruction of the remaining fragments of natural vegetation in the region, it is likely to be threatened.

Phenology. —Flowering collections have been gathered in January, March and June; fruiting collections were made in May, July and November.

Additional Specimens Examined. BRAZIL. Alagoas: Mun. Arapiraca, próximo a torre da Embratel, 9 Jun 1981 (fl), *R. P. Lyra et al. 827* (RB); Mun. Barra de São Miguel, rodovia AL-101, ca. 2 km do entrocamento da AL-215, sentido Piaçabuçu, Dunas do Cavalo Russo, 9°47'14"S, 35°52'18"W, 40–70 m, 18 Jun 2000 (bud), *A. M. Amorim et al. 3511* (CEPEC, MO, NY); Mun. Coité do Noia, Serra do Brejo, 3 Mar 1983 (bud), *M. N. R. Staviski & G. L. Esteves 537* (K); Mun. Coruripe, Usina Coruripe; 09°59’40.3”S–10°0.95’S, 36°14.233’W–36°15.498’W, 130–135 m, 4 Nov 2002 (fr), *W. W. Thomas et al. 13289* (CEPEC, HUEFS, MO, NY); Mun. Igaci, Serra do Breu, 11 May 1982 (fr), *R. P. Lyra & M. N. Staviski 498* (RB); Mun. Marechal Deodoro, encosta de tabuleiro, próximo às dunas do Cavalo Russo, 9 Dec 1998 (fr), *R. P. Lyra-Lemos 4085* (HUEFS); Olho D'Água, encosta de tabuleiro, APA de Santa Rita, 29 Oct 1987 (fl), *L. S. Moreira & M. N. R. Staviski 144* (HUEFS); Mun. Penedo, APA Marituba do Peixe, Estrada para Marituba do Peixe, próximo a Capela, 10°19’41”S, 36°29’38”W, 28 Jul 2008 (fl, fr), *H. C. de Lima et al. 6943* (RB); Mun. Porto Calvo, Bela Vista a 6 km da Zona Urbana, 23 Nov 1982 (fl), *R. P. Lyra & M. N. Staviski 757* (K, RB). **Sergipe:** Mun. Pirambú, estrada para Ponta dos Magues, próximo a ponte, 28 Jan 1992 (fl), *C. Farney et al. 2970* (RB).

Swartzia alagoensis belongs to *Swartzia* section *Acutifoliae* (R. S. Cowan) Torke & Mansano, which among the sections of the genus is characterized by a stipellate and usually marginate or winged leaf rachis, relatively numerous leaflets, estipulate bracts, bracteolate pedicels, a white petal, the ovary stipe and ovary proper of similar length, the style notably shorter and lateral or oblique, a punctiform or truncate stigma, single-compartmented fruits with little or no sub-compartmentalization between seeds, and typically a yellow or orange seed aril. Within section *Acutifoliae*, *S. alagoensis*, is closely allied with taxa of the *S. flaemingii* complex, which have relatively narrow, oblong leaflets and a pubescent gynoecium. It differs from the typical variety of *S. flaemingii* distributed primarily in Rio de Janeiro and São Paulo states in its geographical distribution, smaller bracteoles, thinner, more appressed (versus erect) pubescence, and in having the locule of the ovary glabrous (versus densely tomentose). It is probably most closely related to *S. psilonema*, a widespread species of the dry interior of northeastern Brazil. Both species have the ovary locule glabrous, but, as elaborated in the key that follows, *S. alagoensis* differs from *S. psilonema* not only in its habitat and distribution, but also in its more appressed pubescence, strongly concolorous leaflets, and in having the upper surface of the leaflets essentially glabrous (versus tomentulose).

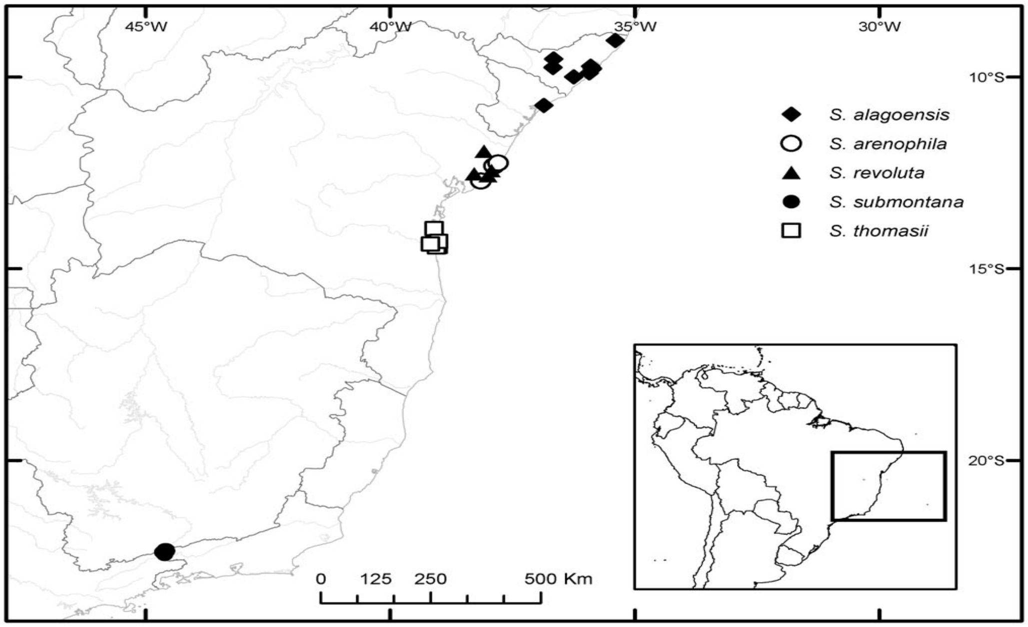

FIG. 2. *Geographic distributions of Swartzia alagoensis*, *S. arenophila*, *S. revoluta, S. submontana*, and *S. thomasii*.

Swartzia arenophila R. B. Pinto, Torke & Mansano, **sp. nov.** Type: Brazil. Bahia: Mun. Entre Rios, Praia de Massarandupió, entroncamento do Km 88 da Linha Verde. Dunas ao lado esquerdo da estrada de terra. 12°18'7"S, 37°52'48"W, 21 Jul 2010 (fl), *R. B. Pinto & T. C. Arantes 115* (holotype: RB; isotypes: CEPEC, MO, NY, UEC). (Fig. 3, 4 A–C)

Rachidibus stipellatis et marginatis vel alatis, bracteis estipulatis, pedicellis bracteolatis, petalo albo, stipito minus quam 1.5-plo longiore quam ovario, stylo obliquo et minus quam 0.3-plo longiore quam ovario, stigmate truncato vel punctiformi, fructibus 1–aliquot-seminatis, ellipticis in cicumscriptio, loculo haud diviso et inter semines pericarpio haud vel leviter constricto ad sectionem *Acutifoliae* (R.S.Cowan) Torke & Mansano referenda; sed foliolorum margine valde revoluto, laminis quasi glabris, foliolis lateralibus 2–5-jugatis, calyce dense piloso-sericeo intus, staminibus maioribus plerumque 2 vel 3, gynoecio glabro, stipito quam longiore vel plus quam longiore quam ovario et arillo lineari singularis.

