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UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL  
INSTITUTO DE BIOCÊNCIAS  
PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

**Sistemática de *Abarema s.s.* (Fabaceae)**

Dissertação de Mestrado

Ethiéne Guerra

Orientação: Prof. Dr. João Ricardo Vieira Iganci

Porto Alegre

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Ethiéne Guerra

Dissertação apresentada ao Programa de Pós-Graduação em Botânica da Universidade Federal do Rio Grande do Sul como parte dos requisitos para obtenção do título de Mestra em Botânica.

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Para meu amado irmão Thalles, que me ensinou da maneira mais doce a valorizar a grandiosidade dos pequenos detalhes.

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## **Sistemática de *Abarema* s.s. (Fabaceae)**

**Resumo:** Um estudo filogenético recente mostrou que *Abarema* (Caesalpinioideae, mimosoid clade) é polifilético. A espécie tipo do gênero, *Abarema cochliacarpus*, está posicionada na Aliança *Inga*, sendo filogeneticamente distante de todas as outras espécies de *Abarema* s.l.. *Abarema cochliacarpus* é uma espécie endêmica do Brasil, que ocorre nos biomas Mata Atlântica e Caatinga. A espécie apresenta uma ampla distribuição geográfica, e diferentes morfotipos ao longo dela. Na presente dissertação, apresentamos a nova circunscrição para o gênero, realizada através de um estudo aprofundado da morfologia dos morfotipos da espécie *Abarema cochliacarpus* e da espécie *Abarema diamantina*, recentemente descrita e proximamente relacionada à *A. cochliacarpus*. Também é apresentada uma análise filogenética molecular baseada nos marcadores ETS e *matK*, realizada com o intuito de elucidar o posicionamento e as relações do gênero *Abarema* com os outros gêneros da Aliança *Inga*. Um estudo morfométrico das espécies de *Abarema* s.s. e seus morfotipos foi realizado, testando a robustez morfológica dos morfotipos citados em associação às características ambientais de suas distribuições geográficas. A nova circunscrição de *Abarema* apresenta como caracteres taxonômicos diagnósticos: lenticelas nos ramos, fruto espiralado, epicarpo do fruto com indumento pulverulento ferruginoso e semente bicolor dividida linearmente. *Macrosamanea* foi confirmado como grupo irmão de *Abarema*. Os morfotipos da espécie *Abarema cochliacarpus* demonstram ser grupos bem definidos morfológicamente ao longo de suas distribuições geográficas

**Palavras-chave:** Caatinga, clado mimosoide, circunscrição, complexo de espécies, ETS, filogenia, Ingeae, Leguminosae, Mata Atlântica, *matK*, morfologia, morfometria.

## **Systematics of *Abarema* s.s. (Fabaceae)**

**Abstract:** Recent phylogenetic studies showed that *Abarema* (Caesalpinioideae, mimosoid clade) is polyphyletic. The type species of the genus, *Abarema cochliacarpus*, is positioned within the *Inga* Alliance, splitting out from the remaining species of *Abarema* s.l.. *Abarema cochliacarpus* is an endemic species from Brazil, which occurs in Atlantic Forest and Caatinga biomes. The species has a wide geographic distribution, and presents different morphotypes along it. In this dissertation, we present a new circumscription for the genus, produced by a detailed study on the morphotypes of *Abarema cochliacarpus* and *Abarema diamantina*, a recently described species, closely related to *A. cochliacarpus*. We also present a molecular phylogenetic analysis, based on ETS and *matK*, aiming to elucidate the position and the relations of *Abarema* with the other genera of *Inga* Alliance. A morphometric study of *Abarema* s.s. species and its morphotypes, testing the morphological robustness of the cited morphotypes, in association to environmental characteristics and their geographic distributions is provided. The new circumscription of *Abarema* highlight as diagnostic taxonomic characters: branches with lenticels, spiraled fruit, epicarp with ferruginous pulverulent indumentum and seed bicoloured, linearly divided. *Macrosamanea* was confirmed as the sister group of *Abarema*. The morphotypes of *Abarema cochliacarpus* are morphologically delimited along their geographic distributions.

**Key words:** Atlantic Forest, Caatinga, circumscription, ETS, Ingeae, Leguminosae, *matk*, mimosoid clade, morphology, morphometry, phylogeny, species complex.

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# INTRODUÇÃO GERAL

## 1. Conceito de espécie

Desde os primórdios da Ciência, os sistematas foram os responsáveis por descrever e nomear todas as variações morfológicas observadas entre táxons distintos, mas sem necessariamente se preocupar com os processos que produziam estas modificações. Entretanto, no início do século XX, começaram a se questionar sobre a origem destas variações, percebendo que o status de “espécie” estava sendo aplicado indiscriminadamente a populações discretas, que apresentavam pequenas variações (Wheeler & Meier 2000). A partir de então, conceitos de espécie foram criados e entre os mais conhecidos estão o conceito morfológico de espécie (Du Rietz 1930), o conceito biológico de espécie (Mayr 1942), o conceito filogenético de espécie (Hennig 1966) e o conceito ecológico de espécie (Van Valen 1976). É amplamente reconhecido que a definição de um conceito único para espécie é uma tarefa praticamente inalcançável e taxonomistas escolhem e aplicam determinado conceito para cada estudo (Colley & Fischer 2013). A escolha do conceito de espécie aplicado a um determinado estudo deve ser explicitada para facilitar uma compreensão plena do pensamento taxonômico do autor (Wheeler & Meier 2000, Futuyma 2009, Butlin *et al.* 2012, Naciri & Linder 2015). O conceito de espécie afeta o status de populações diagnosticáveis (unidades); as estimativas de diversidade de espécies; a análise da história dessas unidades; o entendimento sobre os padrões de fluxo gênico; o delineamento de áreas de endemismo; e estudos e ações para conservação de espécies e áreas (Wheeler & Meier 2000).

No entanto, a definição sobre o que é uma espécie e sobre os processos históricos relacionados à especiação continuam sendo um grande questionamento e tema de debates e controvérsias entre evolucionistas (Wheeler & Meier 2000, Futuyma 2009). Isto ocorre mesmo após 150 anos da publicação da obra clássica de Darwin (1859) “On the origin of species by means of natural selection”. Darwin reconheceu espécies como variedades bem marcadas, definidas pelo grau de diferenças morfológicas (Mallet 2008, Futuyma 2009). A partir desta amplitude morfológica, o estabelecimento de uma nova espécie só acontece quando a seleção natural divergente promove uma lacuna visualmente detectável na distribuição destas morfologias (Mallet 2008). Esta definição foi criticada, principalmente pelo fato de Darwin não ter discorrido sobre como é a evolução das barreiras que promovem as lacunas nas

distribuições das diferentes morfologias (Futuyma 2009). Assim, não é explícito o quão forte necessitam ser estas barreiras e o quão distante devem ser as lacunas para se admitir o isolamento entre dois táxons irmãos.

Dentre os conceitos de espécie, o conceito biológico (CBE) (Mayr 1942) define espécies como grupos de populações reprodutivamente isoladas. Este conceito é aceito principalmente por zoólogos, e vem sendo muito utilizado (Mallet 2008, Butlin *et al.* 2012). Entretanto, é rejeitado e criticado por botânicos e por pesquisadores que têm como objeto de estudo organismos que apresentam reprodução assexuada (Wheeler 1999). O CBE pode ser inaplicável a plantas que se reproduzem de maneira vegetativa, não ocorrendo cruzamentos entre indivíduos, nem entre populações. Da mesma forma, muitas espécies de plantas possuem ciclo de vida longo, sendo necessário um grande período de tempo até a maturidade dos possíveis descendentes para se avaliar o isolamento reprodutivo entre espécies. Além disto, a utilização, mesmo que majoritariamente teórica, do CBE fez com que a importância da hibridação fosse negligenciada, principalmente em estudos envolvendo animais (Jiggins *et al.* 2008). Embora alguns estudos afirmem que, tanto para plantas quanto animais, nas espécies com boa delimitação, a hibridação é rara (Mallet 2008), atualmente existem experimentos provando que a hibridação é um mecanismo extremamente importante e comum para as plantas (Futuyma 2009) e também para os animais, sendo mais comum do que até então documentado (Jiggins *et al.* 2008). A hibridação é vista como um evento importante de especiação. No entanto, Butlin *et al.* (2012) alertam para o fato de que a hibridação é apenas a origem do isolamento reprodutivo, sendo necessários outros processos para completar a especiação, tal qual a ocupação de um novo nicho (Gompert *et al.* 2006), que pode levar ao total isolamento reprodutivo e então à completa especiação, resultando em diferenciações morfológicas e possivelmente comportamentais, que possibilitam a adaptação a novas condições.

O conceito ecológico (CEE) (Van Valen 1976) define espécie como uma linhagem que ocupa o mesmo nicho ou zona adaptativa, evoluindo separadamente de todas as outras linhagens que não ocupam a amplitude de seu nicho. O isolamento reprodutivo é o primeiro passo necessário para que ocorra especiação em uma linhagem que ocupa o mesmo nicho (Abbott *et al.* 2008). Um modelo de especiação definido a partir do nicho ecológico de espécies é o conservantismo de nicho, que defende que a alta capacidade de dispersão de algumas linhagens sugere que elas estão mais susceptíveis a colonizarem ambientes semelhantes, mesmo que a longas distâncias, do



que evoluir e conquistar ambientes adjacentes, porém distintos (Donoghue 2008). Desta forma, espécies irmãs tenderiam a ocupar nichos semelhantes, mesmo que isolados no espaço. A plasticidade fenotípica é considerada por muitos pesquisadores como uma barreira para a especiação, no entanto, a partir do momento em que a plasticidade fenotípica promove a formação de novos fenótipos, pode ser peça chave para a ocupação de nichos adjacentes e ao longo do tempo, pode ser responsável por especiação de alguns táxons, mesmo que apresentem distribuição próxima (Butlin *et al.* 2012).

Com o advento da cladística e da sistemática filogenética, houve importantes mudanças nos paradigmas da classificação de espécies (Amorim 2002). A sistemática filogenética busca distinguir grupos monofiléticos, reconhecidos por estados derivados de caracteres compartilhados (Hennig 1966). Utiliza dados morfológicos ou moleculares para testar hipóteses evolutivas sobre a transformação de caracteres de estados plesiomórficos para apomórficos. O conceito filogenético de espécies (CFE) define apenas agrupamentos monofiléticos. Desta forma, é possível verificar a existência de fluxo gênico entre populações e inferir sobre o grau de isolamento e distanciamento genético entre elas através de análises moleculares (Lavin *et al.* 2003, Forrest & Hollingsworth 2003, Cozzolino & Scopece 2008, Lexer & Widmer 2008, Jiggins *et al.* 2008, Acosta & Premoli 2009). A possibilidade de testar o intercâmbio de diásporos entre populações, ou espécies próximas, através da ocorrência de introgressão e posterior fecundação, faz da biologia molecular uma importante ferramenta para complementar as análises em biologia reprodutiva requeridas pelo CBE. O CFE pode ser interpretado de diferentes formas ao admitir ou não a possibilidade de transferência horizontal de genes entre espécies (Wheeler & Platnick 2000). Entretanto, estes e outros processos de evolução reticulada podem mascarar os resultados sobre relações filogenéticas entre espécies (Naciri & Linder 2015). Métodos baseados em coalescência têm se mostrado eficazes para elucidar estes processos mais complexos na história evolutiva de espécies proximamente relacionadas (Pante *et al.* 2014).

Apesar de muitos estudos destacarem a importância de utilizar métodos filogenéticos e reprodutivos para testar a delimitação entre espécies, a dificuldade no reconhecimento de espécies a partir do CBE e do CFE requer a identificação taxonômica de espécies com base nas diferenças morfológicas (Abbott *et al.* 2008, Naciri & Linder 2015). No conceito morfológico de espécie, cada táxon é reconhecido por um conjunto de características morfológicas que o diferenciam de outros táxons

relacionados (Du Rietz 1930). Este conceito é o mais aplicado em estudos biológicos em geral, principalmente em análises florísticas e taxonômicas. Estudos taxonômicos baseados em morfologia são essenciais para fornecer subsídios a outras análises sistemáticas. A presença de uma boa amostragem de espécies e de identificações corretas em coleções de herbário são essenciais para fundamentar análises filogenéticas completas ao nível de espécies (Hardy *et al.* 2008). O uso de análises moleculares tem se tornado indispensável, no entanto, admite-se que espécies podem incorporar informações genéticas de outras espécies, podem sofrer reestruturações genéticas, sofrer mudanças na variabilidade e até mesmo incorporar plastídios de outras espécies, mas que, sobretudo, precisam ser unidades facilmente reconhecidas por suas características morfológicas e por seus padrões ecológicos (Naciri & Linder 2015). Sendo assim, aliar dados morfológicos aos dados moleculares é a maneira mais eficaz para obter análises filogenéticas confiáveis (Wheeler 2008).

Atualmente, a “taxonomia integrativa” vem sendo utilizada para a delimitação de espécies. Ela caracteriza-se por utilizar vários métodos em conjunto, como dados moleculares, morfológicos (incluindo anatomia, citologia), ecológicos (fenologia, nichos), testes de cruzamento, comportamento, propriedades químicas, entre tantos outros distinguíveis de acordo com o grupo estudado, que unidos, acarretam em uma delimitação mais robusta e confiável de espécies (Pante *et al.* 2014).

Diferentes hipóteses sobre a diversificação de plantas contribuem para o avanço na discussão sobre as possíveis origens da biodiversidade observada hoje. Apesar de o conservantismo de nicho ser considerado o grande responsável pela diversificação de várias linhagens no Neotrópico (Wiens & Donoghue 2004, Wiens 2007) ele pode não ser uma regra geral. Simon *et al.* (2009) mostraram que muitas linhagens no Cerrado dispersaram a partir de ecossistemas adjacentes, como as florestas ombrófilas, florestas sazonais, campos subtropicais, entre outros, e se adaptaram de forma independente às condições locais. Vários outros estudos têm mostrado que uma permuta biótica considerável ocorreu entre biomas neotropicais, bem como entre zonas altitudinais dentro de um mesmo bioma (Perret *et al.* 2006, Antonelli *et al.* 2009, Dušková *et al.* 2010, Hoorn *et al.* 2010).

## **2. Família Fabaceae**

Fabaceae é a terceira maior família de angiospermas, com cerca de 19.325 espécies, subordinadas a 727 gêneros. Ocorre nas regiões tropicais, subtropicais e

temperadas, sendo considerada entre as famílias com maior riqueza de espécies arbóreas nas florestas neotropicais (Lewis *et al.* 2005). Na flora do Brasil a família está representada por 222 gêneros (15 endêmicos) e detém o maior número de espécies dentre as angiospermas do país (2.807 espécies), sendo que destas, 1.508 são restritas ao território brasileiro (BFG 2015).

Estudos filogenéticos sustentam Fabaceae como uma família monofilética (Wojciechowski 2003, Lewis & Schrire 2003, Wojciechowski *et al.* 2004, Lewis *et al.* 2005). A divisão clássica em três subfamílias – Caesalpinioideae, Mimosoideae e Papilionoideae (Bentham 1859, 1870, 1876) – é ainda amplamente empregada (Lewis *et al.* 2005). Entretanto, após estudos moleculares comprovarem a necessidade de reorganizações sistemáticas ao nível de subfamílias e respectivas tribos (LPWG 2013), uma nova classificação para as subfamílias foi recentemente apresentada (LPWG 2017). A antiga subfamília Mimosoideae DC. é monofilética, mas está posicionada em uma linhagem que abrange parte das espécies que eram reconhecidas em Caesalpinioideae (LPWG 2017). Mimosoideae é agora reconhecida como um grupo informal chamado clado Mimosoida dentro da subfamília Caesalpinioideae (LPWG 2017). O clado Mimosoida abrange cerca de 3.270 espécies subordinadas a 78 gêneros de distribuição tropical e subtropical (Lewis *et al.* 2005). No Brasil, o clado é representado em todos os ecossistemas, totalizando 37 gêneros e 824 espécies (BFG 2015).