Shrub or small tree to ca. 2 m tall; trunk cylindrical; bark scaly, exfoliating in small more or less square plates, light-gray; pubescence mostly of weakly flexuous to fairly straight, appressed to semi-erect, unbranched, whitish or ferruginous hairs, mostly 0.2–0.5 mm long, ca. 1 mm long on the interior face of the calyx, in some places mixed with triangular, subulate, or clavate, muticellular glands, these 0.05–0.6 mm long; leaf-bearing branchlets 1.2–5.5 mm thick, tomentose to thinly sericeo-strigose, glabrescent. Stipules lanceolate to triangular, 1.3–9 X 0.5–2.3 mm, sericeo-strigose, glabrescent, often bearing subulate to clavate glands marginally, caducous. Leaves imparipinnate, with 2–5 pairs of opposite lateral leaflets; petioles marginate to somewhat winged, basally pulvinate, 0.8–3 cm long, sparsely pilose or sericeo-strigose, glabrescent; rachis 3–14 cm long, stipellate, winged adaxially, often bearing clavate to subulate multicellular glands at leaflet insertions or between leaflets adaxially, sparsely pilose or sericeo-strigose, the wings narrowly obtriangular or clavate, 1.8–4.5 mm wide measured across the rachis, the margin recurved, the stipels triangular to filiform, 2–4.9 mm long; petiolules terete, dilated basally, 1.2–1.5 X 1.3–1.6 mm, thinly pilose, glabrescent; leaflet blades coriaceous, glabrous or essentially so, ovate to elliptic, the margin strongly revolute, 1.7–3.6 times longer than wide, those of the terminal leaflets 6.5–8.4 X 2.3–3.4 cm, those of the lowermost lateral leaflets 3.4–6.5 X 1.6–2.5 cm, those of the largest distal or medial lateral leaflets 5.3–9 X 2–3.4 cm, the base asymmetrically cordate, largely concealing the petiolule, the apex broadly acute, the adaxial surface glabrous, lustrous, somewhat rugose from the impressed venation, the abaxial surface dull, mostly glabrous, sparsely pilose to sericeo-strigose on the midrib, the midrib and secondary veins impressed adaxially, raised-cariniform abaxially, other venation prominulous to immersed on both surfaces, the secondary veins ca. 10-paired, fairly straight, ascending at 15°–30°. Inflorescenses simple or compound racemes with a single order of branching, borne in leaf axils or on annotinous or somewhat older, defoliated branches, the flowers spirally arranged, the axes green, more or less terete, 10–35 cm long, 1.5–4 mm thick, densely ferruginous-tomentulose to strigose; bracts triangular, 1.7–3.4 X 1.5–2.1 mm, densely sericeo-strigose abaxially, glabrous adaxially, caducous; pedicels dorso-ventrally compressed, dilated apically, 5.8–10.7 X 1.2–1.6 mm, densely ferruginous-tomentulose to sericeo-strigose; bracteoles opposite, inserted at the apex of the pedicel, ovate-lanceolate to narrowly triangular, 2.5–3.4 X 1–1.5 mm, densely sericeo-strigose abaxially, glabrous adaxially; flower buds ovoid to ellipsoid, 6–6.9 X 5–5.5 mm, densely ferruginous sericeo-strigose. Calyx entire in bud, splitting irregularly to reveal densely silvery-cream to light-golden pilose-sericeous interior, the segments 4–6, subequal, ovate to elliptic, 5.5–9 X 2.7–7.4 mm. Corolla monopetalous; petal adaxial, white, membranous, sparsely villous abaxially, glabrous adaxially, the claw basally truncate, apically dilated, ca. 4.2 mm long, 1.2 mm wide at base, 3.2 mm wide at apex, the limb oblate-elliptic or ovate, apically rounded, basally cordate to truncate, ca. 9.3–14 X 11.9–15.2 mm, the venation subpalmate with ca. 9 primary veins, the central vein more robust than the others. Androecium zygomorphic, the stamens dimorphic; larger stamens 2–3 (–4), abaxial in a single row, the filaments white, sparsely villous, dorso-ventrally compressed, 7.2–7.4 mm long, tapering apically, 0.8–0.9 mm thick at middle, the anthers cream-colored, bright-yellow when dehisced, ovate to elliptic in outline, 2.1–3 X 1.1–1.5 mm, the smaller stamens ca. 100, adaxial in several irregular rows, glabrous, the filaments white, terete, 3.7–9.5 X 0.1–0.2 mm, the anthers bright yellow, elliptic to circular in outline, 0.7–1 X 0.8–0.9 mm. Gynoecium monopistillate, light green, whitish at base, glabrous, the stipe terete to elliptic in cross section, dilated basally and apically, 5–6.7 mm long, 0.3–0.5 mm thick at middle, the ovary inequallaterally arcuate-elliptic, laterally compressed, 3.5–4.6 X 1.4–1.7 mm, the ovules ca. 8, the style conical, more or less terminal, but essentially perpendicular to the long-axis of the ovary due to the abrupt curvature of the ovary apex, 0.6–1.5 X 0.2–0.4 mm, the stigma truncate to punctiform. Pods maturing brown or greenish- brown, coriaceous, glabrous, dehiscing along both margins, the stipe terete, dilated basally and apically, 1.3–1.8 cm long, 1–3 mm thick at middle, the body smooth to striate, compressed-ellipsoid, somewhat dilated at the seed chamber, the sutures not constricted, 3.5–7.5 X 3.5–5 cm, the base rounded to broadly acute, briefly decurrent on the stipe, the apex obtuse to rounded, sometimes briefly apiculate from the persistent style. Seeds 1–several per fruit, smooth, lustrous, brown or golden-brown, ellipsoid, somewhat laterally compressed, 2.5–3 X 1.7–2 X 1–1.5 cm, the funicle ca. 5 mm long, the raphe extending from the apex to base of seed, the hilum not apparent, the cotyledons unequal, the radicle triangular, much less than half of the length of the cotyledons and exterior to them, the plumule minute, the aril linear, white, fleshy, 2–2.5 cm X 1–2 mm, covering most of the raphe.

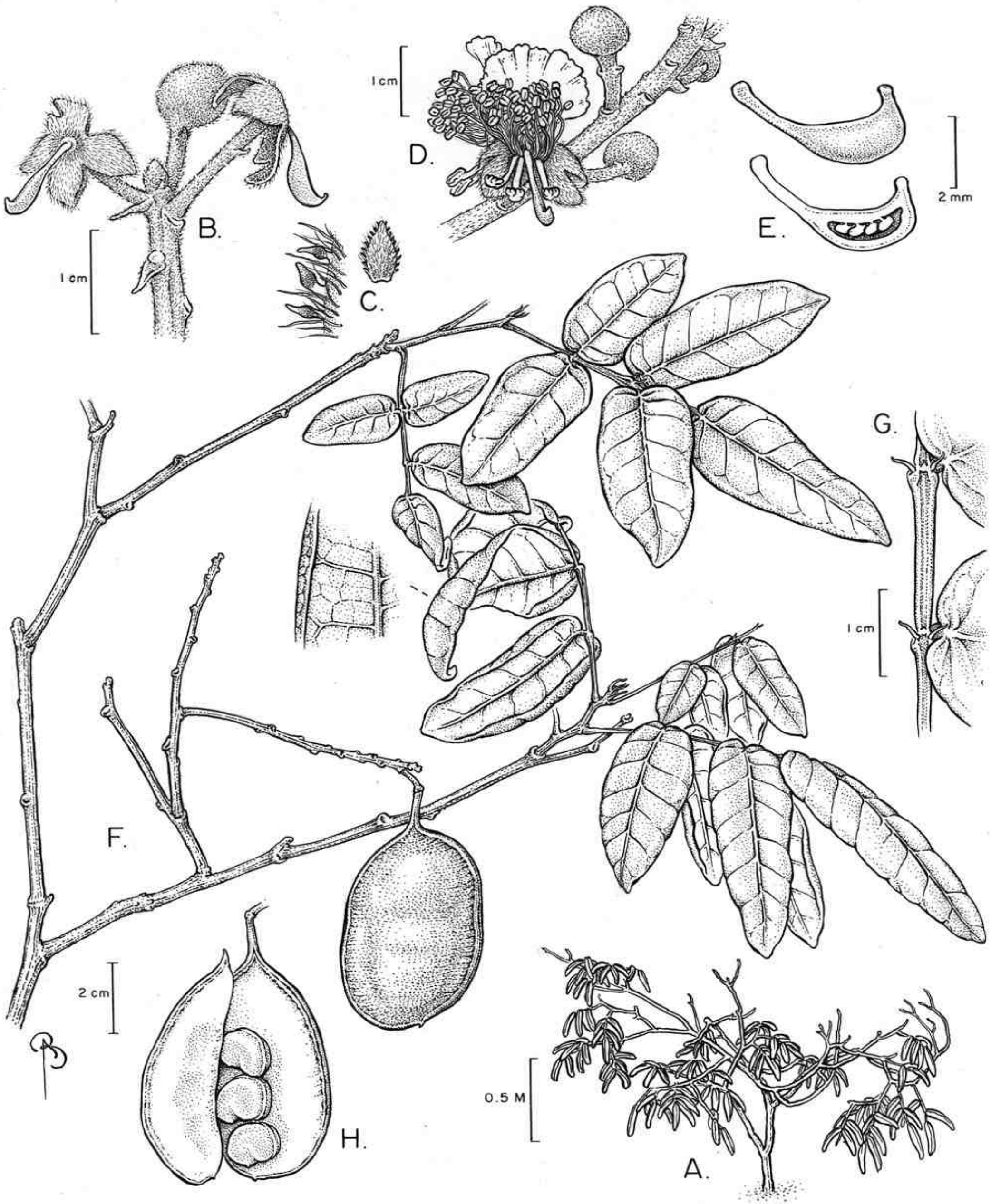

FIG. 3. *Swartzia arenophila*. **A.** Habit. **B.** Inforescence detail with flower bud and post-anthesis flowers. **C.** Bract, with margin detail showing glandular trichomes. **D.** Inflorescence detail with flower buds and anthesis flowers. **E.** Gynoecium, lateral view, with dissection showing ovary locule and ovules. **F.** Fruting branchlet, with detail of leaflet undersurface. **G.** Detail of rachis and leaflet bases. **H.** Sub-mature fruit opened to show developing seeds. (A, from photo vouchered by *Pinto & Arantes 117*, RB; B–E, from *Hatschbach et al. 63121*, G; F–G, from *Mansano et al. 644*, NY.)

FIG. 4. A–C. *Swartzia arenophila*. **A.** Habit. **B.** Inflorescence. **C.** Immature fruit, opened to show seeds. **D–E.** *Swartzia revoluta*. **D.** Habit. **E.** Mature fruit. **F–H.** *Swartzia thomasii*. **F.** Anthesis flower. **G.** Immature fruits, opened to show seeds; leaflet in upper left corner. **H.** Mature seeds, the one on the left with the aril removed. Photo credits: V. F. Mansano (A, C, D), S. A. Mori (G), R. B. Pinto (B, E), W. W. Thomas (F, H).

Distribution, habitat and conservation status.—Swartzia arenophila occurs near sea level in the municipalities of Baixio, Camaçari, Entre Rios, and Mata de São João in northeastern Bahia (Fig. 2). Within its limited distribution, the species is essentially confined to coastal scrub ("restinga arbustiva") habitats on white sand dunes of marine origin, where it is often one of the dominant species. The species is probably threatened, given its restricted geographical distribution in an area with a rapidly expanding tourist resort and summer home industry and the well-known fragility of the coastal dune scrub.

Phenology.—Flowers have been observed in July and August; fruits in November and December.