A família possui grande potencial econômico e importância ecológica e, dentre estes, se destaca o uso na alimentação humana e de animais (Wojciechowski 2003, Doyle & Luckow 2003) e a associação com bactérias fixadoras de nitrogênio, nos táxons mimosoides 52% dos gêneros tem nodulação atestada (Sprent 2001).

A antiga subfamília Mimosoideae DC., agora clado Mimosoida, conta com quatro tribos: Mimoseae, Mimozygantheae, Acacieae e Ingeae (Lewis *et al.* 2005). Assim como para as antigas subfamílias, a atual divisão das tribos do clado mimosoida é reconhecidamente não monofilética. A tribo Ingeae foi originalmente estabelecida por Bentham (1865), tendo como principal característica o androceu formado por numerosos estames com filetes unidos em tubo. Abrange 36 gêneros, 24 destes endêmicos do Neotrópico, e cerca de 950 espécies, distribuídos nos trópicos, subtropicais e regiões temperadas (Lewis & Rico Arce 2005). No Brasil ocorrem 16 gêneros e cerca de 300 espécies (BFG 2015).

## **2.1. Gênero *Abarema* Pittier**

A primeira menção a espécies do gênero *Abarema* foi feita por Pisonis (1658) em um dos primeiros tratamentos para a flora brasileira, com o nome pré-Lineano “*De Abaremo temo arbore, ejulque facultatibus*” não considerado validamente publicado (Figura 1). Assim como em vários outros gêneros atualmente reconhecidos na tribo Ingeae, *Abarema* foi desmembrado do gênero *Pithecellobium* Mart., que originalmente abrangia um grande número de espécies neotropicais. Martius (1837) circunscreveu *Pithecellobium* de forma ampla, abrangendo táxons com distintos padrões morfológicos. Bentham (1844) dividiu o gênero *Pithecellobium* em seções e dentre elas estabeleceu a seção *Abaremotemon*, a qual subordinou espécies inermes, com estames de tubo incluso e com legumes planos ou curvos. Este tratamento foi mantido em suas obras posteriores (Bentham 1875, 1876).



Figura 1. Primeira menção ao gênero *Abarema* feita por Guilhelmi Pisonis M.D. em 1658, em tratamento para a flora brasileira em “*De Medicina Brasiliensi*”, p. 77, cap. XXIX.

O gênero *Abarema* foi descrito por Pittier (1927) com base em *Pithecellobium* sect. *Abaremotemon* sensu Bentham (1844). Desde então, diferentes circunscrições

taxonômicas foram adotadas e implicaram em inclusão ou retirada de espécies a este subordinadas, bem como em modificações quanto ao seu posicionamento em relação aos gêneros afins (Britton & Killip 1936, Cowan 1959, Nielsen *et al.* 1984). Grimes (1995) e Barneby & Grimes (1996) posicionaram o gênero na tribo Ingeae, no grupo informal denominado Aliança *Abarema*, que abrangia os gêneros *Abarema*, *Hydrochorea* Barneby & J.W.Grimes e *Balizia* Barneby & J.W.Grimes, este último sinonimizado posteriormente a *Albizia* Durazz. (Rico Arce 1999). Barneby & Grimes (1996) no estudo sobre os táxons sinandroides neotropicais destacaram que os limites de *Abarema* em relação a gêneros afins da tribo Ingeae não são de fácil estabelecimento. No tratamento mais recente para a tribo Ingeae, realizado por Lewis & Rico Arce (2005), o grupo Aliança *Abarema* abrange, além de *Abarema* e *Hydrochorea*, o gênero *Pararchidendron* I.C.Nielsen.

Segundo Iganci & Morim (2012), *Abarema* compreende cerca de 50 espécies (Iganci & Morim 2012). As espécies ocorrem predominantemente nas formações florestais da Região Neotropical, distribuindo-se desde o sul do Brasil, passando pelas formações florestais do Domínio Atlântico e do Cerrado no sudeste e nordeste do país, pela Amazônia brasileira, venezuelana, guianense, colombiana, peruana e boliviana, ao longo dos vales andinos desde a Bolívia até a Colômbia e o Equador; nos países da América Central e ainda apresenta algumas espécies restritas às ilhas caribenhas (Barneby & Grimes 1996). Apesar da ampla distribuição geográfica no Neotrópico, há uma tendência, em diferentes espécies, por ocupar ambientes abertos e de solo arenoso, mesmo em distintas formações vegetacionais (Iganci & Morim 2012). Para a flora do Brasil são conhecidas 24 espécies que ocorrem nos seguintes domínios fitogeográficos: 15 spp. na Amazônia (Iganci & Morim 2010); 9 spp.no Domínio Atlântico (Iganci & Morim 2009b, 2012); e 3 spp. no Cerrado (Iganci & Morim 2010). Até o momento, do total de espécies conhecidas para a flora brasileira, 52% são endêmicas. As espécies de *Abarema* são atualmente caracterizadas como árvores ou arbustos inermes, que apresentam folhas bipinadas, com nectários extra-florais, com inflorescências em racemos espiciformes ou capitados, com flores homomórficas ou heteromórficas e com frutos do tipo legume, com endocarpo rubro e sementes bicolores.

Apesar da grande contribuição do trabalho de Barneby & Grimes (1996) para o reconhecimento de *Abarema* e de seus táxons específicos e infra-específicos, o monofiletismo do gênero, as relações filogenéticas com os demais táxons da tribo Ingeae e as relações infragenéricas não eram evidentes. Tais questões se refletem na

dificuldade do reconhecimento da identidade taxonômica de algumas espécies, atualmente subordinadas a *Abarema*, principalmente, em relação àquelas que ainda são pouco conhecidas *in loco* e/ou nas coleções de herbários. O mesmo se verifica para as espécies que apresentam plasticidade morfológica, por vezes mais ampla do que nas circunscrições estabelecidas por Barneby & Grimes (1996).

O primeiro estudo filogenético molecular da Aliança *Abarema* (Iganci *et al.* 2016) demonstrou que *Abarema* é polifilético. A filogenia indica que a espécie-tipo do gênero, *Abarema cochliacarpus* (Gomes) Barneby & J.W.Grimes, está afastada das outras espécies de *Abarema*, fazendo parte da Aliança *Inga*, apontando a necessidade de novos estudos e uma nova circunscrição do gênero (Iganci *et al.* 2016).

## **2.2. O complexo *Abarema cochliacarpus***

*Abarema cochliacarpus* é uma espécie endêmica do Brasil, encontrada nos biomas Mata Atlântica e Caatinga (Iganci 2008). Distribui-se do estado de São Paulo até o Ceará, ocorre em floresta ombrófila densa, floresta estacional semi-decidual, restinga e Caatinga, sendo comum no litoral dos estados do Rio de Janeiro, Espírito Santo e Bahia (Iganci 2008). A espécie é representada por árvores ou arbustos de 1 - 30 m de altura, os ramos possuem lenticelas, as inflorescências são homomórficas e os racemos capitados, o legume é espiralado, o epicarpo possui indumento ferrugíneo, as sementes são globosas a lentiformes e apresentam pleurograma mediano-basal aberto, que acompanha a coloração da semente (Iganci 2008, Iganci & Morim 2012).

Lewis (1987) sugeriu estudos para avaliação e possível recircunscrição da espécie ao registrar a ocorrência de diferentes morfotipos no estado da Bahia: um morfotipo representado por indivíduos arbóreos, de 10 metros ou mais de altura, distribuídos nas formações florestais costeiras; e o outro, distribuído no interior da Bahia, formado por indivíduos de até 4 metros de altura com foliólulos menores e mais coriáceos. Lewis (1987) cita ainda, uma variação extrema do morfotipo do interior da Bahia, representado por arbustos de até 2 metros, com foliólulos arredondados, de ápice emarginado e venação proeminente em ambas as faces. Barneby & Grimes (1996) indicaram que os legumes das populações na Paraíba e em Pernambuco tendem a ser mais grossos que os das populações da Bahia e do sudeste do Brasil. Iganci (2008), além de reconhecer estes morfotipos, registra a presença de um outro morfotipo diminuto também na Ilha de Cabo Frio, no estado do Rio de Janeiro, e observa que a plasticidade morfológica apresentada pela espécie provavelmente está ligada a

características ambientais nas diferentes áreas de ocorrência, como a umidade e profundidade do solo, a altitude e a luminosidade.

A partir dos estudos filogenéticos recentes e da constatação do polifiletismo do gênero, *Abarema* necessita, então, de uma nova circunscrição. Em um primeiro momento, *Abarema cochliacarpus* não está relacionada com nenhuma outra espécie de *Abarema*, possivelmente tornando o gênero monoespecífico em uma nova circunscrição (Iganci et al. 2016). No presente estudo foram aplicadas diferentes abordagens em busca de uma análise taxonômica integrativa para recircunscrever o gênero *Abarema* com base em evidências morfológicas, filogenéticas e ecológicas.

Com o objetivo de verificar quais as relações filogenéticas de *Abarema cochliacarpus* com outras espécies de *Abarema s.l.* e entender qual o posicionamento de *Abarema s.s.* dentro da tribo Ingeae, realizou-se uma análise filogenética para o grupo, que é apresentada no primeiro artigo desta dissertação “Phylogenetic placement and new circumscription of *Abarema* (Fabaceae)”. O estudo de campo nas áreas de ocorrência de *Abarema cochliacarpus* aliado a um exame minucioso das coleções de herbários mais representativas para a espécie é o que possibilita uma análise e reavaliação dos caracteres morfológicos de importância taxonômica para o gênero, subsidiando uma nova circunscrição morfológica e filogenética robusta. Este artigo está formatado de acordo com as normas para publicação na revista “Taxon”, à qual será submetido.

O exame minucioso da morfologia dos espécimes dos herbários, aliado às coletas das populações em campo e observação das características ambientais das diferentes áreas de distribuição, nos alertou sobre a importância de delimitações taxonômicas pormenorizadas para o grupo, que apresenta diferentes morfotipos. Um estudo morfométrico do complexo é apresentado no artigo “Taxonomic delimitation and future conservation challenges”. O artigo encontra-se formatado de acordo com as normas para publicação na revista “Diversity and distributions”, à qual será submetido.

Uma nova espécie, representada por um dos morfotipos do complexo *Abarema cochliacarpus* é descrita no artigo “A new species of *Abarema* (Fabaceae) from Brazil”. O artigo foi publicado em dezembro de 2016, no volume 289 (1) da revista “Phytotaxa” e na dissertação é apresentado como apêndice.

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## **ARTIGO 1.**

### Phylogenetic placement and new circumscription of *Abarema* (Fabaceae)

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## Phylogenetic placement and new circumscription of *Abarema* (Fabaceae)

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**Abstract** In recent phylogenetic studies the genus *Abarema* (Caesalpinioideae, mimosoid clade) emerged as polyphyletic. The type-species, *Abarema cochliacarpus*, is positioned within the *Inga* Alliance, as sister to *Macrosamanea*, apart from the remaining species of the genus. Here we present a new circumscription of *Abarema*, based on molecular phylogenetic and morphological analyses. *Abarema* s.s. comprises two species in the Atlantic Forest and Caatinga biomes in Brazil. We provide a new morphological description for the genus, and its species, along with an identification key, comments, distribution map and illustrations.

**Key words:** ETS, Ingeae, Leguminosae, *matK*, mimosoid, morphology.

**Short title:** New circumscription of *Abarema*

## INTRODUCTION

Fabaceae is the third most representative family of angiosperms in the world, with approximately 770 genera and over 19500 species (Lewis & Rico Arce, 2005; LPWG, 2013). The family presents a Pan-tropical distribution, being represented in almost all the ecosystems of the world (Schrire & al., 2005). Until the end of the 1980s, the morphology has been widely used in the traditional division of Fabaceae in three subfamilies: Mimosoideae, Caesalpinioideae and Papilionoideae (LPWG, 2013). With the increasing molecular studies since the last 30 years, there are a lot of resolutions given to the phylogenetic relationships within Fabaceae (LPWG, 2013, 2017). A recent classification of Fabaceae was produced, dividing the family into six subfamilies: Caesalpinioideae DC. (recircumscribed), Cercidoideae LPWG, Detarioideae Burmeister., Dialioideae LPWG, Duparquetioideae LPWG, and Papilionoideae DC., (LPWG, 2017). The former Mimosoideae subfamily is now recognized as the mimosoid clade, within Caesalpinioideae (LPWG, 2017). Considering the novelties presented in recent continuous molecular phylogenies, the generic delimitations within the mimosoids are in a considerable flux, and the tribal division (Mimoseae, Mimosigantheae, Acacieae and Ingeae) (Lewis & al., 2005) seems to be non-monophyletic (LPWG, 2013, 2017).

The tribe Ingeae was first established by Bentham (1865), and is characterized principally by the presence of many stamens with united filaments forming a tube. Barneby & Grimes (1996) studied the species of the tribe from the Neotropics. In this study, a broad taxonomic revision was presented, besides the establishment of Alliances: *Abarema* Alliance, *Chloroleucon* Alliance, *Inga* Alliance, *Samanea* Alliance, *Pithecellobium* Alliance, and unplaced genera. Souza & al. (2013), in a molecular phylogenetic study of *Calliandra* Benth. indicated that the *Inga* Alliance does not represent a monophyletic group, while *Abarema* and *Pithecellobium* Alliances represented monophyletic groups, but only one species of each genus of the *Abarema* Alliance was sampled.

The *Abarema* Alliance currently comprises the genera *Abarema*, *Balizia* Barneby & J.W.Grimes and *Hydrochorea* Barneby & J.W.Grimes (Barneby & Grimes, 1996). The genera are recognized mainly by the type of fruits, a legume in *Abarema*, a follicle in *Balizia* and a loment in *Hydrochorea* (Barneby & Grimes, 1996). In another morphological study, Lewis & Rico Arce (2005) recircumscribed the *Abarema* Alliance adding the Asian genus *Pararchidendron* Nielsen, and excluding *Balizia*, synonymized to *Albizia* Durazz. (Rico Arce, 1999), not positioned in their phylogeny.



The genus *Abarema* (Pittier, 1927) was described based in *Pithecellobium* sect. *Abaremotemon* sensu Bentham (1844). Barneby & Grimes (1996), despite naming the *Abarema* Alliance, signalized that the relationships of the genus with other genera of the tribe Ingeae are of difficult establishment. Since its description, *Abarema* had different taxonomic circumscriptions, incorporating and losing species (Brown, 2008). The first mention to the genus *Abarema* Pittier occurred in 1658, in the publication “*De Medicina Brasiliensi*” of Guilielmi Pisonis M.D. (1658: 77), under the pre-Linnean name of “*De Abaremo temo arbore, ejusque facultatibus*”, which is not considered validly published. After almost 180 years, with the Linnean system already established, Martius (1837) described the genus *Pithecellobium* Mart.. The first circumscription of *Pithecellobium* encompassed taxa with a wide morphological variation. Bentham (1844) divided the genus *Pithecellobium* in eight sections, among them, Bentham established the section *Abaremotemon* Benth.. The circumscription of *P. sect. Abaremotemon* covered the unarmed species, with staminal tube included in the corolla and legumes flat or curved (Bentham, 1844, 1875, 1876). Kuntze (1891) established the genus *Feuilleea* Kuntze transferring species from *Pithecellobium*. Pittier (1927) described the genus *Abarema* and combined the species *A. filamentosa* (Benth.) Pittier and *A. trapezifolia* (Benth.) Pittier from *Pithecellobium*. At the same time the genera *Punjuba* Britton & Rose, *Jupunba* Britton & Rose, and *Klugiodendron* Britton & Killip were described (Britton & Rose, 1928; Britton & Killip, 1936), also including species segregated from *Pithecellobium*, especially from Central and North America. These three genera were lately synonymized to *Abarema* by Barneby & Grimes (1996).