Additional Specimens Examined. BRAZIL. Bahia. Mun. Baixio, BA-099, Km 109, beira da estrada, 12º09’15”S, 37°48’8”W, 23 Jul 2010 (fl), *R. B. Pinto & T. C. Arantes 140* (RB); BA-099 Km 107, beira da estrada, 12º00’15”S, 37°48’39”W, 23 Jul 2010 (fl), *R. B. Pinto & T. C. Arantes 137* (CEPEC, K, MO, NY, RB, UEC). Mun. Camaçari, Rodovia Linha Verde, próximo ao Km 90, 18 Aug 1995 (fl), *G. Hatschbach et al. 63121* (G); Mun. Entre Rios, Subaúma, 8 Dec 1982 (fr), *J. Arouck et al. 216* (RB); Mun. Mata de São João, Praia de Massarandupió, estrada para praia, 12°18’63”S, 37°52’46”W, 21 Nov 2009 (fr), *V. F. Mansano et al. 644* (NY, RB); *V. F. Mansano et al. 645* (NY, RB); Massarandupió, 12°18’6”S, 37°52’47”W, 21 Jul 2010 (fl), *R. B. Pinto & T. C. Arantes 117* (NY, RB); 12°18’7”S, 37°52’48”W, 21 Jul 2010 (bud), *R. B. Pinto & T. C. Arantes 118* (NY, RB); 12°18’6”S, 37°52’47”W, 21 Jul 2010 (bud), *R. B. Pinto & T. C. Arantes 116* (RB).

Swartzia arenophila is confidently assigned to section *Acutifoliae*, within which it belongs to a distinct species group characterized by having the calyx adaxially pubescent. Among the several species in this group, *S. arenophila* may be most closely related to *S. pickelii*, a species found immediately to the north in the states of Sergipe, Alagoas, and Pernambuco. The latter species grows in "mata de tabuleiro" rainforests on low hills, a relatively more inland, higher elevation habitat than that of the new species. *Swartzia arenophila* differs from *S. pickelii* in its shrubby (versus arborescent) habit, in the length of the bracteoles (2.5–3.4 mm versus 1–1.4 mm), in having 2 or 3 (versus 4 or 5) larger stamens with sparsely villous (versus glabrous) filaments, and relatively more coriaceous, discolorous, adaxially lustrous leaflets, with the margin more strongly revolute. It is also very closely related to the next novelty described herein (*S. revoluta*), with which it probably co-occurs in northeastern Bahia. Both species possess multi-celled, glandular epidermal appendages on the leaf rachis, around and between the leaflet insertions, and on the margins of the bracts and bracteoles (Fig. 3C). Although these often-caducous structures have not been previously reported in *Swartzia*, we suspect that they will be found in other species of the genus and that they may function in attracting ants to deter general herbivory. In our own fieldwork, we have frequently observed ants congregating on the inflorescences and/or leaves of many species of *Swartzia*.

Swartzia revoluta R. B. Pinto, Torke & Mansano, **sp. nov.** Type: Brazil. Bahia: Mun. Mata de São João, Praia do Forte, 24 Jan 2006 (fl), *A. M. Miranda et al. 5415* (holotype: RB; isotype: HUEFS). (Fig. 4 D–E, 5)

Rachidibus stipellatis et marginatis vel alatis, bracteis estipulatis, pedicellis bracteolatis, petalo albo, stipito minus quam 1.5-plo longiore quam ovario, stylo obliquo et minus quam 0.3-plo longiore quam ovario, stigmate truncato, fructibus 1-aliquot-seminatis et ellipticis in cicumscriptio, loculo haud diviso et inter semines pericarpio haud vel leviter constricto, ad sectionem *Acutifoliae* (R.S.Cowan) Torke & Mansano referenda; sed foliolorum margine valde revoluto, laminis abaxialibus strigulosis, foliolis lateralibus plerumque 5–9-jugatis, calyce dense piloso-sericeo intus, staminibus maioribus 4 vel 5, gynoecio sericeo, stipito minus quam longiere quam ovario et arillo lineari singularis.

Shrub or small tree, to ca. 4 m tall; bark scaly, exfoliating in irregular flakes or scales, light gray; exudate red; pubescence mostly of simple, appressed, straight to moderately flexuous, whitish or ferruginous hairs, 0.1–0.3 mm long; leaf-bearing branchlets 3–10 mm thick, strigulose, glabrescent. Stipules orbicular, ovate, elliptic, or triangular, apically acute to briefly acuminate, 2.6–7.7 X 2.2–3.3 mm, sericeo-strigulose, glabrescent, notably persistent on defoliated annotinous or older branchlets. Leaves often clustered distally on branchlets, leaving behind clustered, raised leaf scars, imparipinnate, with (2–) 5–9 pairs of opposite lateral leaflets; petioles basally pulvinate, distally bicarinate to marginate, 0.8–2 cm long, 1.5–2 mm thick at middle, pilose-strigulose; rachis adaxially bicarinate to narrowly winged between leaflet pairs, caniculate between ridges or wings, stipellate at leaflets, 5–15 cm long, 1–2 mm thick at middle of segments, pilose-strigulose, glabrescent, the wings when present 1.5–2.5 mm wide measured across the rachis, the stipels ovate to triangular, convex, 0.8–1 x 0.3–0.4 mm, pilose-strigulose, glabrescent; petiolules pulvinate, partially covered by the lamina base, 0.8–1.1 x 1.2–1.6 mm, pilose-strigulose, glabrescent; leaflet blades coriaceous, strongly discolorous, ovate to elliptic, the margin strongly revolute, mostly 1.7–3.1 X longer than wide, those of the terminal leaflet 3.1–5.1 X 0.9–2.5 cm, those of the lowermost lateral leaflets 2.2–3.8 X 0.8–1.7 cm, those of the distal lateral leaflets 3.8–5.9 X 1.4–2.5 cm, the base inequallaterally obtuse, rounded, truncate, or subcordate, the apex broadly acute, the adaxial surface glabrous, lustrous, minutely rugose, the abaxial surface strigulose, drying ferruginous, the bases of the trichomes rufescent, apparently glandular, the midrib and secondary veins strongly impressed adaxially, raised abaxially, the secondary veins ca. 16, fairly straight, initially ascending at 10–30°, other venation immersed and inconspicuous adaxially, prominulous to immersed abaxially. Inflorescences simple or compound racemes

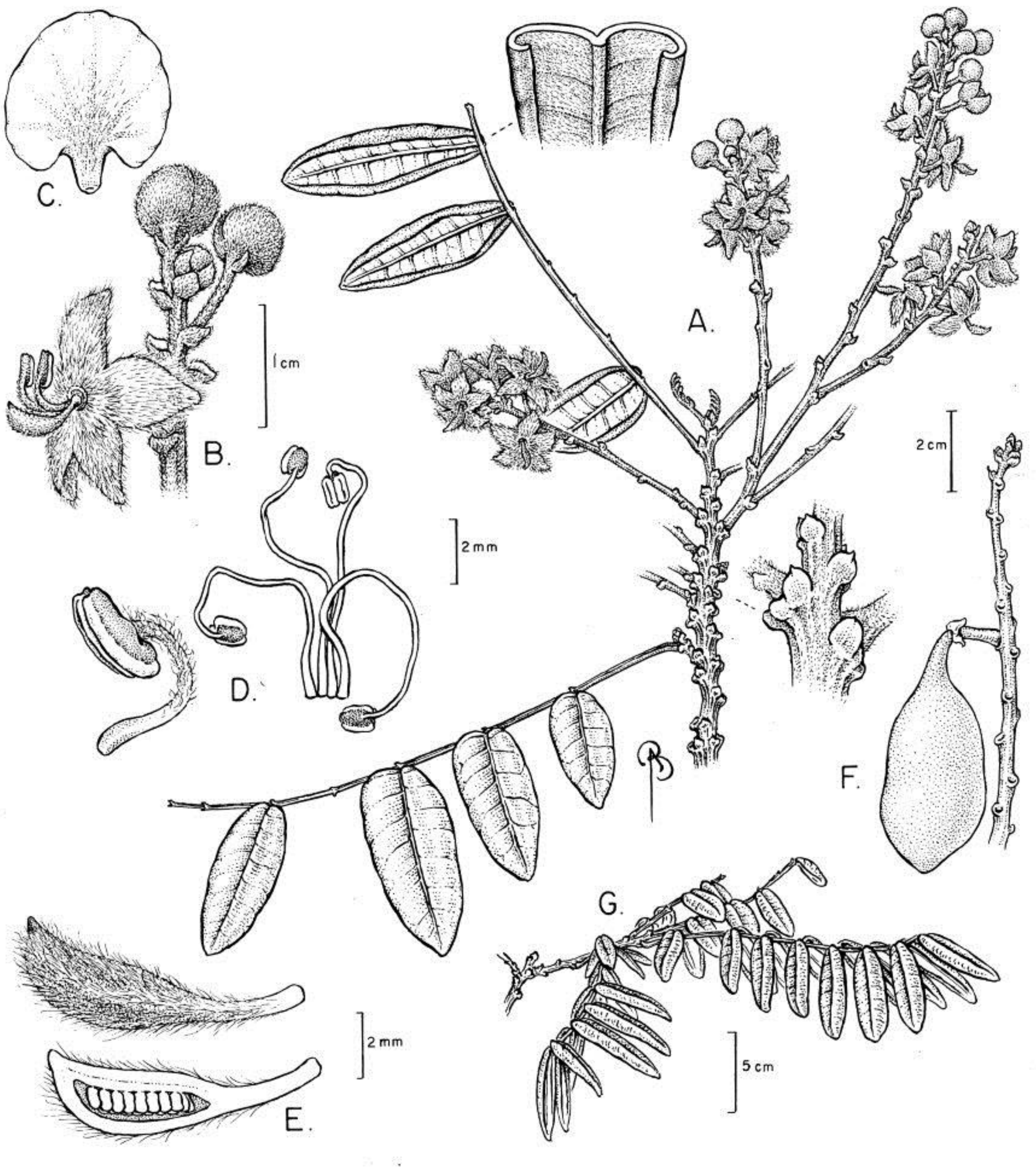

FIG. 5. *Swartzia revoluta*. **A.** Flowering branchlet, with detail of leaflet undersurface. **B.** Inflorescence detail with flower buds and post-anthesis flower. **C.** Petal, abaxial view. **D.** Smaller stamens. **E.** Larger stamen. **F.** Infructescence bearing a mature fruit. **G.** Vegetative branchlet. (A–E, from *Miranda 5415*, RB; F, from photo vouchered by *Pinto & Arantes 119*, RB; from photo vouchered by *Mansano et al. 644*, RB.)

with a single order of branching, arising from leaf axils or from defoliate, annotinous branchlets, to ca. 20-flowered, the flowers spirally arranged, the axes ca. 7–27 cm long, 1–3 mm thick, densely ferruginous-strigulose; bracts broadly ovate to triangular, convex, 2.8–3.7 X 2.5–3.6 mm, densely strigose abaxially, glabrous adaxially; pedicels dorso-ventrally compressed, 6.5–10 mm long, 1.5–1.8 mm thick at middle, apically dilated, densely ferruginous-strigulose; bracteoles opposite, inserted in the distal third of pedicel, ovate to triangular, 1.9–2.3 X 1–1.4 mm, densely strigulose abaxially, glabrous adaxially, caducous; flower buds oblate-ellipsoid, 5.5–7.5 X 6–8 mm, densely ferruginous-strigulose. Calyx entire in bud, splitting irregularly, the interior densely whitish or golden pilose-sericeous, the segments 4–5 (–6), subequal, ovate to elliptic, apically acute, 7–10 X 3.5–9 mm. Corolla monopetalous, the petal adaxial, white, membranous, glabrous adaxially, sparsely sericeo-strigose abaxially, the claw apically dilated, basally rounded, 3.2–3.6 mm long, 2.8–3.5 mm wide at the apex, 1.7–2.3 mm wide at the base, the limb deltoid or broadly ovate, 8.5–11 X 11–13 mm, the apex rounded, the base truncate to cordate, the venation palmate, with 10–12 primary veins, the central vein more robust than the others. Androecium zygomorphic, stamens dimorphic, the larger stamens 4–5, abaxial in a single row, the filaments dorso-ventrally compressed, apically tapering, 7–9 mm long, 0.7–0.9 mm thick at middle, thinly sericeo-pilose, the anthers oblong in outline, 2.5–3.8 X 1–1.4 mm, glabrous except on the sericeo-pilose connective, the smaller stamens ca.100, adaxial in several irregular rows, glabrous, the filaments terete or dorso-ventrally compressed, 7.5–13 X 0.1–0.2 mm, the anthers ovate, elliptic or oblate in outline, 0.7–1.5 X 0.8–1 mm. Gynoecium monopistillate, the stipe densely light-tan sericeous, more or less terete, dilated at base and apex, 3.2–3.9 mm long, 0.7–1 mm thick at middle, the ovary densely light-tan sericeous, inequallaterally arcuate-elliptic in outline, laterally compressed, 4.5–5.8 X 2–2.6 mm, the ovules ca. 16–20, the style essentially lacking or conical and 0.2–0.4 mm long, equally thick, the stigma truncate. Pods maturing brown or yellowish-brown, coriaceous, minutely strigulose, glabrescent, dehiscing along both margins, the stipe terete, strongly dilated at apex, less so at base, 8.8–9.4 mm long, 1.8–2.1 mm thick at middle, the body smooth to striate, more or less ellipsoid, somewhat dilated at the seed chamber, the sutures not constricted, 4.5–5 X 2.5–3 cm. Seeds 1–several per fruit, smooth, lustrous, brown or golden, ellipsoid, somewhat compressed laterally, 1.9–2 X 1.7–2.2 X 1.5–1.7 cm, the funicle ca. 7 mm long, the raphe extending from the apex to base of seed, the hilum not apparent, the aril more or less linear, white, fleshy, 2.5–3 cm X 2–3 mm, covering most of the raphe.

Distribution, habitat and conservation status.—Like *Swartzia arenophila*, *S. revoluta* is known only from costal scrub (shrubby restinga) on white sand dunes in the northern coastal region of Bahia, where it is apparently even more restricted in distribution, having been collected only in the municipality of Mata de São João (Fig. 2). In its xerophytic habitat, *S. revoluta* is one of the dominant species, in some places forming dense populations. The species is threatened by rapid habitat destruction, although part of its known distribution is contained within the nominally protected Reserva Particular do Patrimônio Natural Dunas de Santo Antônio.

Phenology.—Flowers have been observed in December, January, and June; fruits in July and October.

Additional Specimens Examined. BRAZIL. Bahia. Mun. Mata de São João, Sauípe, 12°31’S, 38°17’W, 13 Jun 2000 (fl), *M. L. Guedes et al. 7029* (ALCB, CEPEC); Costa do Sauípe, Fazenda Sauípe, 12°31’S, 38°17’W, 17 Oct 2003 (im fr), *D. M. Loureiro et al. 696* (ALCB); Reserva Particular do Patrimônio Natural Dunas de Santo Antônio, 12°26’S, 37°56’W, 21 Dec 2005 (fl), *C. M. Menezes 385* (HUEFS); Vila de Santo Antônio, RPPN Dunas de Santo Antônio, 12º26’32”S, 37º56’15”W, 21 Jul 2010 (fr), *R. B. Pinto & T. C. Arantes 119* (RB); *R.*

B.Pinto & T. C. Arantes 121 (RB); Vila de Sto. Antônio, RPPN Dunas de Santo Antônio, entrada no km 71, estrada do côco BA-099, 12º26’10”S, 37º56’0”W, 21 Nov 2009 (st), *V. F. Mansano et al. 642* (RB); Massarandupió, dunas próximas a área de brejo sazonal que antecede a praia, 12º27’7”S, 37º56’2”W, 21 Jul 2010 (st), *R. B. Pinto & T. C. Arantes 120* (RB); Massarandupió, a 25km, próximo á região de brejos, 11°56’S, 38°5’W, 29 Mar 2001 (bud), *M. L. Guedes & N. G. Jesus 8093* (ALCB, HUEFS).

Swartzia revoluta belongs to section *Acutifoliae* and is closely related to *S. arenophila*. Both species are shrubs or small trees with an adaxially sericeous calyx and strongly revolute leaflets, hence the specific epithet. *Swartzia revoluta* differs from *S. arenophila* most notably in having a densely sericeous (versus glabrous) gynoecium with the stipe somewhat shorter than the ovary (versus as long or longer), 4–5 (versus typically 2–3) larger stamens with the filaments pilose (versus nearly glabrous), the smaller stamens with the filaments 7.5–13 mm long (versus 3.7–9.5 mm), broadly oblate (versus elliptic to globose) flower buds, and typically 5–9 (versus 2–5) pairs of leaflets, with the lower leaflet surface uniformly strigulose (versus essentially glabrous). Although the two species occur in the same region, individual populations seem to be mostly allopatric. Differences in flowering time between nearby populations of *S. revoluta* and *S. arenophila* were observed in the field in 2009 and may represent an effective reproductive barrier between the two species.

Swartzia submontana R. B. Pinto, Torke & Mansano, **sp. nov.** Type: Brazil. Rio de Janeiro: Mun. Itatiaia, Parque Nacional do Itatiaia, caminho entre Maromba e Macieiras, ca. 1820 m, 29 May 1969 (fl), *D. Sucre & T. Plowman 5192* (holotype: RB; isotype: K). (Fig 1 A–E)

Rachidibus stipellatis et marginatis vel alatis, pedicellis bracteolatis, petalo albo, stipito minus quam 1.5-plo longiore quam ovario, stylo obliquo minus quam 0.3-plo longiore quam ovario, stigmate truncato vel punctiformi, fructibus 1–aliquot-seminatis, ellipticis in cicumscriptio, loculo haud diviso et inter semines pericarpio haud vel leviter constricto ad sectionem *Acutifoliae* (R.S.Cowan) Torke & Mansano referenda; sed indumento adpresso, trichomatibus plerumque 0.1–0.4 mm longis, pulvinulis conspicue canaliculatis, foliolis lateralibus 4–6-jugatis, lamanis abaxialibus et inflorescentiis strigulosis, staminibus maioribus 2 et gynoecio glabro vel strigoso pro parte cum ovario glabro pro parte et loculo glabro singularis.