Britton & Killipi (1936) designated *Pithecellobium avaremotemo* Mart. as the lectotype of the genus *Abarema*. Cowan (1959) justified that the lectotype of *Abarema* should be selected among the species studied by Pittier (1927). Between the two species selected from *Pithecellobium* by Pittier in 1927, Cowan (1959) considered *A. trapezifolia* more representative for the genus than *A. filamentosa*, and selected *A. trapezifolia* as lectotype. About 25 years late, Nielsen & al. (1984), based on morphological observations, transferred the species of *Abarema* from the Old World to the genus *Archidendron* F. Muell.. Barneby & Grimes (1996) realized a study on the synandrous Mimosoideae from the New World. In this study, they contested the *Abarema* typification made by Cowan (1959), corroborating the typification of Britton & Killip (1936). They argued that since the genus was based on the section *Abaremotemon* Benth., the species *Pithecellobium avaremotemo*, that is the basionym

of *Abarema cochliacarpus*, must be the lectotype, because it is the type species of the section.

Recently, Iganci & al. (2016) presented the first molecular phylogeny based on *matK* and ETS molecular markers for the *Abarema* Alliance, where all genera cited to the Alliance in all circumscriptions were sampled. This study showed, among other novelties, that the type species of the genus, *Abarema cochliacarpus* (Gomes) Barneby & J.W.Grimes, clustered into the *Inga* Alliance, and not within the other species and genera of the *Abarema* Alliance (Iganci & al., 2016).

*Abarema cochliacarpus* is endemic to Brazil. The species is distributed from Northeast to Southeast Brazilian Atlantic coast and inland in the Bahia state, on Atlantic Forest and Caatinga biomes (Iganci & Morim, 2009). *Abarema cochliacarpus* is characterized as a putative complex of species, since it presents a variety of morphotypes along its distribution. Lewis (1987), studying the legumes of Bahia state, cited the occurrence of a morphotype of up 10 m along the coast of the state, in the Atlantic Forest, and another of at most 4 m in the inland portion of the state, in the Caatinga. Besides this two morphotypes, Lewis (1987) mentioned an extreme form, of a shrub of at most 2.5 m in the inland portion, in the Caatinga. Barneby & Grimes (1996) highlighted that the fruits from populations of Paraíba and Pernambuco states are thicker than the ones from the southeast distribution. Iganci & Morim (2012), besides confirming the differences among those morphotypes, also indicated the occurrence of a population of smaller trees in the Cabo Frio Island, in Rio de Janeiro state. Since the publication of the preliminary phylogeny of the *Abarema* Alliance (Iganci & al., 2016), a meticulous study on the morphotypes of the genus type species, *Abarema cochliacarpus* now considered as a complex, began. *Abarema diamantina* E.Guerra, Iganci & M.P.Morim, was described as the first resolution of the *Abarema cochliacarpus* complex (Guerra & al., 2016).

In this study, we present a new morphological circumscription for the genus *Abarema* s.s, based on a detailed revision of the *Abarema cochliacarpus* complex, and a phylogenetic analysis based on plastidial *matK* and nuclear ETS molecular markers, focused on understanding the relationships of *Abarema* s.s within the *Inga* Alliance.

## METHODS

### *Taxonomic methods*

**Plant material:**—For a detailed evaluation of morphological characters of *Abarema s.s.* species, to generate a robust new circumscription for the genus, we analyzed the most important collections of *Abarema cochliacarpus* and *Abarema diamantina*. We examined the collections deposited in the herbaria ALCB, CVRD, EAC, HST, HUEFS, ICN, PEUFR, RB, SPF, UB, UEC, and UFPE (Thiers, 2017). Fieldwork to collect new samples and to recognize the environmental characteristics of the species distribution were also realized. The field excursions covered the distribution of the species in Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Bahia, Espírito Santo and Rio de Janeiro states, between November 2015 and March 2016, increasing the original number of *Abarema s.s.* collection in 47 registers. Exsiccates were deposited in herbarium ICN and duplicates were sent to RB and others important herbaria for *Abarema* collections. In total, we analyzed 204 exsiccates, almost the whole collection of *Abarema s.s.*.

**Morphology:**—Morphological traits of *Abarema s.s.* were analyzed in 204 exsiccates from herbaria collections and from new samples collected during this study. Flowers of dried material were studied after rehydration in warm water and a drop of detergent. The quantitative characters were measured with a ruler and a digital caliper. The state of qualitative characters were also analyzed. We measured the characters cited by Barneby & Grimes (1996) and Iganci & Morim (2009) as the diagnostics for *Abarema cochliacarpus*. Special attention was given to the whole morphological set, mainly reproductive, aiming to find new taxonomic representative characters to circumscribe the genus.

The following terminology was adopted on the taxonomic descriptions of morphological structures: for habit and branches, Barneby & Grimes (1996); for indumentum, Hickey & King (2000); for foliar nectaries, Garcia (1998); for venation, form, apex, base and margin of leaflets, Rizzini (1977) and Stearn (1992); for inflorescences, Weberling (1992) and Grimes (1999); for flower characters, Barneby & Grimes (1996); for fruit and seed, Barroso & al. (1999), Lima (1985) and Oliveira (1999).

### ***Molecular methods***

**Taxon sampling:**—Based on the results showed by Iganci & al. (2016), we sampled *Abarema cochliacarpus* and other genera included in the *Inga* Alliance. Samples were collected from the wild during fieldwork, the fresh leaves were dried in silica gel for posterior DNA extraction. *Samanea saman* (Jacq.) Merr. and some taxa from the extinct *Abarema* Alliance were sampled as outgroup. Since our objective was not to test the whole delimitations of the *Inga* Alliance, but the positioning of *Abarema* within the Alliance, some taxa traditionally included in the *Inga* Alliance, such as *Calliandra* Benth., *Zapoteca* H.M.Hern. and other species of *Enterelobium* Mart., were not sampled. These taxa have been highlighted as not part of the *Inga* Alliance in recent molecular phylogenetic studies (Souza & al., 2013; Iganci & al., 2016).

**DNA extractions, amplifications, and sequencing:**—The total genomic DNA extractions followed a modified protocol of the cetyltrimethylammonium bromide (CTAB) method from Doyle & Doyle (1987). The choice of molecular markers was based in previous studies in phylogeny of Fabaceae (LPWG, 2013; 2017) and in the phylogeny of the *Abarema* Alliance (Iganci & al., 2016). The molecular markers used were the nuclear ribosomal (nrDNA) external transcribed spacers (ETSs; primers: 18S-IGS-CAC ATG CAT GGC TTA ATC TTT G/AcR2-GGG CGT GTG AGT GGT GTT TGG; Baldwin & Markos 1998; Ariati & al. 2006), and the chloroplast (cpDNA) *trnK* intron including *matK* (primers: *trnK685F*-GTA TCG CAC TAT GTA TCA TTT GA/*trnK2R*-CCC GGA ACT AGT CGG ATG G; Lavin & al.; 2000; 2001; Wojciechowski & al., 2004; Iganci & al., 2013). The polymerase chain reaction (PCR) was conducted with 20 µL of PCR Mix Ludwig Biotec Ltda., 3 µL of DNA template, 1 µL of primer 3' and 1 µL of primer 5', totalizing a reaction volume of 25 µL. PCR conditions followed Iganci & al. (2016): ETS: 95 C° for 5 min and 30 cycles of 1 min at 94 C°, 1 min at 55 C°, and 2 min at 72 C°, followed by a final extension of 7 min at 72 C°; *matK*: 95 C° for 5 min and 30 cycles of 30 s at 94 C°, 30 s at 50 C°, and 2 min at 72 C°, followed by a final extension of 7 min at 72 C°. The purification of PCR products and the sequentiation was conducted by Macrogen (Seoul, South Korea). Alignments of the sequences were made by default settings and the L-INS-i algorithm in MAFFT, version 7.017 (Kato and Toh 2008), implemented within Geneious, version 10.0.9. Gaps were not coded.

**Phylogenetic methods:**—A combined Bayesian analysis using both ETS and *matK* sequences was implemented. The partitioned analyses of nuclear and plastid data

subsets were carried out, and the most likely genealogical species tree was reconstructed with a multispecies coalescent approach implemented in MrBayes 3.2.6. We used the Akaike information criterion implemented in the program JModeltest (Nylander, 2004) to choose the best-fit models of sequence evolution. The GTR I G was chosen as the nucleotide substitution model for ETS, and the GTR G as the nucleotide substitution model for *matK*. The Bayesian analyses initiated from random starting trees in two independent runs of 10,000,000 generations and four chains. Trees were sampled every 100 generations in each run, log-likelihood scores were compared for convergence, we discarded the first 25% of trees as burn-in. Then, 50% majority-rule consensus and Bayesian posterior probabilities were generated for the resulting trees.

## Results

### *Taxonomy*

*Abarema* s.s. Pittier in Trab. Mus. Comercial Venezuela 2: 86. 1927.  $\equiv$  *Pithecellobium* sec. *Abaremotemon* Benth., The London Journal of Botany 3: 203. 1844. Lectotype: *Pithecellobium auaremotemo* Mart. [= *Abarema cochliacarpus* (Gomes) Barneby & J.W.Grimes] (designated by Britton & Killip, 1936).

(Fig. 1)

**Shrubs and trees** without spines; reddish bark, branches pubescent, pulverulent, with conspicuous lenticels; stipules triangular, brown-greenish, usually deciduous. **Leaves** bipinnate, alternate; nectaries sessile, pateliform, between the pairs of pinnae and leaflets; petiole, rachis and rachilla with pubescent and ferruginous pulverulent indumentum, canaliculated; pinnae alternate one to five jugate, leaflets sessile, opposite, chartaceous or membranaceous, asymmetric, lanceolate, obovate or oblanceolate; indumentum present or not, veins brochidromous. **Synflorescences** axillary; cincinnates homomorphic, capitate racemes; peduncle with pubescent and ferruginous pulverulent indumentum; bract triangular, pubescent, deciduous; bracteoles spatuliform and triangular, pubescent, generally deciduous; flowers pentamerous; calyx green, campanulate, gamosepalous, with apex acute, pilose in the laciniations; corolla green, campanulate, infundibuliform, gamopetalous, with apex acute, pilose in the laciniations; androecium with many stamens, white, exerted; filaments fused in tube inserted or exerted to the corolla; anthers with rimose apertures; ovary superior, subsessile, truncate or attenuate at the apex, glabrous or pilose, stigma punctiform. **Legumes** spiraled, valves chartaceous, epicarp brown, with ferruginous pulverulent indumentum, endocarp

brown-orange; seeds obovate, bicoloured, white and dark bluish, with pleurogram opened, median-basal.

**Distribution:**—The genus is distributed along the Atlantic Forest, in coastal Southeast and Northeast Brazil, from São Paulo to Ceará states. In Northeast Brazil it also occurs in the Caatinga, in inland Bahia state (Fig. 2).

**Two species:**—*Abarema cochliacarpus* and *Abarema diamantina*.

#### Identification key for species of *Abarema* s.s.

1. Staminal tube exerted to the corolla; seeds with foveolate testa.....  
..... 1. *Abarema diamantina*  
1'. Staminal tube inserted in the corolla; seed with smooth testa.....  
..... 2. *Abarema cochliacarpus*

**1. *Abarema diamantina*** E.Guerra, Iganci & M.P.Morim in Phytotaxa 289 (1): 77. 2016.

Type: Brasil. Bahia: Morro do Chapéu, Estrada do Feijão, trecho da estrada conhecido como Coreia, 9 a 10 km de Morro do Chapéu [BA 052] km 259 até km 260, 11°35'44,18"S 41°04'11,10"W, 982 m elev., 21 March 2016, *E. Guerra 149* (holotype ICN!, isotypes RB!, HUEFS!).

Fig. 3 and additional illustrations in Guerra & al. (2016).

**Shrubs** 1–2.5 m. **Stipules** 0.5–1.5 mm long. **Leaves** 1–4 pairs of pinnae; petiole 7–22 mm long; rachis 1.3–7 cm long; foliar nectaries on the rachis 1–1.4 mm diam., and on the rachilla 0.4 mm diam. **Leaflets** 2–4 pairs per pinnae, chartaceous and discolorous, light green in adaxial surface, dark green in abaxial surface, obovate to oblanceolate, the proximal (8–9) 14–19 (28) × (5–9) 10–14 (17–19) mm, and the distal (20–25) 27–37 (38–42) × (12–14) 19–23 (24–25) mm, the apex rounded, sometimes emarginate, usually glabrous, sometimes puberulous on the primary veins of the abaxial surface, secondary veins prominent on both surfaces. **Synflorescences** axillary; peduncle 65–85 mm long; **Bracteole** spatuliform, 0.6 mm, pubescent. **Flowers** sessile; calyx 2–2.5 mm long; corolla 4.7–5.6 mm long; stamens 12.3–12.6 mm, staminal tube 5.5–6 mm, exerted to the corolla; anthers 0.1 mm long; ovary puberulous, 1.3 mm, truncate at the

apex. **Legumes** 170–250 × 8–14 mm, apex acute. **Seeds** 7–8 × 5–6 mm, with foveolate testa, mostly on the distal portion.

**Distribution and habitat:**— *Abarema diamantina* has a narrow restrict known geographic distribution, being endemic to the municipality of Morro do Chapéu, in Bahia state. It occurs in the Caatinga biome, in the Chapada Diamantina.

**Phenology:**—Flowers observed in December, old flowers observed in March, fruits observed from March to September.

**Comments:**— In herbarium samples the differentiation from *A. cochliacarpus* is possible by the flowers (exserted staminal tube in *A. diamantina* vs. inserted staminal tube in *A. cochliacarpus*) and seeds (foveolate testa in *A. diamantina* vs. smooth testa in *A. cochliacarpus*). Besides these reproductive characters, the distinction between the two species in field is remarkable by the shrubby habit of *A. diamantina* (up to 2.5 m high vs. 4–30 m high in *A. cochliacarpus*). The reddish bark, an important character for recognizing the genus *Abarema*, in the *A. diamantina* is present mainly in the surface close to the bark.

*Abarema diamantina* presents exactly the vegetative characters cited by Lewis (1987) when referring to the extreme morphotype of inland Bahia: height up to 2.5 meters and leaflets chartaceous with prominent venation. Lewis (1987) associated this morphotype to the sample of Harley & al. 22990. The principal taxonomic characters on the *Abarema diamantina* description are the reproductive ones of the staminal tube excluded to the corolla, and the testa of the seed foveolate. In Harley & al. 22990, these reproductive characters are not evident on the digitized image analyzed by us. Besides it, the leaves in *A. cochliacarpus* presents a wide variation, and the species co-occur with *A. diamantina* in Morro do Chapéu municipality. So, we cannot consider the Harley & al. 22990 as *A. diamantina* before examining the reproductive morphological characters that distinguish it from *A. cochliacarpus*.

**Examined material:**— BRAZIL. Bahia: Morro do Chapéu, Distrito de Palmeiras, 11°55'S 41°15'W, 04.XII.2002, M.E.R. Junqueira 169 (HUEFS); Estrada do Feijão, trecho da estrada conhecido como Coréia, 9 a 10 km de Morro do Chapéu [BA 052] km 259 até km 260, 11°35'44,18"S 41°04'11,10"W, 982 m elev., 21.III.2016, E. Guerra 147 (ICN); Estrada do Feijão, trecho da estrada conhecido como Coréia, 9 a 10 km de Morro do Chapéu [BA 052] km 259 até km 260, 11°35'44,18"S 41°04'11,10"W, 982 m elev., 21.III.2016, E. Guerra 148 (ICN); Estrada do Feijão, trecho da estrada conhecido como Coréia, 9 a 10 km de Morro do Chapéu [BA 052] km 259 até km 260,

11°35'44,18"S 41°04'11,10"W, 982 m elev., 21.III.2016, *E. Guerra 150* (ICN); Estrada para Torre, 27.IV.1999, *R.C.Forzza, A.M.Amorim & S.C.de Sant'ana 1397* (CEPEC, NY, RB, SPF); Serra Pé do Morro, 11°35'27S 41°12'24"W, 1293 m elev., 29.VI.1996, *H.P.Bautista, N.Hind, A.M.Giulietti, R.Harley & S.Smith s.n.* (SPF 130982).

**2. *Abarema cochliacarpus*** (Gomes) Barneby & J.W.Grimes in Mem. New York Bot.

Gard. 74: 94. 1996.  $\equiv$  *Mimosa cochliacarpus* Gomes in Mem. Acad. Real. Sci. Lisboa: pl. 34, t. 4, fig. 3. 1803. Type: *habitat in montibus, frequens, ut tratidur, in Brasiliae provinciis S. Paulo, et Minas Geraes; occurrit raro in Rio janeira* (Lectotype: Mem. Acad. Real. Sci. Lisboa: pl. 34, t. 4, fig. 3, designated by Iganci & Morim, 2009). Brazil. Bahia: Porto Seguro, BR-367, 12 km W de Porto Seguro, 27.XI.1979, *S. A. Mori, A. M. Carvalho & D. Halloran s.n.* (Epitype RB 204952!, designated by Iganci & Morim, 2009).  $\equiv$  *Pithecellobium cochliocarpum* (Gomes) Macbr.. MacBride, Contr. Gray Herb., 59: 3, 1919.

= *Pithecellobium auaremotemo* Mart.. Martius, C.F.P. von in Flora, 2(8): 115, 1837.

Type: not found.

= *Mimosa vaga* Vell. in Flora fluminensis, Vellozo, vol.11, tab 13. 1831. Type: Flora fluminensis, vol.11, tab 13!

Fig. 4 and additional illustrations in Iganci & Morim (2009).

**Shrubs and trees** 2–30 m. **Stipules** 0.3–1.5 mm long, deciduous. **Leaves** (1) 2–4 (5) pairs of pinnae; petiole 5–65 mm long; rachis (1.6) 5–9 (18) cm long; foliar nectaries on the rachis 0.5–1 mm diam., and on the rachilla 0.09–0.8 mm diam. **Leaflets** 2–6 pairs per pinnae, membranaceous, discolours in the aged leaflets, light green in adaxial surface, dark green in abaxial surface, obovate to oblanceolate, apex acute to acuminate, sometimes rounded in the young leaflets, the proximal (6–8) 10–20 (25–31)  $\times$  (4–6) 8–15 (17–21) mm, and the distal (12–30) 35–55 (115)  $\times$  (7–15) 17–30 (50) mm, the apex acute to acuminate, sometimes rounded in the young leaflets, glabrous, venation usually not prominent, sometimes with prominent venation only in the abaxial surface. **Synflorescences** axillary; co-florescences homomorphic, capitate racemes, eventually presents a distal solitary flower; peduncle (28–40) 50–80 (90–110) mm long; bracts sometimes present, 0.3–1.10 mm, deciduous. **Bracteole** triangular 0.4  $\times$  0.3 mm and spatuliform 0.35  $\times$  0.12 mm. **Flowers** sessile, but a few flowers, generally from the base of some racemes, can present pedicels 0.10–0.40 (0.88) mm; calyx 1.2–2.8 mm long; corolla 4.1–7.8 mm long; stamens 9–18.3 mm long, staminal tube 3.1–7.5 mm, inserted



in the corolla; anthers 0.06–0.3 mm long; ovary 0.8–1.7 mm long, glabrous, attenuate at the apex. **Legumes** (6.3) 14–25 (29–32) × 0.7–2.6 cm, apex rounded. **Seeds** 4–8.3 × 3.6–7.7 mm, with smooth testa.

**Distribution and habitat:**— *Abarema cochliacarpus* is distributed along the Brazilian coast, from Ceará to São Paulo states, also occurring in Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia, Espírito Santo, Minas Gerais and Rio de Janeiro. In Bahia state, it occurs also as an inland form, in the Chapada Diamantina, Caatinga biome. In the coastal distribution, it occurs on Atlantic Forest: on dense ombrophilous forest, semi-deciduous forest and restinga (coastal scrub).

**Phenology:**— Flowers and fruits observed all year long. Flowers mature principally from September to December. Fruits mature principally from January to March.

**Comments:**— Along its wide geographical distribution, *Abarema cochliacarpus* presents morphological plasticity in some characters, such as the height, leaves and fruits. In the leaves, even within an individual, it is common to find a remarkable variation of number and size of leaflets. Barneby & Grimes (1996) cited that the fruits in the Northeast distribution up to Bahia are thicker than in the remaining distribution. Lewis (1987) emphasized the occurrence of two different morphotypes in Bahia state, diagnosable principally by the plant height. After detailed analyses of exsiccates, a morphometric study (Guerra & al., *in prep.*) and fieldworks focused on observing the morphotypes in their habitats, we confirm the morphotypes mentioned and highlight that there are climate and environmental differences along the distribution range of the species, that would influence morphological variation observed. It was also possible to observe that in the coastal portion of the distribution, the species can be considered as pioneer, with representative populations in forests of secondary stage of regeneration.

In the northeast portion of the distribution, the species is commonly used in popular medicine, the stem bark is used in infusions, to treat wounds and ulcers, the properties are associated to the presence of tannins in the chemical composition (Dias *et al.*, 2012). The reddish portion in *A. cochliacarpus* bare is deeper than in *A. diamantina*.

Martius (1837) describes *Pithecollobium auaremotemo* based on *Mimosa cochliacarpus* Gomes, as a probable synonym. He used the epithet “auaremotemo”, following the first mention of the species (Piso, 1658, Iganci & Morim, 2009:583). Thus, Martius’s circumscription clearly refers to *A. cochliacarpus*, and not to *A. diamantina*. Many posterior studies erroneously follow Martius’s work as the original description of

the species. However, combinations based on this basionym would clearly be considered as non-validly published names.

**Examined material:**—BRAZIL. Rio Grande do Norte: Goianinha, Mata da Gruta do Bode, 15.XII.1966, *G. Teixeira 2967* (HST); BR 101, km 17, borda de mata na beira da estrada, a direita sentido João Pessoa – Natal, 01.III.2016, *E. Guerra et al. 121* (ICN); BR 101, km 17, borda de mata na beira da estrada, a direita sentido João Pessoa – Natal, 01.III.2016, *E. Guerra et al. 122* (ICN); BR 101, km 17, borda de mata na beira da estrada, a direita sentido João Pessoa – Natal, 01.III.2016, *E. Guerra et al. 123* (ICN); BR 101, km 29, borda de mata na beira da estrada, a direita sentido João Pessoa – Natal, 01.III.2016, *E. Guerra et al. 120* (ICN); Natal, 04.X.1999, *S.M. de Faria et al. 1894* (ICN, RB); São José de Mipibu, BR 101, entre km 142 e 143, de Natal para João Pessoa, a 5km da entrada de Pipa, entrada à direita, aproximadamente 500 m de estrada de chão, em borda da mata à direita, 27.II.2016, *E. Guerra et al. 115* (ICN). Paraíba: Bayeux, Margem da estrada Natal – João Pessoa, 12.IX.1979, *A. Fernandes et al. s.n.* (ICN, RB 460695); Margem da estrada Natal – João Pessoa, 12.IX.1979, *A. Fernandes et al. s.n.* (EAC 6900); Campina Grande, estrada João Pessoa – Campina Grande, 27.IX.1982, *A. Fernandes et al. s.n.* (EAC 11670, ICN, RB 460693); Conde, Área de Preservação Permanente de Tambaba: loteamento de Jacumã, 02.X.2009, *A.A.M. Araújo et al. 169* (JPB, RB); Área de Preservação Permanente de Tambaba, 23.VIII.2011, *L.A. Pereira et al. 303* (JPB, RB); Tambaba, nas bordas das estradas internas do loteamento, 28.II.2016, *E. Guerra et al. 119* (ICN); Jacaraú, Floresta Estacional Semidecidual das Terras Baixas, Mata da Pitanga fragmento Pb162, 22.III.2012, *P.C. Gadelha Neto 3197* (JPB, NY, RB); João Pessoa, 4.II.1994, *Matos s.n.* (EAC 19722, RB 460709); Bairro Bancários, terreno em área antropizada, 28.II.2016, *E. Guerra et al. 116* (ICN); Parque dos Sonhos, borda de estrada, 28.II.2016, *E. Guerra et al. 117* (ICN); entre João Pessoa e Coqueirinhos, borda de estrada, 28.II.2016, *E. Guerra et al. 118* (ICN); Mamanguape, BR-101, próximo ao km 60, 17.IX.1979, *A.J. Castro et al. s.n.* (EAC 6935, ICN, RB 460694); Marcação, Aldeia Lagoa Grande, 18.X.2006, *G.B. Freitas et al. 187* (ICN, RB); Rio Tinto, Floresta Estacional Semidecidual das Terras Baixas, fragmento Pb114, 29.III.2012, *P.C. Gadelha Neto 3242* (JPB, NY, RB); Santa Rita, Usina Miriri, 1.III.2016, *E. Guerra et al. 125* (ICN); Tabuleiro de Santa Rita, 24.IX.1962, *S. Tavares 1055* (HST). Pernambuco: Goiana, Ponta de Pedras, 26.XI.2013, *L.R. Silva 406* (HST);

RPPN Fazenda Tabatinga, borda do fragmento Mata Atlântica, 16.IV.2011, *D. Cavalcanti et al. 514* (UFP); Igarassu, Cruzinha/Santa Helena, 6.IV.2005, *A.D.C. Cavalcanti 207* (PEUFR); Usina São José, Mata da Zambana, borda da mata, 18.X.2007, *A. Alves-Araújo et al. 645* (UFP); Usina São José, Mata das Vespas, 29.XI.2007, *N.A. Albuquerque 616* (IPA, RB); Usina São José, Mata Dedo de Deus, 19.VI.2008, *L.V. Cunha 150* (HST); Usina São José, Mata Dedo de Deus, 23.X.2008, *L.V. Cunha 192* (HST); Usina São José, Mata da Zambana, 7.III.2016, *E. Guerra et al. 126* (ICN); Usina São José, Mata Dedo de Deus, 7.III.2016, *E. Guerra et al. 127, 128, 129, 130, 131* (ICN); Usina São José, Mata dos Macacos, 8.III.2016, *E. Guerra et al. 132* (ICN); Itamaracá, mata do Engenho Macaxeira, 30.III.1998, *A. Laurênio 985* (PEUFR); estrada do Sossego, 19.IX.2008, *L.R. Silva 205* (HST); Recife, Dois Irmãos, Próximo Est. Macacos, 30.IX.1949, *D.A. Lima 49319* (RB); Dois Irmãos, chão da Tiririca, 17.II.1966, *J.L.S. de Lima 10* (HST); Mata de Dois Irmãos, módulo 3, indivíduo 115, 03.X.1989, *M.L. Guedes s.n.* (ESA 10900); Mata de Dois Irmãos, módulo 11, indivíduo 536, 14.II.1990, *M.L. Guedes et al. 2262* (ESA); Mata de Dois Irmãos, módulo 3, indivíduo 115, *M.L. Guedes et al. 2268* (ESA); Rio Formoso, Horto Florestal de Saltinho, 23.IX.1959, *J.L.A. Falcão et al. 1207* (ICN, RB); Engenho Amaraji, Mata do Ribeiro, 7.III.2002, *S.S. Lira et al. 452* (PEUFR); Tamandaré, Mata da Gia, 27.XI.1999, *A.C. Souza et al. 508* (PEUFR). Alagoas: Barra de Santo Antônio, Bosque Hotel Fazenda, 14.XI.1982, *C. Campelo et al. 2023* (EAC); Colônia Leopoldina, Engenho Arraial, 9.VII.1969, *M.T. Monteiro 21697* (HST); Coruripe, Usina Coruripe, área da barragem de Capiatã, 15.III.2016, *E. Guerra et al. 137* (ICN); Usina Coruripe, 15.III.2016, *E. Guerra et al. 138* (ICN); Usina Coruripe, 15.III.2016, *E. Guerra et al. 139* (ICN); Maceió, APA do Catolé e Fernão Velho, Conjunto Novo Horizonte, Tabuleiro dos Martins, 27.I.1999, *R.P.L. Lemos 4117* (ALCB, MAC); Marechal Deodoro, próximo ao Sítio Malhado, 13.IX.1967, *F. Paiva 3402* (HST); Messias, 10.X.1967, *M. Tenório 21797* (HST, R); Pilar, Fazenda Lamarão, 14.III.2016, *E. Guerra et al. 133, 134, 135* (ICN); Rio Largo, Mata do Rolo, 21.VIII.1968, *M.T. Monteiro 22713* (HST); São Gonçalo, 21.IX.1954, *J.I.A. Falcão et al. 1188* (ICN, RB); São Miguel dos Campos, Mata do Varrela, 14.IX.1968, *M.T. Monteiro 22746* (HST). Sergipe: Aracaju, BR 101, 50km após a cidade, rumo Maceió, 2.II.1976, *P. Montouchet s.n.* (UEC 7330); Capela, Refúgio da Vida Silvestre Mata do Junco, 18.IX.2013, *E. Córdula et al. 1077* (UFP); Pirambu, Povoado Alagamar, Assentamento São Sebastião, 10.VII.2013, *T. Carregosa et al. 386* (ASE, UEC); Povoado Sambaíba, 9.IX.2013, *T.*