Tree, exceeding 13 m tall; pubescence mostly of appressed, fairly straight, unbranched, ferruginous, whitish, or golden hairs, 0.1–0.4 mm long; leaf-bearing branchlets 1.5–3.5 mm thick, strigulose, glabrescent. Stipules narrowly triangular, 2.5–4 X 0.8–1 mm, densely strigulose, caducous. Leaves imparipinnate, with 4–6 pairs of opposite lateral leaflets; petioles strigulose, glabrescent, basally pulvinate, bicarinate or marginate adaxially, 1–2.4 cm long, 1–1.4 mm thick at middle, the pulvinus 2.4–5.3 X 1.4–2.2; rachis strigulose, glabrescent, bicarinate-maginate to narrowly winged adaxially between leaflet pairs, caniculate between wing lobes, stipellate at leaflets, 3.9–9.7 cm long, 0.8–1.3 mm thick at middle of segments, the wings narrowly oblong-clavate, 1.2–2.6 mm wide measured across the rachis, the margin revolute, the stipels triangular, 0.3–0.8 X 0.1–0.5 mm, strigulose, glabrescent; petiolules pulvinate, 1.7–3.2 X 1–1.4 mm, strigulose, strongly caniculate adaxially; leaflet blades chartaceous to subcoriaceous, elliptic to oblong-elliptic, 1.8–3.3 X as long as wide, those of the terminal leaflet 3.1–6.4 X 1.1–2 cm, those of the lowermost lateral leaflets 1.9–3.8 X 1–1.8 cm, those of the distal lateral leaflets 3.2–6.6 X 1.2–2.3 cm, the margin deflexed, the base acute, the apex rounded to broadly acute, the adaxial surface mostly glabrous, but with the midrib pilosulose-strigulose, the abaxial surface evenly strigulose, the midrib strongly depressed adaxially, salient abaxially, other venation prominulous to immersed and inconspicuous on both surfaces, the secondary veins 20+, initially ascending at 20°–40°, straight to continuously curving, then forming submarginal loops, the highest-gauge tertiary veins more or less parallel to the secondaries. Inflorescences simple or compound racemes with a single order of branching, arising from leaf axils or from annotinous branchlets, to ca. 20-flowered, the flowers spirally arranged, the axes 3.9–13.5 cm long, 1–2.2 mm thick, densely ferruginous-strigulose; bracts triangular, occasionally stipulate, ca. 1.9 X 1.4 mm, concave and glabrous adaxially, convex and strigulose abaxially, caducous, the stipules triangular, ca. 0.8 X 0.5 mm long; pedicels flattened-elliptic in cross section, 7–11 mm long, 1.5–2.1 mm thick at middle, densely ferruginous-strigulose; bracteoles opposite to subopposite, inserted at or somewhat above center of pedicel, triangular, 1.3–1.9 X 0.5–0.7 mm, densely strigulose abaxially, glabrous adaxially, caducous; flower buds densely ferruginous-strigulose, ellipsoid to ovoid, 7.1–7.8 X 5.6–6.2. Calyx entire in bud, splitting irregularly to reveal glabrous, light-green interior, the segments 4–5, subequal, elliptic to obovate, apically acute, 6–10 X 3–7.5 mm. Corolla monopetalous, the petal adaxial, white, membranous, adaxially glabrous, abaxially strigulose, the claw basally truncate, apically dilated, 3.7–4.8 mm long, 1.6–2.1 mm wide at the base, 2.8–4.1 mm wide at the apex, the limb oblate-ovate, basally truncate to subcordate 1.5–2.2 X 1.9–2.7 cm, the venation palmate, with ca. 13 primary veins. Androecium zygomorphic, the stamens glabrous, dimorphic, of two sizes; larger stamens 2, abaxial in a single row, the filaments white, dorso-ventrally compressed, 8.5–11.5 mm long, ca. 0.8 mm thick at base, the anthers elliptic in outline, ca. 2.5 X 1.4 mm, the smaller stamens ca. 100, adaxial to central on the floral axis, the filaments white, terete or dorso-ventrally compressed, 6.4–9.6 X 0.2–0.3 mm, the anthers elliptic, circular, or oblate-elliptic in outline, 0.6–1.2 X 0.7–1.1 mm. Gynoecium monopistillate, glabrous to somewhat densely, though incompletely golden-strigose; the stipe glabrous to densely strigose, but then glabrous at base, terete or somewhat dorso-ventrally compressed, dilated at base and apex, 3.5–4.1 mm long, 0.7–0.9 mm thick at middle, the ovary glabrous to densely strigose, but then partially glabrous on sutures and/or lateral faces, arcuate-elliptic in outline, laterally compressed, 5.7–6.9 X 2.3–3 mm, the locule glabrous, the ovules 6–10, the style glabrous or nearly so, obliquely terminal, recurved, terete, apically tapering, 1.4–2 mm long, 0.4–0.6 mm wide at the middle, glabrous, the stigma obliquely truncate to punctiform. Immature fruits glabrous, 1–several-seeded, the stipe 8.1–12 mm long, ca. 1–1.5 mm thick at middle, dilated at apex, the body inequallaterally ovate to elliptic in outline, laterally compressed, not obviously constricted along the sutures, the base and apex acute or attenuate.

Distribution, habitat and conservation status.—Swartzia submontana is known only from the Parque Nacional do Itatiaia in the Serra da Mantiquera mountain range in the northwestern corner of the state of Rio de Janeiro, near the border of Minas Gerais and São Paulo states. As indicated by the specific epithet, *S. submontana* was collected in humid pre-montane forest at ca. 1800 m elevation. The species may be more widespread than the few available collections attest to, as most of the wet southern front of the Serra de Mantiquera range is poorly collected. The conservation status of *S. submontana* is unknown.

Phenology.— Flowering and fruiting individuals have been encountered in May.

Additional Specimens Examined. BRAZIL. Rio de Janeiro: Mun. Itatiaia, Parque Nacional do Itatiaia, Macieiras, ca. km 14, 1830 m, 16 May 1941 (fl), *W. D. Barros 288* (RB, US); Parque Nacional do Itatiaia, caminho entre Maromba e Macieras, ca. 1820 m, 29 May 1969 (fl), *T. Plowman & D. Sucre 2892* (GH, K, US).

Another new member of section *Acutifoliae*, *S. submontana* is closely allied to the *S. flaemingii* and *S. macrostachya* species complexes. However, it is unusual among these taxa and unique in having the combination of distinctly caniculate petiolules, two (versus four) larger stamens, the external surface of the gynoecium glabrous to patchily sericeous (versus densely and evenly pubescent), and a glabrous ovary locule. *Swartzia submontana* is perhaps most closely related to the typical variety of *S. flaemingii*, with which it shares rounded oblong leaflets. However, it differs in having four to six (versus nine to twelve) pairs of leaflets, smaller bracteoles, and a more appressed indument. The distribution of *S. submontana* is probably discontinuous with that of *S. flaemingii*, a more coastal species of lower elevation wet forest.

In its known habitat, *S. submontana* co-occurs with *S. pilulifera* Benth. Although the latter has much smaller apetalous flowers, the two species have superficially similar leaves and are difficult to distinguish in vegetative state. Upon close inspection, the leaves of *S. submontana* differ from those of *S. pilulifera* in having appressed (versus erect) pubescence, a glabrous (versus pubescent) leaflet margin, and a more strongly winged rachis.

Swartzia thomasii R. B. Pinto, Torke & Mansano, **sp. nov.** Type: Brazil. Bahia: Mun. Uruçuca, Serra Grande study site, 7.3 km N of Serra Grande on road to Itacaré, transect tree no. 45, 14°25'S, 39°1'W, 7 May 1992 (fl, fr), *W. W. Thomas et al. 9182* (holotype: NY; isotypes: ALCB, K, MO, US). (Fig. 4 F–H, 6)

Organis maturis totis glabris, rachidibus nudis et estipellatis, foliolis magnis, coriaceis et reticulato-venosis, bracteis estipulatis, pedicellis bracteolatis, petalo albo, fruitibus magnis, 1–4-sematibus et ellipticis obovatis vel oblongis in cirumscriptio, inter semines pericarpo leviter constricto, et arillo margine integro ad secionem *Glabriplantae* Torke & Mansano referenda; sed foliolorum venis secundariis 10–32° ascendens et parallelis ad venas tertias, staminibus maioribus 3 vel 4, ovario ca. 13 mm longis, plus quam 2-plo longiore quam stipito et stigmate capitellato singularis.

Tree to ca. 15 m tall, glabrous on mature organs; trunk to ca. 20 cm in diameter; bark smooth; leaf-bearing branchlets, 5–8 mm thick. Stipules not seen. Leaves imparipinnate or paripinnate by abortion of the rachis, with 2 pairs of opposite to subopposite lateral leaflets; petioles terete, basally pulvinate, 6–15 cm long, 2.8–4.5 mm thick at middle, the pulvinus 7.5–14.7 X 4.5–7.5 mm; rachis terete, estipellate, unwinged, 12–40 cm long, 2–4 mm wide at middle of segments; petiolules pulvinate, 10–19.5 X 2.5–5.5 mm; leaflet blades coriaceous, broadly ovate to elliptic, mostly 2–3 times longer than wide, those of terminal leaflet 16–24 X 9.5–15 cm, those of the basal lateral leaflets 13.5–20 X 7–13.5 cm, those of the distal lateral leaflets 19–25.5 X 10–14.5 cm, the margin slightly deflexed, the base rounded to obtuse, the apex obtuse or rounded, then usually briefly acuminate, the acumen 4–12 (–18) mm long, sometimes aborted, the midrib depressed adaxially, salient abaxially, other venation raised-reticulate on both surfaces, the secondary veins ascending initially at 10–32°, relatively straight, then curving distally and forming submarginal loops, the included intersecondary and highest-gauge tertiary veins closely parallel to the secondaries. Inflorescences simple racemes, often fasciculate, arising from annotinous or somewhat older branches, to ca. 10-flowered, the flowers spirally arranged, the axes green, ca. 3.5–10 cm long, 1.5–2.8 mm thick; bracts triangular, abaxially convex, the apex acute to acuminate, 1–1.8 X 0.8–1.4 mm, pedicels green, dorso-ventrally compressed, dilated apically, 11–19 mm long, 2.5–3.1 mm thick at middle; bracteoles opposite to strongly subopposite, inserted at the middle of pedicel or somewhat above or below the middle, triangular, 0.7–1.1 X 0.3–0.5 mm; flower buds green, ellipsoid to globose, 7.6–10.7 X 5.3–9.5 mm. Calyx, more or less actinomorphic, entire in bud, splitting irregularly to reveal light green interior, the segments 4–5, sub-equal, more or less elliptic, apically acute, 11–15 X 4–10 mm. Corolla monopetalous, the petal adaxial, white, membranous, the claw basally truncate, apically dilated, 1.2–3 mm long, 0.5–1 mm wide at base, 2.4–2.6 mm wide at apex, the limb deltoid-ovate, basally cordate, 1.8–2 X 1.8–2.2 cm, the venation subpalmate with 11–13 primary veins, the central vein more robust than the others. Androcium zygomorphic, the stamens dimorphic; larger stamens 3–4, abaxial in a single row, the filaments cream-colored or pale yellow, dorso-ventrally compressed, tapering apically, ca. 16.5 mm long and 1 mm thick near base, the anthers elliptic in outline, ca. 3.6 X 1.7 mm, the smaller stamens ca. 100, adaxial, the filaments cream-colored or pale yellow, 7.5–10.5 X 0.1–0.2 mm, the anthers ovate in outline, 1–1.6 X 0.9–1.5 mm. Gynoecium monopistillate, cream-colored or pale-yellow, the stipe terete or oval in cross section, dilated basally and apically, ca. 5 mm long and 1 mm thick near middle, the ovary narrowly arcuate-elliptic in outline, laterally compressed, ca. 13 X 3 mm, sometimes abortive, the ovules ca. 6, the style oblique-terminal, terete, ca. 3.8 mm long and 0.7 mm thick at middle, the stigma capitellate. Pods green to pale yellow, short-stipitate, the body irregularly elliptic to oblong in outline, weakly compressed laterally, somewhat dilated at seed chambers but only weakly constricted along the prominently raised sutures, 14–30 X 7–7.5 cm. Seeds 1–4 per fruit, brown, flattened-ellipsoid, ca. 9.5–9.7 X 5.5–5.8 cm, often irregularly shaped and about half as long in multi-seeded fruits, the aril smooth, maturing bright yellow-orange, bilobed, the lobes elliptic, ca. 7–7.5 X 4.8–5 cm, covering most of the lateral faces of the seed, the cotyledons asymmetrical.