*Carregosa et al. 468* (ASE, UEC); Santa Luzia do Itanhy, cerca de 2 km do Distrito de Crasto, na estrada para Santa Luzia do Itanhy, 9.X.1993, *S.C. Sant'Ana et al. 431* (CEPEC, RB). Bahia: Alagoinhas, Campus II/UNEB, 16.I.2001, *N.G. Jesus et al. 498* (HUEFS); Almadina, Serra do Corcovado, 17.XII.2006, *R.A.X. Borges et al. 380* (CEPEC, ESA, HUEFS, MBM, NY, RB, SP, SPF, SPFR, UEC); Andaraí, Rio Apiaba, 17.IX.1984, *G. Hatschbach 48345* (UEC); entre Andaraí e Mucugê, *A. Fernandes et al. s.n.* (ICN, RB 460697) Barra da Estiva, estrada para o povoado Sincorá da Serra, 17.XI.1988, *R.M. Harley et al. 26500* (CEPEC, SPF); estrada de Barra de Estiva para Mucugê, 16.II.1997, *T.R. Santos et al. PCD 5785* (ALCB); Brejões, Fazenda Lagoa do Morro, 17.XI.2007, *F.M. Ferreira et al. 1848* (CEPEC, RB); Fazenda Lagoa do Morro, 17.XI.2007, *F.M. Ferreira et al. 1881* (CEPEC, RB); Caetité, Serra Geral, brejinho das Ametistas, 28.IV.2008, *M.L. Guedes et al. 14319* (ALCB); Caravelas, 5.VI.2012, *N.C.B. Albuquerque 9* (HUEFS); Entre Rios, RPPN Fazenda Lontra/Saudade, 29.III.1998, *N.G. Jesus et al. 350* (HUEFS, HUNEB); Litoral Norte, Subaúma, 20.IV.2002, *M.L. Guedes et al. 9574* (ALCB); Fazenda Experimental da Escola de Medicina Veterinária (UFBA) Litoral Norte, Reserva Florestal do povoado de Aguazinha, 21.XI.2009, *N. Roque et al. 2496* (ALCB); alto do Sempre-verde, 20.XI.2011, *E.N. de Matos et al. 817* (HUEFS); Esplanada, BR-101, cerca de 5 km N de Esplanada, 21.XII.1993, *L.P. de Queiroz et al. 3773* (HUEFS, SPF); Ibicoara, 21.VIII.1986, *R.P. Orlandi et al. 755* (RB); Jeremoabo, Comunidade Baixa dos Quelés, 13.XII.2009, *V.S. Almeida et al. 83* (HUEFS); Lençóis, 8km S da BR 242, 26.XI.1992, *Arbo et al. 5789* (CTES, HUEFS, MBM, NY, SPF, UB); 2.VIII.1998, *S. Bridgewater et al. S1051* (UB, UEC); vertente E do Morro do Pai Inácio, 26.I.2000, *J.G. Jardim et al. 2528* (CEPEC, RB); Fazenda Salobrinho, 12.III.2004, *R.Funch 26* (HUEFS); 19.X.2009, *E.P. Queiroz et al. 3913* (RB); Maracás, 13 a 22 km ao S de Maracás, 27.IV.1978, *S.A. Mori et al. s.n.* (CEPEC, RB); Fazenda Vale Aprazível, 22.IV.2002, *K.R.B. Leite et al. 191* (HUEFS); Cruzeiro, 27.X.2012, *E. Melo et al. 11627* (HUEFS); estrada para Lajeado do Tabocal, 27.X.2012, *E. Melo et al. 11690* (HUEFS); Mata de São João, Vila Sauípe, 9.VII.2002, *E.von S. Medeiros et al. 185* (RB); Miguel Calmon, Serra das Palmeiras, 21.VIII.1993, *L.P. de Queiroz et al. 3513* (HUEFS); Piemonte Da Diamantina, entorno da entrada do Parque Sete Passagens, 21.XII.2006, *M.L. Guedes et al. 13022* (ALCB); Piemonte Da Diamantina, entorno da entrada do Parque Sete Passagens, 23.XII.2006, *M.L. Guedes et al. 13270* (ALCB); Morro do Chapéu, 26.IX.1965, *A.P. Duarte et al. 9202* (ICN, K, RB); near base of Morro do Chapéu,

19.II.1971, *H.S. Irwin et al. s.n.* (NY 32557, UB); near base of Morro do Chapéu, 20.IX.1985, *G.C.G. Pinto 99a/85* (ESA, HRB, RB, UB); próximo a Moreira, 31.III.1986, *A.C. Sarmiento et al. 830* (RB); rodovia para Utinga, 15.IX.1990, *H.C. de Lima et al. 3894* (ICN, RB); rodovia para Utinga, 15.IX.1990, *H.C. de Lima et al. 3902* (ICN, RB); cerca de 12km E do entroncamento para Cafarnaum, na BA 052, 22.VIII.1993, *L.P. de Queiroz et al. 3541* (HUEFS); cerca de 12 km do Morro do Chapéu, 11.III.1996, *A.M. Giulietti et al. PCD 2277* (SPF); 5 km ao sul de Morro do Chapéu, 14.III.1996, *R. Atkinson et al. PCD 2365* (SPF); Fazenda Santa Maria, 16.III.1996, *R. Atkinson et al. PCD 2458* (SPF); Serra Pé do Morro, 29.VI.1996, *H.P. Bautista et al., PCD 3220* (SPF); arredores do povoado de Fedegosos, 30.IV.1999, *F. França et al. 2749* (HUEFS, UB); 11 km W de Morro do Chapéu, 2.V.1999, *F. França et al. 2833* (HUEFS, SPF); Estrada para Utinga, 18.VII.2001, *V.C. Souza et al. 26432* (ESA, SPF); estrada para o Morrão, 03.XII.2003, *E.B. Miranda et al. 588* (HUEFS); Estrada do Feijão, BA 052, km 259 a km 263, 21.III.2016, *E. Guerra 140, 141, 142, 143, 144, 145, 146* (ICN); Mucugê, Santa Cruz, 9.IV.1992, *G. Hatschbach et al. 56880* (MBM, UEC); estrada Andaraí-Mucugê, 26.II.2001, *A.A. Ribeiro-Filho 229* (HUEFS); Guiné, Serra do Esbarrancado, 30.X.2001, *A.A. Conceição 974* (SPF); Chapadinha, 6.II.2005, *R.Funch 598* (HUEFS); Parque Nacional da Chapada Diamantina, Serra do Esbarrancado, 17.IV.2005, *D. Cardoso et al. 455* (HUEFS); estrada para Igatu, 25.II.2007, *R.M. Harley et al. 55611* (HUEFS); entre Andaraí e Mucugê, *A. Fernandes et al. s.n.* (EAC 20480); Palmeiras, Serras dos Lençóis, 23.V.1980, *R.M. Harley 22516* (ICN, RB, UEC); estrada Seabra, 18.V.1982, *A. Fernandes et al. s.n.* (EAC 11391); BR 242, 2 km antes do entroncamento para Palmeiras, 15.IX.1990, *H.C. de Lima et al. 3965* (ICN, RB); 5.IX.1996, *E. Nunes et al. s.n.* (EAC 24357, ICN, RB 460712); Campo de São João, 15.XII.2002, *L.S. Funch et al. 1531* (HUEFS); Campo de São João, 15.XII.2002, *L.S. Funch et al. 1532* (HUEFS); 06.IV.2004, *C. van den Berg et al. 1400* (HUEFS); estrada para Pratinha, 29.I.2005, *J.P. Souza et al. 5008* (ESA, RB); Cerrado no caminho do Morro do Camelo, 16.IV.2009, *E. Silveira s.n.* (EAC 44703); Morro do Pai Inácio, 10.VI.2012, *L.P. de Queiroz et al. 15538* (HUEFS, RB); Porto Seguro, BR 367, 27.XI.1979, *A.A. Mori et al. s.n.* (CEPEC 13006, UEC 24 391); Salvador, Área de Pituauçu, 15.II.1992, *H.P. Bautista et al. 1609* (HRBN, RB, SPF); Biribeira, Paralela, 8.XI.1994, *J.A.R. Jesus et al. s.n.* (ALC 26179, SPF 118169); Parque Metropolitano de Pituauçu, 20.XII.2003, *D.F. Gomes et al. 10* (HUEFS); Parque Metropolitano de Pituauçu, XI.2011, *M.C. Bellintani et al. 10* (ALCB); Parque Metropolitano do Pituauçu,

24.III.2016, *E. Guerra 151* (ICN); São Sebastião do Passé, Fazenda Maju, 27.III.2001, *G. Carvalho et al. 32* (ALCB); Seabra, Serra da Água de Rega, 24.II.1971, *H.S. Irwin et al. s.n.* (NY 30882, UB, UEC 40922); 13.II.1987, *J.R. Pirani et al. 2009* (F, K, SPF); entre Lagoa Boa Vista e Água de Rega, 25.VI.2010, *E. Melo et al. 8400* (HUEFS); Utinga, 17.X.1994, *L.P. de Queiroz et al. 4230* (HUEFS); Vitória da Conquista, 4.III.1978, *S.A. Mori et al. s.n.* (CEPEC 9431, RB 204935); matinha da UESB, XI.2010, *A.F.P. Machado et al. 1014* (HUEFS). Espírito Santo: Itapemirim, Fazenda do Ouvidor, 27.III.2016, *E. Guerra et al. 152* (ICN); Linhares, Reserva Natural Vale, 7.XI.1977, *J. Spada 6/77* (CVRD, ICN), 14.IX.2004, *D.A. Folli 4931* (CVRD, ICN), 02.V.2008, *G.S. Siqueira 412* (CVRD, ICN), Canto Grande, III.2016, *M.P. Morim 587* (RB, ICN); Fazenda 3 Maria, 21.X.2011, *D.A. Folli 6801* (CVRD, ICN, RB). Minas Gerais: Itueta, 29.IX.2004, *A.A. da Luz 235* (CVRD, ICN). Rio de Janeiro: Armação de Búzios, Rasa, 27.VIII.2004, *H.G. Dantas 408* (ICN, RB); Reserva Tauá, 17.V.2005, *R.D. Ribeiro et al. 467* (ICN, RB); Arraial do Cabo, Ilha de Cabo Frio, vertente N, 22.XI.2001, *C. Farney et al. 4413* (ICN, K, MBM, RB SPF, US), 01.IX.2004, *R.D. Ribeiro et al. 326* (RB), no Lageado após o farol velho, 17.XI.2015, *E. Guerra et al. 105, 106* (ICN), na parte baixa, 17.XI.2015, *E. Guerra et al. 107, 108* (ICN); Maricá, Ponta do Fundão, margem da Lagoa da Barra, 03.IV.1996, *M.C.L. Ramos 1112* (ICN, RB); Nova Iguaçu, Parque Municipal de Nova Iguaçu, estrada da Cachoeira, 4.IX.2002, *M.C.F. Santos et al. 908* (RB); Rio de Janeiro, Chácara do Guimarães, Leblon, 10.X.1947, *O.X. de B. Machado s.n.* (ICN, RB 76099); Estrada de acesso ao Corcovado, entrada do Sumaré, 16.X.1972, *J. Almeida de Jesus 2036* (ICN, RB); subida para a Pedra da Gávea, 16.IV.1974, *D. Sucre et al. 10702* (ICN, RB); Parque Nacional da Tijuca, estrada para Corcovado, 22.IX.1982, *H.C. de Lima 1787* (ICN, RB); Jardim Botânico do Rio de Janeiro, seção XIV, canteiro A, indivíduo 3077, 28.IX.1989, *V.F. Gonçalves et al. 41* (ICN, RB); Maciço da Tijuca, 15.IV.1994, *J.M.A. Braga 1138* (RB); Paquetá, Morro do Parque Ducke, 9.V.1998, *R.M. Araújo et al. 260* (ICN, RB); Floresta da Tijuca, Pedra da Gávea, Pé de Carrasqueira, 09.III.2004, *R.D. Ribeiro et al. 97* (ICN, RB); Jardim Botânico do Rio de Janeiro, canteiro 37a, 13.XI.2015, *E. Guerra et al. 104* (ICN); Floresta Nacional da Tijuca, Vista Chinesa, 23.XI.2015, *E. Guerra et al. 109* (ICN); Morro da Viúva (APA), 23.XI.2015, *E. Guerra et al. 110* (ICN); Parque Natural Municipal Catacumba, 24.XI.2015, *E. Guerra et al. 111, 112, 113, 114* (ICN); Saquarema, Reserva Ecológica Estadual de Jacarepiá, 29.X.1991, *C. Farney et al. 2782*

(RB). São Paulo: São Paulo, Horto Faculdade de Farmácia de São Paulo, 22.I.1945, *Hoehne s. n.* (RB).

### ***Phylogenetic Analyses***

The molecular phylogenetic analysis included 18 terminal taxa and 1318 bp. The ingroup sampling included *Abarema cochliacarpus*, *Macrosamanea* Britton & Rose ex Britton & Killip (two accessions), *Inga* Mill. (four accessions), *Zygia* P.Browne (five accessions), plus *Enterolobium schomburgkii* (Benth.) Benth. For the outgroup we choosed *Samanea saman* (Jacq.) Merr., one representant of the tribe Ingeae, not close related to the *Inga* Alliance. We also sampled few accessions of the former *Abarema* Alliance, including *Abarema langsdorffii* (Benth.) Barneby & J.W.Grimes, *Abarema filamentosa* (Benth.) Pittier, *Abarema centiflora* Barneby & J.W.Grimes and *Hydrochorea corymbosa* (Rich.) G.P.Lewis & Owen.

*Abarema cochliacarpus* grouped together with genera from the *Inga* Alliance with 100% of posterior probabilities (Fig. 5). *Abarema* emerged as sister to *Macrosamanea* (92% of posterior probability). The remaining taxa from the extinct *Abarema* Alliance clustered together, next to *Samanea saman* in the outgroup.

### **Discussion**

#### **Systematic relationships of *Abarema s.s.* within the *Inga* Alliance**

*Abarema* used to be considered as a monophyletic genus, and the morphological features used to delimit and circumscribe the genus were considered as robust. Even in the morphological phylogeny of Barneby & Grimes (1996), and other recent molecular phylogenetic analysis (Souza & al., 2013 ) the monophyletic circumscription of the genus was not contested. However, previous phylogenetic analyses made their conclusions based in sampling only few accessions of *Abarema* (Souza & al., 2013). Moreover, all the taxonomic changes encompassing taxa once described as *Abarema* and further combined to other genera, and vice versa, highlight the ambiguity applied in different circumscriptions (Britton & Rose, 1928; Britton & Killip, 1936). The first molecular analyses focused on the genus *Abarema* and its closest related taxa, showed *Abarema* as polyphyletic (Iganci & al., 2016). Thus, the morphological diagnostic characters used to circumscribe the genus were considered as homoplastics. Curved fruits with reddish endocarp were once used to delimit *Abarema* as also including Asian species currently circumscribed into *Archidendron* F.Muell. and *Pararchidendron*

I.C.Nielsen (Kostermans, 1954), which is phylogenetic unrelated to *Abarema*. However, this homoplastic character was still considered strong on the delimitation of *Abarema* s.l. by Barneby & Grimes (1996), besides the bicoloured mimetic seeds.

The type species of *Abarema*, *Abarema cochliacarpus* is segregated from the remaining species of *Abarema* s.l., and strongly sustained as part of the *Inga* Alliance (Iganci & al., 2016). The new circumscription for *Abarema* presented here, is based on the detailed analyses of the morphological characters of *Abarema cochliacarpus* and *Abarema diamantina* species. We highlight the conspicuous lenticels in the branches, the spiraled fruits, the ferruginous pulverulent indumentum in the fruit epicarp and the seed bicoloured in a straight division between the dark and white portions as good taxonomic characters to support *Abarema* s.s. (Fig. 2). The capitate raceme present in *Abarema* s.s. is recurrent in species of the *Inga* Alliance, including *Zygia*, *Macrosamanea* and *Enterolobium*, besides being less common in *Inga*. Vegetative morphological characters are strongly similar between species and genera of Ingeae, and the fruits are still one of the most important characters to distinguish the genera. Future morphological analyses should contribute together with a more robust molecular analysis, for a more comprehensive systematic organization of the Alliances within the tribe. Our phylogenetic analysis showed *Abarema* close related to the *Inga* Alliance, similarly to the results presented by Iganci & al. (2016). *Abarema* merged as sister to the Amazonian genus *Macrosamanea* with moderate posterior probability, and also close to *Inga*, *Zygia* and *Enterolobium schomburgkii*.

The current new circumscription to *Abarema* implies in the need of a new taxonomic circumscription to the remaining species traditionally recognized under *Abarema*. These remaining species of *Abarema* s.l. showed to be polyphyletic, splitting out in two clades in the *Abarema* Alliance phylogeny by Iganci & al. (2016). The Y clade is compound by *Abarema* s.l. species from Andes, that are morphologically differentiated mainly by the flowers that are clustered in a long spike-like inflorescence (Iganci & al., 2016). The W clade is composed by the remaining *Abarema* s.l. nested together with the genera *Balizia* and *Hydrochorea* with low internal resolution (Iganci & al., 2016). These unresolved taxa represent the next steps towards the resolution of the dissolved *Abarema* Alliance group, and a new taxonomic treatment to name and describe those groups is being produced (Soares & al., *in prep.*).



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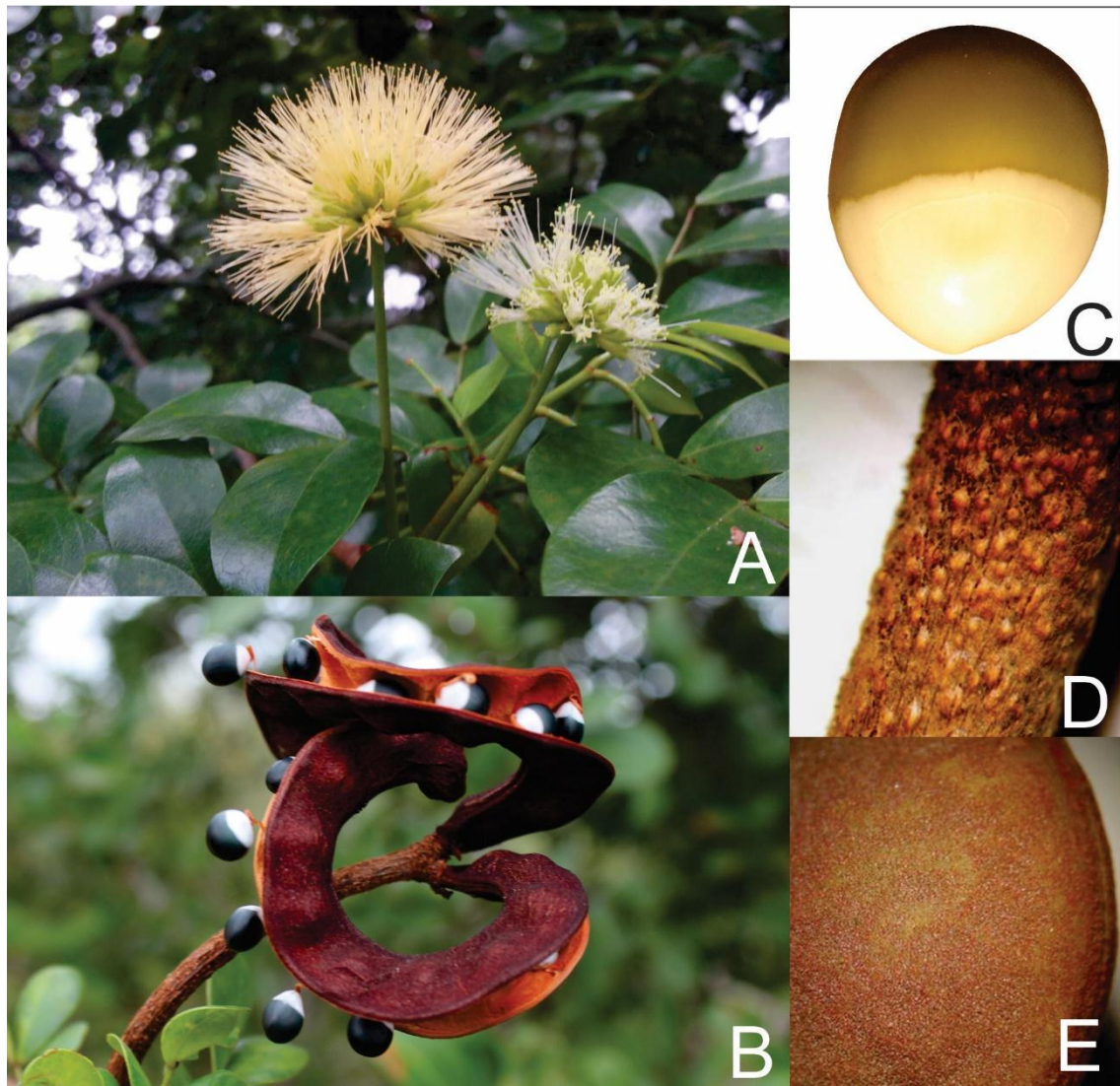
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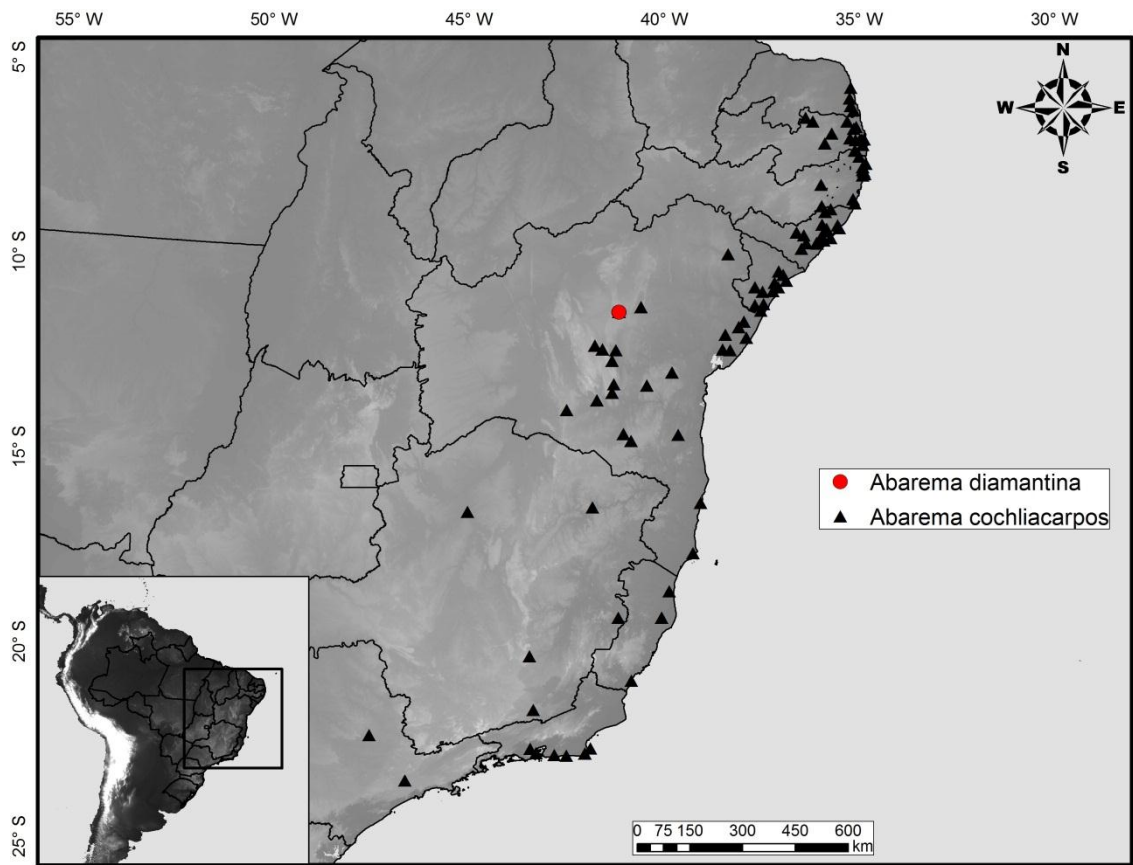
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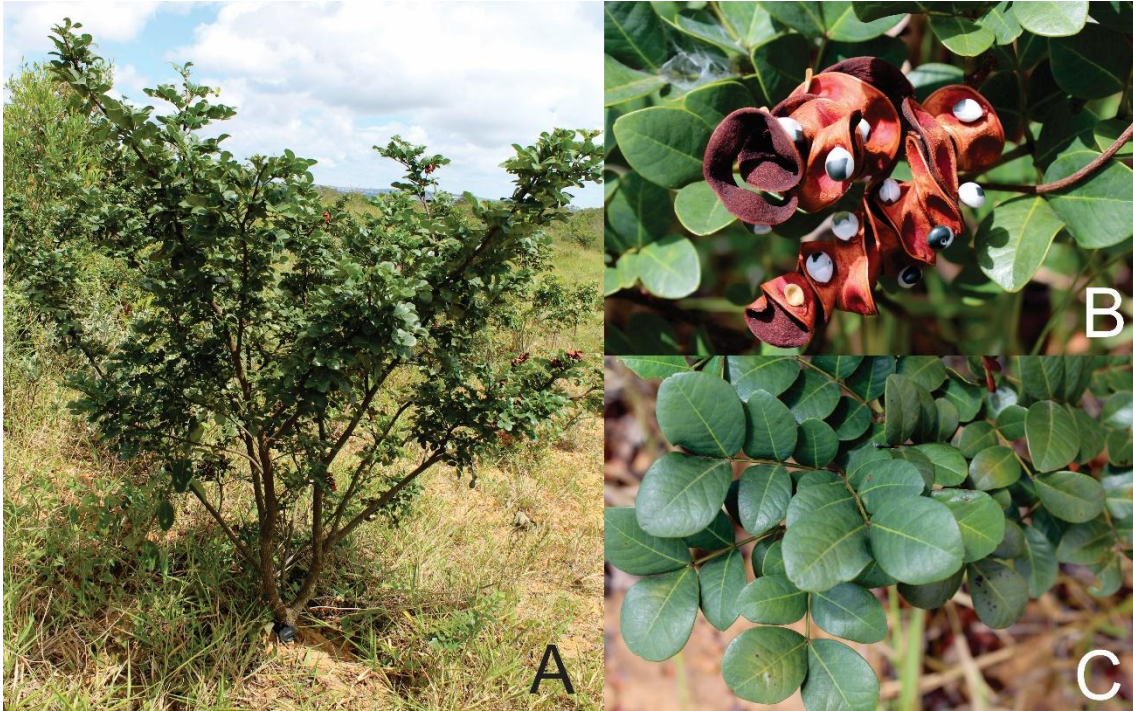
## Figures



**Fig. 1** - Taxonomic diagnostics characters of the genus *Abarema* Pittier. **A.** homomorphic flowers in capitulate racemes (photo: Iganci, J.R.V); **B.** spiraled fruit (photo: Guerra, E.); **C.** seed bicoloured in a straight division between the dark and white portions (photo: Iganci, J.R.V); **D.** branches with conspicuous lenticels (photo: Iganci, J.R.V); **E.** ferruginous pulverulent indumentum in the fruit epicarp (photo: Iganci, J.R.V).



**Fig. 2** - Geographic distribution of the genus *Abarema* Pittier.

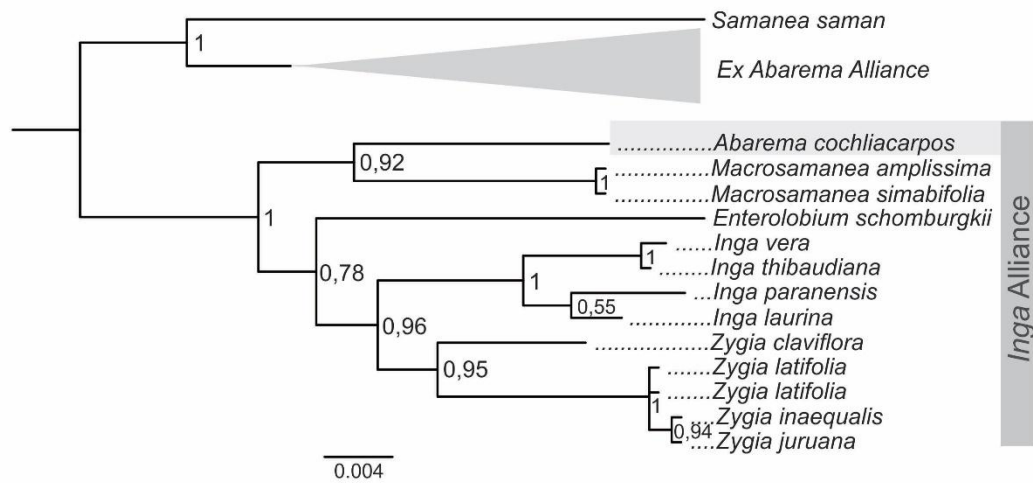


**Fig. 3** - *Abarema diamantina* E.Guerra, Iganci & M.P.Morim. **A.** habit (photo: Guerra, E.); **B.** fruit (photo: Guerra, E.); **C.** prominent venation of the leaflets (photo: Guerra, E.).



**Fig. 4** - *Abarema cochliacarpus* (Gomes) Barneby & J.W.Grimes. **A.** habit (photo: Guerra, E.); **B.** fruit (photo: Guerra, E.); **C.** non prominent venation of the leaflets (photo: Guerra, E.).





**Fig. 5** - Bayesian phylogenetic tree, based on the combined analysis of *matK* and ETS sequences, showing the positioning of the genus *Abarema* s.s. within the *Inga* Alliance. Node labels indicate Bayesian posterior probabilities.

Node labels indicate Bayesian posterior probabilities.

## **ARTIGO 2.**

### **Taxonomic delimitation in species complexes and the future challenges of conservation**

Artigo a ser submetido para publicação na revista  
“Diversity and Distributions”

## **Taxonomic delimitation in species complexes and the future challenges of conservation**

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Short running title: Taxonomic delimitation and conservation

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## **ABSTRACT**

**Aim** The taxonomic and ecological knowledge of plant species complexes legitimate its conservation concern. Non-well delimited species boundaries may lead to wrong assessments of biodiversity. At the same time, a rare species might have its distribution range overestimated by considering other close related species as a unique taxon. The present study aimed at investigating the level of morphometric variation within the *Abarema cochliacarpus* complex, as a case study, throughout its distribution, and the sources of its variation.

**Location** Northeast to Southeast Brazilian Atlantic Forest hotspot and the Caatinga.

**Methods** We examined all available herbarium material, and sampled new specimens along the entire distribution of the *Abarema cochliacarpus* complex. Morphometric traits of the complex were measured and environmental variables were detected along its geographical gradient. A morphometric study using cluster and NMDS analyses was conducted on reproductive and vegetative features. We analyzed patterns of variation among and within groups, and how it is related with environmental features.

**Results** We found that some morphological groups of the complex form consistent groups. Some of the morphological characters that represent good taxonomic features to differentiate the groups were highlighted by our analyses. Plant morphometric data showed to be correlated to environmental traits. The climatic and environmental variables that seem to drive the morphology along the distribution complex were presented.

**Main conclusions** The development of conservation strategies and actions for protecting species complex deals with understanding the range of morphological characteristics within the complexes. In the study case of the *Abarema cochliacarpus* complex, we conclude that there are morphotypes well delimited by morphometric analyses linked to climatic and environmental variables, but further studies using molecular techniques are still required. While these resolutions are forthcoming, we highlight the importance of conserving the morphotypes of species complex with a large distribution range.

**Keywords** Atlantic Forest, biodiversity, Caatinga, distribution, environmental gradient, morphometry, species complex.

## Introduction

Uncertainties on the taxonomic boundaries between species play an important role on conservation (Mace, 2004). The distribution range of species within a complex of two or more poorly known species may vary according to its delimitation, leading to overestimate the species distribution or even underestimate its diversity (Eldridge *et al.*, 2014). Precise taxonomic delimitation of close related species may directly affect their habitat occupation and extension of occurrence and, consequently their conservation status individually (IUCN, 2001). At the same time, recurrent changes on species concept lead to taxonomic inflation by the raising of subspecies to species what may overestimate the red lists (Isaac *et al.*, 2004).

To apply conservation actions, a well resolved taxonomy of the group of interest is essential (Vogel-Ely *et al.*, 2017). There are a variety of techniques to delimit species, reflecting the different species concepts that are recognized, like the morphological, ecological and phylogenetic concepts (Agapow *et al.*, 2004). Aleixo (2009) highlight the difficult on delimiting species, evenmore dealing with the variety of species concepts and species complexity, and suggest that for conservation strategies really be effective, the protection should be addressed to Evolutionary Significant Units (ESU). The ESU are classified by Aleixo (2009) as entities of biodiversity, that even if not well delimited by taxonomists, are classified as representative on being protected. Taxonomists can apply a variety of methodologies focusing on clarifying the relationships between close related species, species complexes, and even cryptic species, testing more than one species concept for the studied group, resulting in a well delimited taxa to apply conservation strategies.

Ennos *et al.* (2005) suggest that for conservation of taxonomically complex groups, in specific those where uniparental reproduction, hybridization and polyploidy occurs, it is worth to recognize the evolutionary processes of the groups and then to implement conservation strategies to maintain the evolutionary processes generating biodiversity. Understanding these processes is a challenge since it is required to reconstruct the evolutionary history of diversification and ecological interactions within a determined group (Levin, 2001; Rieseberg & Wendel, 2004).