Distribution, habitat and conservation status.—Swartzia thomasii is known from a handful of wet forest fragments on heavy loam soils at less than 200 m elevation in the municipalities of Camamu, Itacaré and Uruçuca in the southern Bahian coastal region (Fig. 2). Most of the original forest in this region was long ago converted to cacao plantation, and little of what remains is well protected. The species, which is undoubtedly threatened, is present in the recently protected Serra Grande Forest Reserve, and it has been reported from the Serra do Conduru State Park (as "*S. reticulata*;" Martini et al., 2007). We have not been able to examine voucher material from the latter area.

Phenology.—Flowering and fruiting appear to be sporadic, possibly with two peaks. According to specimen labels, flowers have been observed in December, January, May, and July, fruits in December, May, and September.

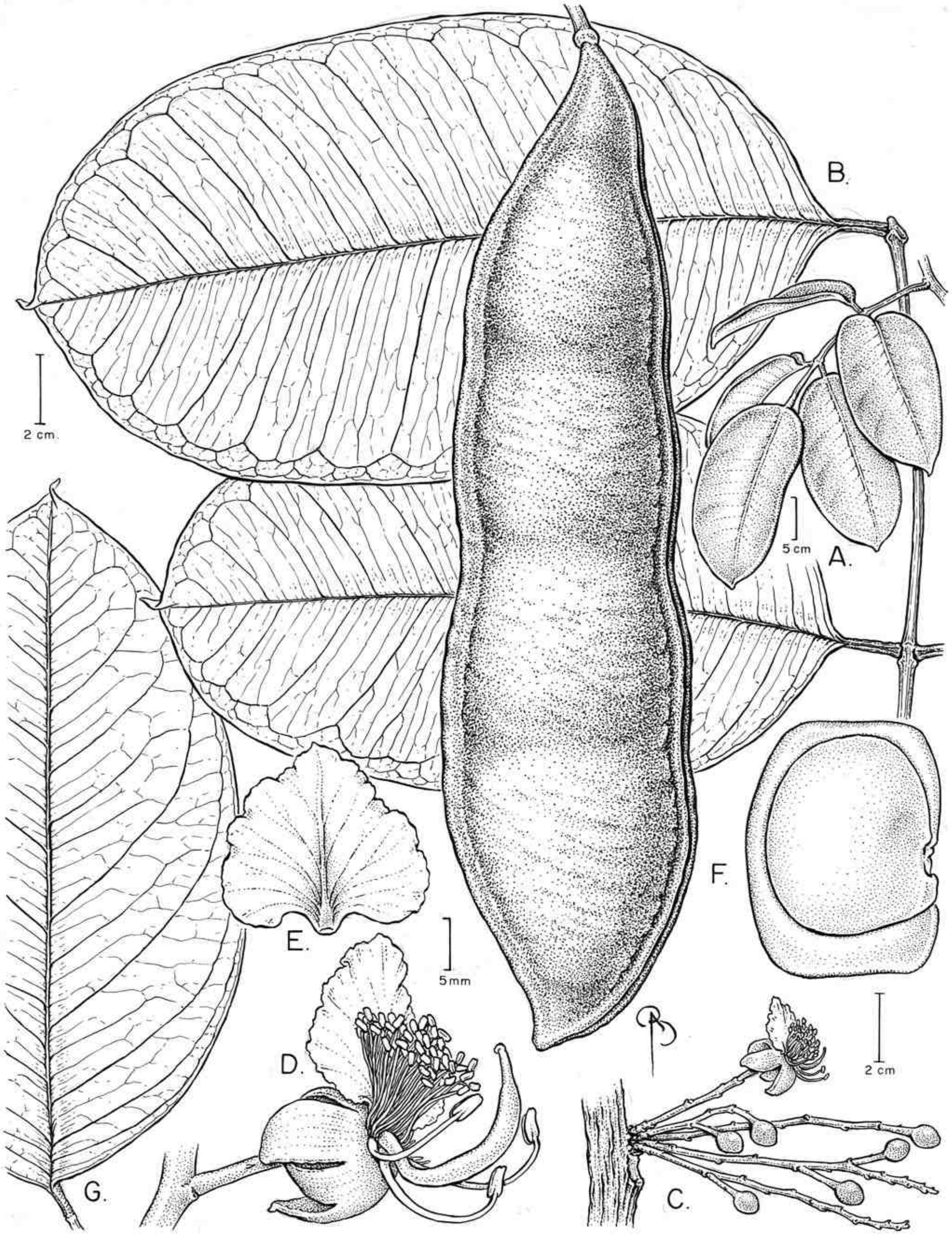

FIG. 6. A–F. *Swartzia thomasii*. **A.** Leaf. **B.** Detail of rachis and leaflets, adaxial view. **C.** Inflorescences. **D.** Anthesis flower. **E.** Petal, abaxial view. **F.** Fruit and arillate seed. **G.** *Swartzia reticulata,* leaflet, for comparison. (A, F, from *Mori et al., 13060*, NY, and photos; B, D, E, from *Thomas et al. 9182*, NY, and photo; C, from *Amorim et al. 919*, NY; G, from *Ackerly et al. s.n., INPA/WWF 1302.980.2*, NY.)

Additional Specimens Examined. BRAZIL. Bahia: Mun. Camamu: Acaraí rodovia, lado sul, 2 Jul 1971 (fl), *T. S. Santos 1719* (CEPEC); Mun. Itacaré, estrada de Itacaré/Taboquinhas, ca. 6 km de Itacaré, loteamento da Marambaia, 14 Dec 1992 (fl), *A. M. Amorim et al. 919* (CEPEC, K, NY, RB); rodovia Itacaré/Ilhéus, ca. 6 km a partir da sede do município, assentamento da Marambaia, 11 Nov 1998 (bud), *A. M. Amorim et al. 2652* (CEPEC); ca. 6 km SW of Itacaré, on side road S from the main Itacaré/Ubaitaba road, S of the mouth of the Rio de Contas, 14°19'S, 39°1'W, 0–100 m, 29 Jan 1977 (st), *R. M. Harley et al. 18364* (CEPEC, K, NY, US); ca. 8 km SW of Itacaré, along side road S from main Itacaré/Ubaitaba road, S of the mouth of the Rio de Contas, 14°20'S, 39°3'W, 0–100 m, 31 Jan 1977 (fl), *R. M. Harley et al. 18437* (CEPEC, K, NY, US); Mun. Uruçuca, Distrito de Serra Grande, 7.3 km na estrada Serra Grande/Itacaré, Fazenda Lagoa do Conjunto Fazenda Santa Cruz, 14°25'S, 39°1'W, 7 Sep 1991 (fr), *A. M. Carvalho et al. 3664* (NY); estrada que liga Uruçuca com Serra Grande, a 28 km ao NE de Uruçuca, 2 Dec 1979 (fr), *S. A. Mori et al. 13060* (CEPEC, K, NY); 4.6 km de Serra Grande em direção a Itacaré, 14°25'50"S, 39°3'13"W, 24 Jan 2004 (bud), *T. S. Nunes et al. 998* (HUEFS); 7.3 km N of Serra Grande on road to Itacaré, Fazenda Lagoa do Conjunto Fazenda Santa Cruz, parcel 2, tree no. 48, 14°25'S, 39°1'W, 1–12 Jul 1991 (st), *W. W. Thomas et al. 6861* (NY); 7.3 km N of Serra Grande on road to Itacaré, Fazenda Lagoa do Conjunto Fazenda Santa Cruz, parcel 3, tree no. 9, 14°25'S, 39°1'W, 1–12 Jul 1991 (st), *W. W. Thomas et al. 6903 (CEPEC, NY)*; 7.3 km N of Serra Grande on road to Itacaré, Fazenda Lagoa do Conjunto Fazenda Santa Cruz, parcel 5, tree no. 169, 14°25'S, 39°1'W, 1–12 Jul 1991 (fr), *W. W. Thomas et al. 7022* (CEPEC, MO, NY); 7.3 km N of Serra Grande on road to Itacaré, Serra Grande study site, 14°25'S, 39°1'W, 7 Sep 1991 (fr), *W. W. Thomas et al. 9754a* (NY).