## A case study on *Abarema cochliacarpus*

The first molecular phylogeny of *Abarema* Pittier (1927) showed that the genus was polyphyletic and its type species, *Abarema cochliacarpus* (Gomes) Barneby & J.W.Grimes, grouped to the informal clade *Inga* Alliance, splitting out from the other species as a monospecific genus (Iganci *et al.*, 2016).

*Abarema cochliacarpus* occurs in the coastal Atlantic Forest from Northeast and Southeast Brazil, and as an inland form in the Caatinga biome in Bahia state, also in Northeast Brazil (Barneby & Grimes, 1996; Iganci & Morim, 2012). On this large latitudinal distribution range, the species presents a variety of morphotypes cited on literature. Lewis (1987) studying the legumes of Bahia highlighted the existence of two morphotypes of *A. cochliacarpus*, the first represented by trees of ten or more meters high, occurring in the coastal region, and the second represented by shrubs up to four meters high, occurring in the Caatinga. A third morphotype was cited by Lewis (1987), which referred to an extreme form of the smaller morphotype, as a shrub up to two meters high, with more coriaceous leaflets. Barneby & Grimes (1996) highlighted that the fruits in specimens from Pernambuco and Paraíba states in Northeast Brazil, were thicker than the other populations. Iganci & Morim (2012) also reported the occurrence of another distinct morphotype in the Island of Cabo Frio, in Rio de Janeiro state, Southeast Brazil. The morphological distinction between all these morphotypes suggests that *A. cochliacarpus* might be better recognized as a species complex than a unique taxon, including the recently described *Abarema diamantina* E.Guerra, Iganci & M.P.Morim, endemic to the Caatinga biome (Guerra *et al.*, 2016) (Fig. 1).

*Abarema cochliacarpus* was considered Vulnerable by the IUCN Red List, but considering its wide distribution it is now evaluated as Least Concern since it does not fit any of the criteria for the threatened categories (Watkinson, 2012). However, the doubts concerning its threats still remain when we question the identity of different morphotypes or species as a complex. *Abarema cochliacarpus* has an extensive distribution, comprising a wide environmental range, and its distribution coincides with two of the most threatened biomes in Brazil, the Atlantic Forest and the Caatinga. The Atlantic Forest is recognized as a Hotspot of Biodiversity, having as main threats human occupation, land use change and habitat loss (Myers *et al.*, 2000). The specific habitats where the species is found are dense ombrophilous forest, semi-deciduous forest and restinga (coastal scrub) (Iganci & Morim, 2012). The Caatinga is the largest

semiarid ecoregion from South America, being threatened by the expansion of agriculture and cities, that modify the structure and the diversity of this ecosystem (Leal *et al.*, 2005). Two of the complex morphotypes occur in the open shrublands in Caatinga biome.

Considering this background, we look for possible boundaries that allow us to recognize if the *Abarema cochliacarpus* complex has only the two known species or a more intricate taxonomic circumscription. Thus we test if qualitative and quantitative morphological characters of the morphotypes and species sustain robust morphological groups along the geographical distribution of the complex. Thus, we test if the variation on the morphometric features are related or not to the environment to understand what are the ecological traits that drive the morphological variation along the complex geographical distribution. The possibility of new taxonomic delimitations will implicate in developing new conservation strategies.

## Methods

### Study area

The *Abarema cochliacarpus* complex is widespread in contrasting environments: along the Northeast and Southeast Brazilian coast in the Atlantic Forest biome, and in the inland Caatinga biome, a seasonally dry forest biome, in the Bahia state, Northeast Brazil. The study covers the entire distribution of the complex, which ranges more than 20° in latitude, covering 11 states of Northeast and Southeast Brazil: Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo (Fig. 2).

Most of the study area is under tropical climate, however there are arid areas in the north and subtropical ones in the south along the species complex distribution (Alvares *et al.*, 2013). The areas of occurrence of the complex varies in altitude from the sea level to about 1.200 m a.s.l. in the inland areas. The mean annual precipitation varies from 850 mm in the driest area, in the Caatinga biome, up to 2.050 mm in wettest area, in the extreme Northeast Brazil, in the Atlantic Forest biome (INMET, 1992). The annual insolation varies, in hours, from 1.800 hours in the southeast, to 2.800 hours in the northeast of the distribution (INMET, 1992). The average annual temperature does not present a great variation, it goes from 20°C to 26°C, the maximum annual

temperature varies from 25°C to 31°C, and the minimum varies from 14°C to 24°C (INMET, 1992).

#### Morphological database

We analyzed the most important collections of the *Abarema cochliacarpus* complex along its complete distribution in the Atlantic Forest and the Caatinga biomes, examining samples from 1945 to 2016. Thirteen Herbaria collections ALCB, CVRD, EAC, ESA, HST, HUEFS, ICN, PEUFR, RB, SPF, UB, UEC e UFPE (Thiers, 2017) were analyzed, representing a total of 157 specimens. Additional fieldwork excursions to Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Bahia, Espírito Santo and Rio de Janeiro states were performed aiming to fill the gaps concerning the morphotypes information and sites underrepresented along the entire environmental gradient. The field trips were conducted between November 2015 and March 2016, increasing the original number in 47 new records. In total, we examined 194 specimens of the *Abarema cochliacarpus* complex, seven of them, representing *A. diamantina*, and the remaining representing all the different morphotypes of *A. cochliacarpus* along its entire geographical distribution (see Appendix S1 in Supporting Information).

Within the complex there are four groups pre-established by the literature and our field observations: (i) the upper northeast group (nt; n=67), (ii) the typical group (tp; n=113), (iii) the Cabo Frio island group (cf; n=8), and (iv) the *Abarema diamantina* group (di; n=6). For all the 194 specimens, we measured 19 quantitative characters and 11 qualitative characters, totalizing 30 variables for each sample, nine variables were relative to vegetative and 21 to reproductive characters (see Appendix S2).

The *Abarema cochliacarpus* complex rarely present flowers and fruits at the same period, thereby our final matrix contains missing data, since just few exsiccate present the complete set of reproductive characters. To deal with the missing data, we used the data matrix in two different sizes, one objective and another more subjective, with a more restrict set of variables (due the incomplete morphological information for some samples) respectively. The first matrix has the total number of samples, and the number of variables determined by the clustering of variables, which lump together strongly related variables, avoiding redundancy and favoring variable selection. The selected variables were the height of the plants, consistency of leaflets, corolla length, insertion of the staminal tube in the corolla, staminal tube length, anthers length, ovary



length, ovary apex, peduncle length, fruit length, fruit width. In the second matrix, we selected eight variables, that according our expertise in the study group are the most representative taxonomically, focusing mainly on the fruits characters, which are one of the most important morphological characters to recognize the mimosoid legumes (fruit length, fruit turns, fruit width, and fruit thickness), and others that were also well represented in our database (the height of the plants, consistency of leaflets, insertion of the staminal tube in the corolla, peduncle length), and then we excluded the samples with less than four measured variables, resulting in a matrix of 122 samples, also representing the whole morphological and geographical ranges within the complex.

#### Climatic/Environmental data

We extracted current climate data from WorldClim database (time period ~1960-1990, resolution ~18km) (<http://www.worldclim.org/current>) for the georeferenced point location of each analyzed specimen. The *Abarema cochliacarpus* complex distribution coincides with the area with higher density of weather stations in Brazil, from which the records were used to derive the set of bioclimatic variables (BIO) used in this study. From the available set of variables in WorldClim, we selected the altitude and another seven variables which are biologically meaningful variables and represent the extremes or limiting environmental factors that most strongly constrain species distribution (Toledo *et al.*, 2012). The following variables were used to assess the association among environment and morphology: BIO2 = Mean diurnal temperature range (mean of monthly maximum temperature minus minimum temperature); BIO3 = Isothermality ( $\text{BIO2} / \text{Temperature Annual Range} * 100$ ); BIO5 = Maximum temperature of warmest month; BIO6 = Minimum temperature of coldest month; BIO13 = Precipitation of wettest month; BIO14 = Precipitation of driest month; BIO16 = Precipitation of wettest quarter (i.e. precipitation of four consecutive wettest months); BIO17 = Precipitation of driest quarter.

#### Data analyses

Cluster analyses were performed to yield a dendrogram depicting the morphological relatedness within all the samples of the *Abarema cochliacarpus* complex along its entire distribution for each data matrix. The distance matrices were

used to calculate a cluster, where Ward method was employed. Since the Gower dissimilarity index can handle with missing data, it was applied to detect underlying ecological gradients in both data matrices (Faith *et al.*, 1987).

We estimated the association between environmental features and plant morphology using Mantel test (Legendre & Legendre, 1998). The test consists of calculating a correlation between environmental and morphometric dissimilarity matrices, then permuting and calculating the same statistic test under 999 Monte Carlo randomizations, and then comparing the original test to the distribution of statistic tests to generate a p-value.

The morphological variables measured are mixed (qualitative and quantitative), so for the ordination analyses, we used nonmetric multidimensional scaling (NMDS). NMDS is a constrained ordination technique, that uses both information from the matrix of sample morphologies, and the environmental matrices, aiming to explain the differences in the samples between sites, by the differences in environmental variables (Kindt & Koe, 2005). Besides accepting mixed data, NMDS is the most robust ordination method for detect ecological patterns (Minchin, 1987).

To individually test each pre-established group, we applied additional analyses of variance to test and highlight some key taxonomic characters identified as potentially strong morphological features to distinguish the groups. Those morphological traits include the height of the plants, the length of the distal leaflet, the insertion of the staminal tube in the corolla, anthers length, the fruits width, and the fruits thickness.

All the statistical analyses were carried out with R 3.2.3 (R Development Core Team, 2010) using cluster, ClustOfVar, MASS and vegan packages.

## **Results**

### Groups definition

The cluster dendrogram obtained from the complete matrix (194 samples and 11 variables), presented five major morphological groups (Fig. 3(a)). The pre-established group *Abarema diamantina* (di) was remarkably distinguished by grouping all its six samples. A second group was mostly composed by samples from pre-established northeast group (nt) (33 samples), together with 11 representatives of the typical group (tp), in addition to one sample from the Cabo Frio island group (cf). The samples from

the pre-established typical group (tp) was splitted out into three independent groupings, with the presence of some samples from the other pre-established groups. In the first one (tp1), there are 15 samples from the typical group, eight from the upper northeast group, and four from the Cabo Frio island group; in the second one (tp2), there are 26 representatives of the typical group, seven from the upper northeast group, and one from the Cabo Frio island group; the third cluster presented 61 representatives of the typical group, 19 from the upper northeast group and two from the Cabo Frio island group.

The diagram design obtained by the cluster analyses was similar between the two matrix size studied, highlighting that its main structure was maintained regardless the effect of missing data, mostly found in the complete matrix.

The second cluster dendrogram (Fig. 3(b)), obtained from the reduced matrix of 122 samples and eight variables, presented a similar design of the complete matrix cluster. Five major morphological groups were formed. The pre-established *Abarema diamantina* group samples clustered. Also the pre-established upper northeast group clustered, but on this analysis, with only five representatives of the typical group clustering together. The samples from the typical group splitted out again into three independent clusters, in the first one, compounded by eight samples of typical group and one representative of the upper northeast clustering together; in the second one, there are 29 samples from the typical group, plus five representatives from the upper northeast pre-established group, and four from the Cabo Frio island pre-established group; the third cluster is compounded by 29 samples of the typical group, three representatives of the upper northeast group, and two of the Cabo Frio island group.

#### Environmental sources of variation

The ordination analyses and Mantel test were realized with the same matrices used for the cluster analyses. For the complete samples matrix, with eleven variables, the Mantel test presented a positive correlation between the two dissimilarity matrices from morphological and environmental data ( $r = 0.1101$ ,  $P = < 0.001$ ), confirming that plant morphological traits are related to environment. The NMDS ordination clearly split the *Abarema diamantina* group from the main group (Fig. 3(a)). In the main group, the upper northeast seems to be gradually replaced the typical group. The Cabo Frio island group specimens can be found scattered among the typical group. The NMDS most important environmental and climate variables that drive the distribution and

morphological features of *Abarema diamantina* group were the altitude ( $r = 0.2121$ ,  $P = 0.001$ ) and the isothermality ( $r = 0.0853$ ,  $P = 0.001$ ). While the others are mainly driven by the maximum temperature of warmest month ( $r = 0.1454$ ,  $P = 0.001$ ), minimum temperature of coldest month ( $r = 0.1283$ ,  $P = 0.001$ ), and the precipitation of wettest quarter ( $r = 0.0809$ ,  $P = 0.002$ ), wettest month ( $r = 0.0622$ ,  $P = 0.005$ ), and driest month ( $r = 0.0333$ ,  $P = 0.040$ ).

For the second matrix, with the restricted number of samples and eight variables, the Mantel test also presented a positive correlation between morphological and environmental data ( $r = 0.1732$ ,  $P = 0.001$ ). The NMDS ordination separated the *Abarema diamantina* group from all other groups (Appendix S3). The upper northeast group grouped consistently. The typical and Cabo Frio Island groups grouped together as a continuum. The NMDS indicated that the most important variable that drive the geographical distribution and morphological features of *Abarema diamantina* group is the altitude ( $r = 0.2650$ ,  $P = 0.001$ ). For the upper northeast group, the most important variables that drive its geographical distribution and morphological features are the maximum temperature of warmest month ( $r = 0.3046$ ,  $P = 0.001$ ), minimum temperature of coldest month ( $r = 0.3454$ ,  $P = 0.001$ ), and the precipitation of wettest quarter ( $r = 0.3766$ ,  $P = 0.001$ ) and of the wettest month ( $r = 0.3441$ ,  $P = 0.001$ ).

### Morphometric variation

The four reproductive morphological features tested as possible key taxonomic characters, proved to be effectively valuable on the circumscription of the pre-established groups (Fig. 5(a, d, e, f)). The anthers length and the insertion of the staminal tube in the corolla distinguished the *Abarema diamantina* group from the remaining. The fruit thickness and the fruit width distinguished the upper northeast group.

Plant height is one of the morphological vegetative features analyzed, and distinguished the *Abarema diamantina* group from the remaining ones (Fig. 5(c)). The morphological vegetative feature length of the distal leaflet showed no potential to distinguish any group (Fig. 5(b)).

## Discussion

The formulation of conservation strategies begins with the decision of what effectively should be protected. Conservation strategies can be focused on protecting ecosystems, ecological and evolutionary processes, but the undoubted base for actions in conservation are the species (Mace, 2004). Despite being the basic unit in biology, the delimitation of species is sometimes hard and controversial (Ellis *et al.*, 2006). The definition of species can follow a variety of species concepts, studies at the same group, but dealing with different concepts, can arrive at different entities, with different geographical ranges, and different numbers of individuals (Agapow *et al.*, 2004). However, independently of the species concept used, the taxonomic studies must look forward a strong and sustainable base for conservation. Taxonomy and conservation are known as intricate areas and it is impossible to conserve what is not known or delimited (Mace, 2004). Besides the importance of knowing the biodiversity for its protection, a good taxonomic delimitation is crucial when dealing with rare species, that can be exposed to fast extinction process (Eldridge *et al.* 2014).