The affinities of *Swartzia thomasii* lie with the species of the small section *Glabriplantae* Torke & Mansano, which is characterized by having the combination of entirely glabrous mature organs, a naked, estipellate leaf rachis, large coriaceous leaflets with reticulate venation, estipulate bracts, bracteolate pedicels, a white petal, relatively massive, 1–4-seeded fruits, with a single compartment, and large seeds that are nearly covered by an entire-margined aril. *Swartzia thomasii* is very closely related to and probably the sister taxon of the Amazonian species *S. reticulata*, found north of the Amazon River from the vicinity of Manaus, Brazil to southern Guyana and Suriname. Although it has for decades been filed under *S. reticulata* in herbaria, the new species differs subtly but consistently from the Amazonian species in the venation of its leaflets; in *S. thomasii* the secondary veins are relatively straighter and less ascending (initially at 10–32° with respect to the latitudinal axis of the leaflet versus 35–48° in *S. reticulata*), and the secondary, intersecondary, and tertiary veins are more closely parallel (Fig. 6). In addition, examination of the few available flowering collections of the two species suggest that they differ in the number of abaxial stamens (3–4 in *S. thomasii* versus 5–7 in *S. reticulata*), the length of the ovary-stipe relative to the ovary proper (less than half as long versus more than half as long), the length of the style (ca. 3.8 mm in versus ca. 2.5 mm), and the shape of the stigma (capitellate versus punctiform).

The specific epithet honors the collector of the type specimen, Dr. William Wayt Thomas of The New York Botanical Garden, for his long-standing collaborative research on the flora of northeastern Brazil.

Key to the Species and Varieties of *Swartzia* in Extra-Amazonian Brazil

1\. Leaflet midrib raised-cariniform above; pedicels lacking bracteoles; flower bracts usually supplied with a pair of stipules basally; petal yellow; mature pods orange; mature seeds black; mature aril white; stigma capitate or capitellate; inflorescences usually borne in the axils of current leaves and less than 8-flowered; trunk slash lacking red or pinkish exudate; bark smooth.

  2\. Lateral leaflets lacking, leaves unifoliolate. ....*S. simplex var. continentalis* Urb.

  2\. Lateral leaflets 1–7 paired.

    3\. Lateral leaflets 1-paired; flower buds 7–13 mm in diameter; larger stamens 6–11. ....*S. simplex var. grandiflora* (Raddi) R. S. Cowan

    3\. Lateral leaflets 1–7-paired; flower buds 4–9.3 mm in diameter; larger stamens 4–8. .... *S. myrtifolia var. elegans* (Schott) R. S. Cowan

1\. Leaflet midrib usually impressed or more or less flush with the laminar surface above, rarely raised; pedicels (or base of calyx) with or without paired bracteoles; flower bracts usually lacking stipules (if stipulate, the pedicels bracteolate); petal usually white or absent, occasionally yellow; mature pod green, brown, yellow, or orange; mature seeds variously colored, sometimes black; aril maturing yellow, orange, red, or white; stigma usually punctiform or truncate, rarely capitellate; inflorescences often borne on stems or on branches below leaves, sometimes axillary, often more than 8-flowered; trunk slash often with red or pinkish exudate; bark usually exfoliating.

4. Flowers apetalous; pedicels without bracteoles; leaflet venation finely reticulate above; mature pods usually orange, mostly single-seeded, the body globose or plumply ellipsoid, less than 5 mm long, with the apex and base rounded; seeds maturing black; aril white.

  5. Ovary densely and uniformly pubescent; pods retaining pubescence, at least at the base and/or on the stipe.

    6. Leaf rachis naked, estipellate at leaflet pairs; leaflets apically acuminate, sparsely strigulose below; ovary sericeous, the pubescence appressed; indumentum mostly whitish. …...……..…………… *S. capixabensis* Mansano

    6. Leaf rachis alate or marginate, stipellate at leaflet pairs; leaflets apically rounded or retuse, densely pilose below; ovary pilose, the pubescence erect; indumentum mostly ferrugineous. ……………………….......................….....*S. pilulifera* Benth.

  5. Ovary glabrous or very incompletely pubescent; pods entirely or essentially glabrous.

    7. Leaflets densely pilose-tomentose below. …...............……..*S. riedelii* R. S. Cowan

    7. Leaflets glabrous to thinly strigulose below.

      8. Pedicels mostly 2–8 mm long; ovary stipe to 2.6–3.5 mm long; gynoecium black when dry. …..................…..………………..…*S. apetala* Raddi *var. apetala*

      8. Pedicels mostly 12–30 mm long; ovary stipe 4.5–7.5 mm long; gynoecium green or pale yellow-green when dry.
      ....*S. apetala var. glabra* (Vogel) R. S. Cowan

4. Flowers usually petalous, rarely apetalous; pedicels with or without paired bracteoles; leaflet venation various, often immersed above, sometimes reticulate; mature pods green, brown, yellow, or orange; often multi-seeded, the body variously shaped, usually more than

5 cm long, frequently with the apex and/or base acute or attenuate; seeds usually brown, white, yellow or green; aril usually yellow, orange, red or absent, rarely white.

9. Petal yellow; stamens fewer than 30.

  10. Lateral leaflets alternate; pedicels with paired bracteoles, androecium strongly zygomorphic, with the two larger stamens abaxial. ....*S. alternifoliolata* Mansano

  10. Lateral leaflets opposite; pedicels without bracteoles; androecium semi-actinomorphic with the 2–7 larger stamens more or less encircling the smaller stamens. ....*S. jorori* Harms

9. Petal white or lacking; stamens more than 30.

  11. Pistils two per flower. …...............................………*S. dipetala* Willd. ex Vogel

  11. Pistils one per flower.

    12. Leaflets large, frequently more than 8 cm wide, thickly coriaceous, the venation raised-reticulate; plants entirely glabrous; mature seeds large, usually more than 5 cm wide; aril, with two lobes, these lacking columnar or cellular divisions, the margins entire. ....*S. thomasii* R. B. Pinto, Torke & Mansano

    12. Leaflets smaller with various texture and venation; plants usually at least partially pubescent; mature seeds smaller; aril variously shaped, with obvious columnar or cellular divisions, the margins rugose or undulate.

      13. Gynoecium glabrous; pods glabrous.

        14. Calyx adaxially pubescent, i.e., pubescent within; aril lacking or linear.

15. Bracteoles 2.5–4.9 mm long.

16. Lateral leaflets 6–12-paired; leaflet margin plane; larger stamens 4; trees to ca. 12 m tall. …..*S. bahiensis* R. S. Cowan

16. Lateral leaflets 2–5-paired; leaflet margin strongly revolute; larger stamens usually 2–3, shrubs or treelets to ca. 2 m tall. ……...............….*S. arenophila* R. B. Pinto, Torke & Mansano

15. Bracteoles 0.8–1.8mm long.

17. Lateral leaflets 6.1–12.3 X 2.1–3.7 cm, the apex usually acute; flower buds (5–) 6–8 mm wide, often somewhat costate. ....……………..*S. pickelii* Killip & Ducke

17. Lateral leaflets 2.6–4.7 X 1.3-2 cm, the apex usually rounded to slightly retuse; flower buds 4–5 (–6) mm wide, smooth, never costate. ....…….*S. glazioviana* (Taub.) Glaz.

14. Calyx adaxially glabrous; aril well developed, variously shaped.

18. Lateral leaflets 3–6-paired.

19. Leaflets essentially glabrous; flower buds glabrous; petal persistent long after anthesis, deciduous after stamens. ....*S. langsdorffii* Raddi

19. Leaflets strigulose below; flower buds strigulose; petal soon caducous after anthesis, deciduous before stamens. …...................…*S. submontana* R. B. Pinto, Torke & Mansano

18. Lateral leaflets 7–15-paired.

20. Petal limb basally cordate or subcordate; larger stamens 4–6.

21. Inflorescence axes velutinous-tomentose, with the hairs flexuous and semi-erect; lateral leaflets with the base usually truncate, rounded or subcordate, the apex usually rounded or retuse, sometimes bluntly acute. ……………………………………………….*S. multijuga* Vogel

21. Inflorescence axes strigulose, with the hairs fairly straight and appressed; lateral leaflets with the base angular-obtuse to acute, the apex acute.

......*S. submarginata* (Benth.) Mansano var. *submarginata*

20. Petal limb basally acute-angustate to truncate, or the petal absent; larger stamens 0–2.

22. Ovary less than 2 X as long as wide; style less than 1 mm long; leaflet apex usually rounded-acute or retuse.

..............................*S. parvipetala* (R. S. Cowan) Mansano

22. Ovary more than 2 X as long as wide; style more than 1 mm long; leaflet apex pointed-acute.

..............*S. submarginata* var. *leiogyna* (Benth.) Mansano

13. Gynoecium pubescent; pods usually retaining at least some pubescence on the base and/or stipe.

23. Calyx adaxially pubescent, i.e., pubescent within.

24. Lateral leaflets 12–20-paired, the blades mostly more than 4 X as long as wide . ……………......……………….*S. pinheiroana* R. S. Cowan

24. Lateral leaflets 2–9-paired, the blades mostly less than 3 X as long as wide.

25. Leaflet margin strongly revolute; stipules persistent.
…..................................*S. revoluta* R. B. Pinto, Torke & Mansano

25. Leaflet margin plane; stipules caducous.
....*S. curranii* R. S. Cowan

23. Calyx adaxially glabrous.

26. Flowers apetalous; body of pod usually flattened-discoid, less than 1.3 x as long as wide. ....*S. linharensis* Mansano

26. Flowers petalous; body of pod usually elliptic, oblong, ovate, or obovate in outline, more than 1.3 x as long as wide, if less, the body more or less globose or ellipsoid, not strongly flattened.

27. Pedicels without paired bracteoles; ovary less than 1.7 X as long as wide; body of pod more or less globose to broadly ellipsoid, less than 1.3 X as long as wide. ....*S. acutifolia* Vogel

27. Pedicels with paired bracteoles, ovary more than 1.7 X as long as wide; body of pod variously shaped, more than 1.3 x as long as wide.

28. Filaments of the larger stamens glabrous or essentially so.

29. Larger stamens 6–14; lateral leaflets mostly 12–25-paired.
....*S. polita* (R. S. Cowan) Torke

29. Larger stamens 2–4; lateral leaflets mostly 4–11-paired.

30. Pubescence on leaflets erect and flexuous; upper leaflet surface distinctly pubescent.

…………...............………….……*S. psilonema* Harms

30. Pubescence on leaflets appressed and fairly straight; upper leaflet surface glabrous or nearly so.

31. Ovary glabrous to incompletely strigose, with at least the sutures and/or face of the ovary partially glabrous; trichomes on lower leaflet surface often more than 0.2 mm long; larger stamens 2.

……..…*S. submontana* R. B. Pinto, Torke & Mansano

31. Ovary densely and uniformly pubescent, the pubescence covering the entire surface of the ovary; trichomes on lower leaflet surface mostly less than 0.2 mm long; larger stamens 4.

............…*S. alagoensis* R. B. Pinto, Torke & Mansano

28. Filaments of the larger stamens distinctly pubescent.

32. Buds less than 5 mm in diameter and the lateral leaflets 3–4-paired. ……..……........……….*S. micrantha* R. S. Cowan

32. Buds exceeding 5 mm in diameter and/or the lateral leaflets 5–14-paired.

33. Petal limb basally obtuse to truncate; inflorescence axes somewhat thinly strigulose; ovary closely appressed-sericeous, with the faces often rugose.

....*S. oblata* R. S. Cowan

33. Petal limb basally cordate; inflorescence axes densely

tomentose or villous; ovary tomentose, pilose, or loosely-appressed sericeous, with the faces smooth.

34. Leaflets mostly 9–14-paired; pedicels frequently more than 11 mm long. ....*S. flaemingii* Raddi

34. Leaflets mostly (2–) 5–8-paired; pedicels usually less than 11 mm long.

    35. Pubescence on gynoecium loosely pilose-sericeous, the trichomes mostly straight to slightly flexuous; leaflet base usually subcordate, partially concealing the petiolule adaxially; plants shrubs or small trees rarely exceeding 10 m tall; dry lands. ....*S. macrostachya* Benth. var. *macrostachya*

    35. Pubescence on gynoecium tightly tomentose, the trichomes strongly flexuous and tangled; leaflet base usually obtuse, not obscuring the petiole adaxially; plants trees, often over 10 m tall; wet forest and coast scrub. ....*S. macrostachya* var. *riedelii* R. S. Cowan

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CONSIDERAÇÕES FINAIS

Swartzia é um gênero fascinante em diversos sentidos. São desde pequenos arbustos que ocupam uma restrita área em dunas da Bahia, como *S. arenophila,* até árvores emergentes nas terras firmes da floresta amazônica do Pará, como *S. polyphylla*. Em áreas sazonalmente alagadas da amazônia, indivíduos de *S.acuminata* permanecem vivos com seus troncos submersos e dispersam grandes sementes que flutuam nos rios amazônicos. Ambientes peculiares, como os tabuleiros do Espírito Santo, também são ocupadas por diversas espécies, como *S. acutifolia*, *S. apetala* var. *glabra*, *S. linharensis*, *S. micrantha*, *S. myrtifolia* var. *elegans* e *S. simplex* var. *continentalis*.

A seiva avermelhada confere uma aparência de que as árvores sangram ao sofrerem injúrias no tronco e nos ramos, tanto que algumas espécies chegam a ser conhecidas popularmente como 'Pau-sangue'(e.g. *S. alternifoliolata*, *S. apetala*, *S. macrostachya* e *S. polita*). As flores de *Swartzia* possuem uma morfologia exótica para a família, porém, dentro do gênero, a morfologia apresenta um padrão. As características mais marcantes são o cálice inteiro nos botões florais, que demonstraram proteger os órgãos internos da flor até mesmo contra fervura. Foi observado que era necessário danificar a parede do botão para rehidratação dos órgãos florais nos estudos taxonômicos. A corola com apenas uma pétala ou apétala e os estames dimórficos também são características compartilhadas entre a maior parte das espécies. Exceções são encontradas para todas estas características, como, por exemplo, a presença recorrente de duas pétalas em *S. dipetala* e *S. microstyles* (estas também apresentam com frequência a presença de dois carpelos). O cálice, que é geralmente glabro internamente, apresenta pilosidade na parede interna das sépalas em um seleto grupo de espécies da seção *Acutifoliae*, característica também encontrada em algumas espécies da seção *Swartzia* como *S. sericea* e *S. emarginata*. Assossiada a esta característica especificamente, estas mesmas espécies apresentam ausência de arilo nas sementes. A partir do desenvolvimento deste trabalho, *S. arenophila* e *S. revoluta* passaram a fazer parte deste grupo. Contudo, ainda não se sabe se esta correlação apresenta implicações filogenéticas. Pôde-se observar entretanto, através dos levantamentos, que a ausência do arilo parece estar relacionado com a restrição da distribuição geográfica.

A diversidade de frutos e sementes pôde ser constatada através dos exemplares coletados em campo pela equipe deste trabalho e por colegas. Pôde-se observar variações no revestimento, nas cores, nos tamanhos, na deiscência e na quantidade de sementes apresentadas entre todas as espécies analisadas nos dois capítulos. As sementes também apresentaram ampla diversidade de arilos que variaram em cor, odor, textura e área revestida da semente. Todos estes aspectos tornam o gênero um atrativo para contemplações e inferências biológicas.

Apesar desta grande diversidade morfológica, foi constatado um padrão conservado de características citogenéticas em todas as espécies analisadas. O número cromossômico 2n=26 foi compartilhado entre as espécies, independentemente da seção a que pertencem. Um tipo de autopoliploidia, com poucos registros na literatura foi detectada em *S. leptopetala*, mediante a observação de sementes coletadas de uma única árvore, que apresentaram níveis de ploidia diferentes (diploide/tetraploide). Estas observações sugerem a ocorrência de poliploidia modular, ou seja, alguns ramos (módulos) da árvore poderiam estar sofrendo duplicação do número cromossômico em células somáticas e nos meristemas. Esse processo estaria levando os meristemas a produzirem células germinativas 2x, com a possibilidade de produzir embriões 4x. Relatos de fenômenos semelhantes são raros na literatura e até o momento era inexistente em Leguminosae, sendo mais uma peculiaridade interessante encontrada para *Swartzia*.

Os dados relativos ao tamanho dos cromossomos, também inéditos para o gênero, demonstraram que *Swartzia* tem cromossomos pequenos quando comparados a casos disponíveis na literatura. Geralmente é possível construir cariótipos baseado nas comparações entre os tamanhos dos braços e dos cromossomos como um todo. Entretanto, em *Swartzia*, além de pequenos, os cromossomos apresentam uma variação de tamanho relativa entre eles muito baixa, como demonstrado pelos valores do tamanho relativo entre maior e menor cromossomos, tornando-os visualmente muito semelhantes e impossibilitando a identificação de pares.

Bandamento CMA/DAPI e FISH enrriqueceram as informações citológicas do grupo. Assim como as demais características citogenéticas, o gênero apresentou seu número de bandas CMA^{+}/DAPI^{-} e sítios de sequências de rDNA para 45S e 5S conservados entre as espécies analisadas.

Este padrão conservado para as características citogenéticas foi útil para a análise de *S. euxylophora*, cuja inclusão no gênero já havia sido citada na literatura como um possível equívoco. Uma vez que as características citológicas e morfológicas observadas em campo foram semelhantes ao restante das espécies analisadas, concluímos que o táxon é verdadeiramente uma *Swartzia*.

As características citogenéticas de *Swartzia* eram pouco conhecidas (apenas uma contagem imprecisa para *S. laevicarpa*) até o desenvolvimento deste trabalho. A partir dos dados obtidos é possível sugerir que o clado swartzioide apresenta variações sistemáticas de número cromossômico entre os gêneros. Entretanto, em nível infragenérico, não foi possível observar agrupamento de espécies por caraterísticas cromossômicas. Mesmo no nível infra-específico, como no caso de *S. simplex*, as duas variedades diferiram apenas pelo tamanho dos cromossomos. Estudos citogenéticos adicionais continuam sendo necessários, uma vez que o gênero possui um amplo número de espécies. Pode-se dizer que é são conhecidas características citogenéticas para quase 10% do gênero a partir do trabalho atual.

Na região extra-amazônica *Swarztia* demonstrou possuir uma grande diversidade, principalmente na seção *Acutifoliae*. Novas espécies foram descritas, porém, estas estão localizadas em regiões ameaçadas principalmente pela indústria imobiliária.

Sendo assim, observações minuciosas sobre a morfologia continuam sendo a melhor ferramenta para apontar descontinuidades em *Swartzia*. Este trabalho contribuiu amplamente com os estudos sistemáticos e taxonômicos no gênero, apresentando informações citológicas inéditas, descrição de novas espécies, tratamentos taxonômicos e elaboração de uma chave para identificação dos táxons extra-amazônicos no Brasil. Contudo, ainda são necessários mais estudos citogenéticos para garantir conclusões mais contundentes acerca dos processos cromossômicos envolvidos na evolução do gênero e do clado swartzioide.

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Rafael Barbosa Pinto
Universidade Estadual de Campinas
Rua Monteiro Lobato 970
Cidade Universitária Zeferino Vaz, Barão Geraldo
Campinas – SP 6190
Brasil

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Joy E. Runyon, Managing Editor
The New York Botanical Garden Press
jrunyon@nybg.org • tel 718 817.8574 • fax 718 817.8842

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