In species complex studies, there are different methodologies used to clarify the relationships between the species, the morphotypes, the varieties, the populations. Herbert *et al.* (2004) describe the molecular markers as a trustful technique for species delimitation, but highlight that it must be congruent with morphological characters. Newmaster & Subramanyam (2009) used DNA barcoding technique to discriminate multiple populations among a species complex in the pantropical *Acacia* subg. *Acacia*, supporting and proposing a new genera, *Vachellia* Wight & Arn.. On that study, Newmaster & Subramanyam (2009) realized a morphometric study associated with molecular methods, that proved the cryptic nature of those sister species. The classical morphology based taxonomy, together with other evidences, such as the differences in morphology associated with the detectable differences in ecological and climate traits of the geographic distribution, can better elucidate species delimitation (Koffi *et al.*, 2010; Souza *et al.*, 2014). Even in cryptic species complex resolution, a consistent morphometric study, associated with ecological data analyses lead to a clear delimitation of the *Galactia neesii* DC. complex (Ceolin & Miotto, 2012). Studies focused on morphometric plus cytogenetic analyses also are being successful on delimiting species complex (Morales *et al.*, 2014).

Pierre *et al.* (2014) tested the taxonomic circumscription of the genus *Storthocalyx* (Sapindaceae) using only multivariate morphometric analyses, they confirmed the taxonomic circumscription of four species and suggested a new one. On the case study of the *Abarema cochliacarpus* complex that we present here, we tested the three morphological groups and the *Abarema diamantina* species, that together, are recognized as a complex. On applying a variety of morphometric analyses, we could see that three morphological groups cited by previous studies form differentiated entities, the upper northeast group, the typical group and the *Abarema diamantina* group.

In both cluster analyses that we presented, with variables chosen by us and with variables detected by a cluster of variables analysis, *Abarema diamantina* group formed a consistent morphological group, the upper northeast group present a not so consistent, but also representative grouping. We believe that the most representative characters for grouping the upper northeast group are associated with the fruit morphology, which was sampled in both data matrix (Fig. 3(c, d)). García-Lara *et al.* (2015) while testing the validity of *Pithecellobium insigne* Micheli ex Donn.Sm. with morphometric analyses, also found the thickness of the fruit as an important reproductive morphological character to differentiate the species. Coincidentally, *Pithecellobium* and *Abarema*, both genera of Ingeae tribe, passed by many taxonomic circumscriptions, and the fruits are classical diagnostic characters for genera within the tribe (Barneby & Grimes, 1996).

When analyzing the morphological character variance among groups, we observed the representativeness of the fruits thickness and the fruits width on differentiating the upper northeast group. The fruits in the upper northeast group are thicker than in the remaining groups. García-Lara *et al.* (2015) associated the thicker fruits of *Pithecellobium insigne* with the possibility of hybridization. For the *Abarema cochliacarpus* morphotype from the upper northeast group, in a first moment, we do not consider this possibility, because it represents an extreme of the geographical range in the complex, with differentiated environmental and climatic conditions from the remaining groups of the complex.

Differently from the *Mimosa diversipila* Micheli, which forms a species complex that shows no qualitative characters segregating groups, unless the pubescence in some organs (Morales *et al.*, 2014), the *Abarema diamantina* group is detectable by strong qualitative characters confirming its taxonomic circumscription at species level. The insertion of the staminal tube in the corolla is one of the important reproductive characters on the differentiation of *A. diamantina* from the other morphotypes, showed

in the boxplots. In a study that revalidated *Pithecellobium insigne*, the length of the staminal tube was also highlighted as a representative taxonomic character (García-Lara *et al.*, 2015). The height of the plants was another character evidenced by the variance analysis as meaningful on segregating the *Abarema diamantina* group from the remaining. The height is cited on *A. diamantina* taxonomic description as an important character to recognize the species in field (Guerra *et al.*, 2016). The length of the anthers represents a good character to differentiate *Abarema diamantina* from the typical and the Cabo Frio island groups, even if it does not provide a complete segregation. Our study highlight that this character, not usually applied and most times not even measured in other morphometric or taxonomic studies, present potential on differentiating some morphotypes and should be related to the pollination.

The second vegetative morphological character that we tested in the variance analysis, the length of the distal leaflet, showed an amplitude of variation that comprises all the groups. The specimens within the *Abarema cochliacarpus* complex present a wide variation on leaflet length, besides the leaflets characters are recognized as taxonomic representative in many taxonomically related groups (Estrella *et al.*, 2009; Morales *et al.*, 2014). In the *Mimosa diversipila* complex morphometric study, the vegetative characters showed representative variation between the groups (Morales *et al.*, 2014). Also opposing to our results, in a morphometric study of the Fabaceae genus *Daniellia* Benn., the characters highlighted as being taxonomically informative for the differentiation between groups were vegetative, as the petiole indumentum, petiole width, number and position of glands on the leaflets (Estrella *et al.*, 2009).

The pre-established Cabo Frio island group was not consistent in the cluster analyses, always being mixed with the samples from the typical group. It was also not segregated by any character in the variance analyses. Iganci & Morim (2012) warned about the possibility of the morphological variation in the Cabo Frio island morphotype to be associated with minor ecological variations. After analyzing the NMDS ordination of both matrices of variables, we concluded that the morphology of the typical and the Cabo Frio island groups are both driven by the average of the climatic and environmental conditions. So, it is expected that they do not form consistent groups separately, but present only superficial differences when exposed to some extreme variations within a unique ecological pattern.

The distribution of the whole complex encompasses a large latitudinal gradient, and there are important environmental characteristics varying along this wide

geographic area. The altitude is one of the variables that showed to play an important role on the differentiation of morphotypes, leading the morphology of the *Abarema diamantina* species. There are also two climatic variables which vary significantly within the distribution area of the complex, the temperature and the precipitation. Those variables showed, in the ordination analyses, to be correlated to the morphological variation of the upper northeast group. It is important to highlight that the climate variables do represent important drivers in the morphological variation along the specimens distribution range, and could be responsible for speciation events within the complex. So, for protecting the morphotypes along the complex distribution, these climate variables should be taken in consideration. Even if a species is widely distributed, the individually morphological and genetic characteristics of the groups are represented in segregated portions along the geographic distribution. The differentiation between morphologies and defining species circumscription could be a crucial information for conservation purposes using the IUCN Red List criteria.

*Abarema cochliacarpus* also plays an important role in Brazilian popular medicine, especially in the Northeast. There are notes on exsiccates about its medicinal use and the presence of tannins, principally in specimens from Pernambuco and Paraíba. In the states of Alagoas, Bahia and Sergipe, the stem bark of the trees are used as infusion to treat gastritis, ulcers, purulent wounds and other pains (Dias *et al.*, 2012; Sánchez-Fidalgo *et al.*, 2013). The antioxidant, anti-inflammatory, anti-ulcerogenic and healing actions of *Abarema cochliacarpus* are already tested and confirmed (Silva *et al.*, 2010; Dias *et al.*, 2012). In the other hand, Oliveira *et al.* (2013) alerted to the hepatotoxicity of *Abarema cochliacarpus*, and to the relevance of studies to analyze the chemical components responsible for this toxicity. So, for medicinal properties studies and medicinal popular uses, the differentiation of the *Abarema cochliacarpus* morphotypes is very important. In future, it will be necessary to recognize the chemical components and medical properties of each morphotype/species, since *Abarema cochliacarpus* l.s. is no longer recognized as a unique species.

In the present study on the *Abarema cochliacarpus* complex, we first tested the morphological species concept associated with the ecological species concept, to put a first light on the resolution of the complex. The intention of understanding the taxa delimitation is the first step to generate conservation strategies for the complex as a whole. Using morphometry, we could confirm the segregation of the *Abarema diamantina* group and the upper northeast group from the typical group. Since the



recognition of *Abarema diamantina* at the species level, it represents a narrowly restricted distributed taxon, which seeks urgent conservation assessment. Considering our results, the upper northeast group might be possibly recognized as an independent taxon in future studies. Thus, *Abarema cochliacarpus* would possibly be split again in two other taxa of narrower geographic distribution in comparison to its current range. This resolution on taxonomic circumscription and distribution range delimitation will be crucial for establishing a more precise conservation assessment for the group. Here we list the next steps for improving the conservation of the complex: the formulation of strategies to protect the rare species *Abarema diamantina*; and the necessity of testing the remaining groups under a molecular and a chemical approach to better understand their limits and conservation priorities.

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### **Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Table S1** {Table of analyzed material}

**Table S2** {Table of variables measured}

**Figure S3** {NMDS Ordination}

### **Biosketch**

**Ethiéne Guerra** is interested in evolution and speciation of the species of the complex *Abarema cochliacarpus*, aiming to give robust resolution to taxonomy and systematics of Ingeae tribe (mimosoid clade, Fabaceae), and understand the processes that guide speciation and evolution of widely distributed taxa, mainly ecological speciation between biomes.

Author contributions: E.G., M.P.M and J.R.V.I. drafted the research and collected the samples; E.G. measured the data set; B.O.A. drafted the analyses; B.O.A. and E.G. analyzed the data. E.G., J.R.V.I. and B.O.A. led the writing. All authors read, commented on, and approved the final manuscript.

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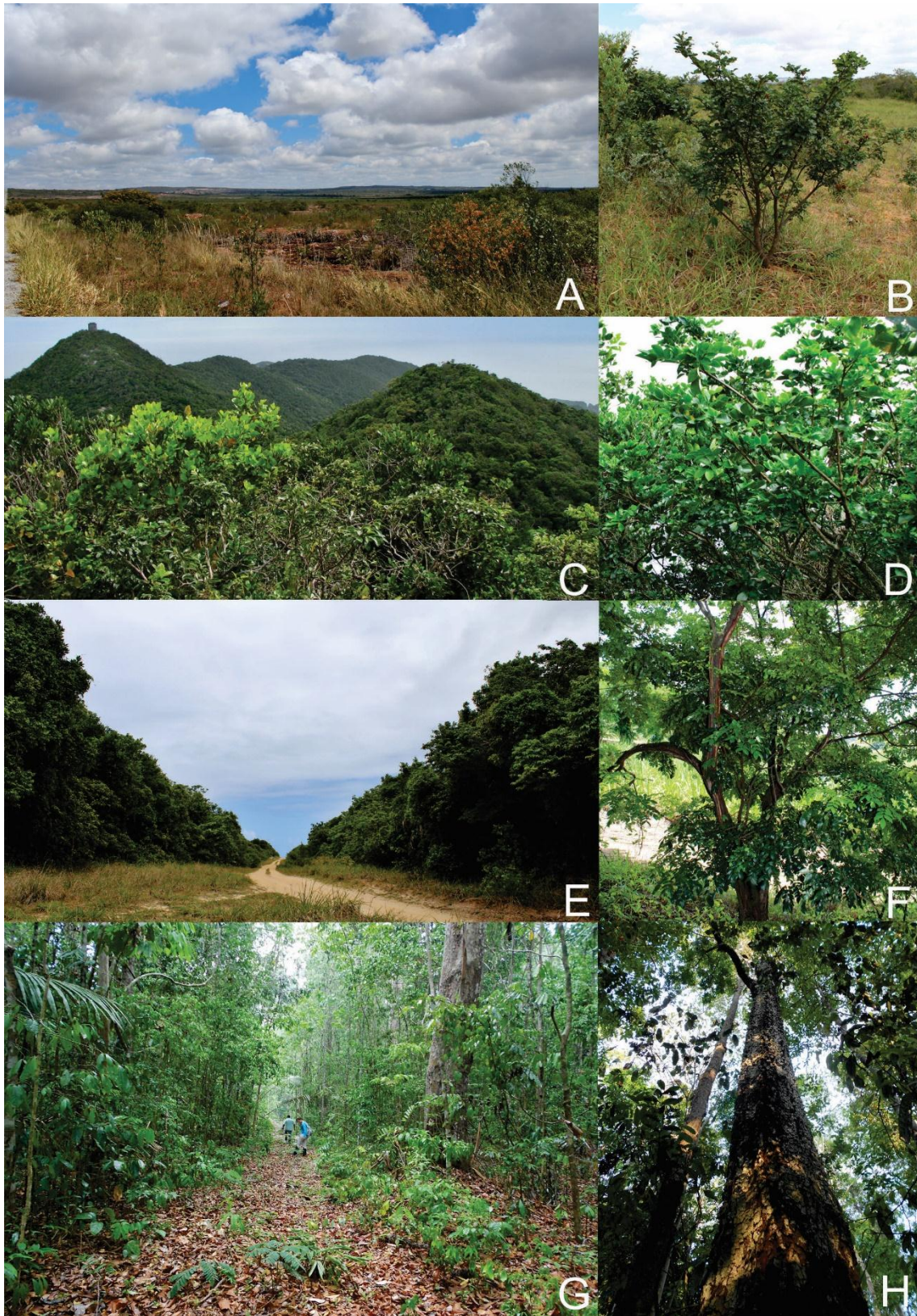
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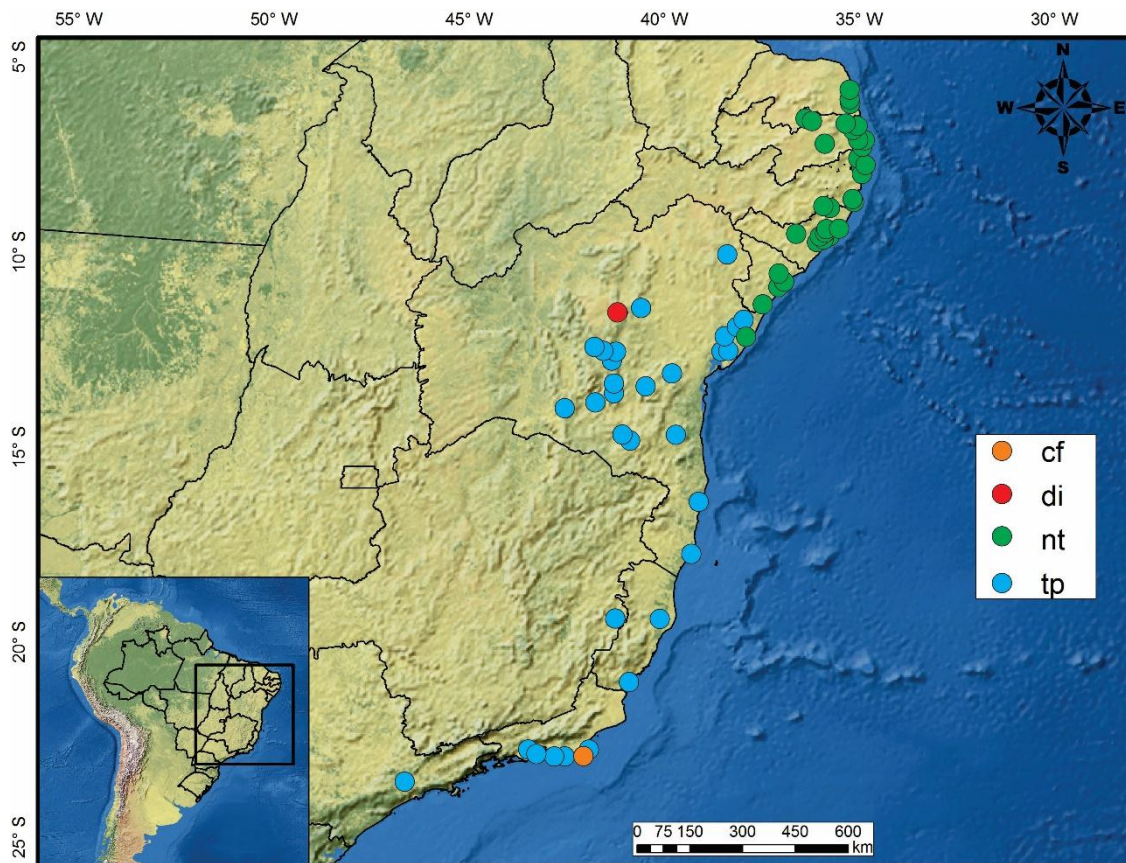
doi: 10.2305/IUCN.UK.2012.RLTS.T36560A20013204.en

## Figures



**Fig. 1** - The habitats and habits of *Abarema diamantina* E.Guerra, Iganci & M.P. Morim and the morphotypes of *Abarema cochliacarpus* (Gomes) Barneby & J.W. Grimes

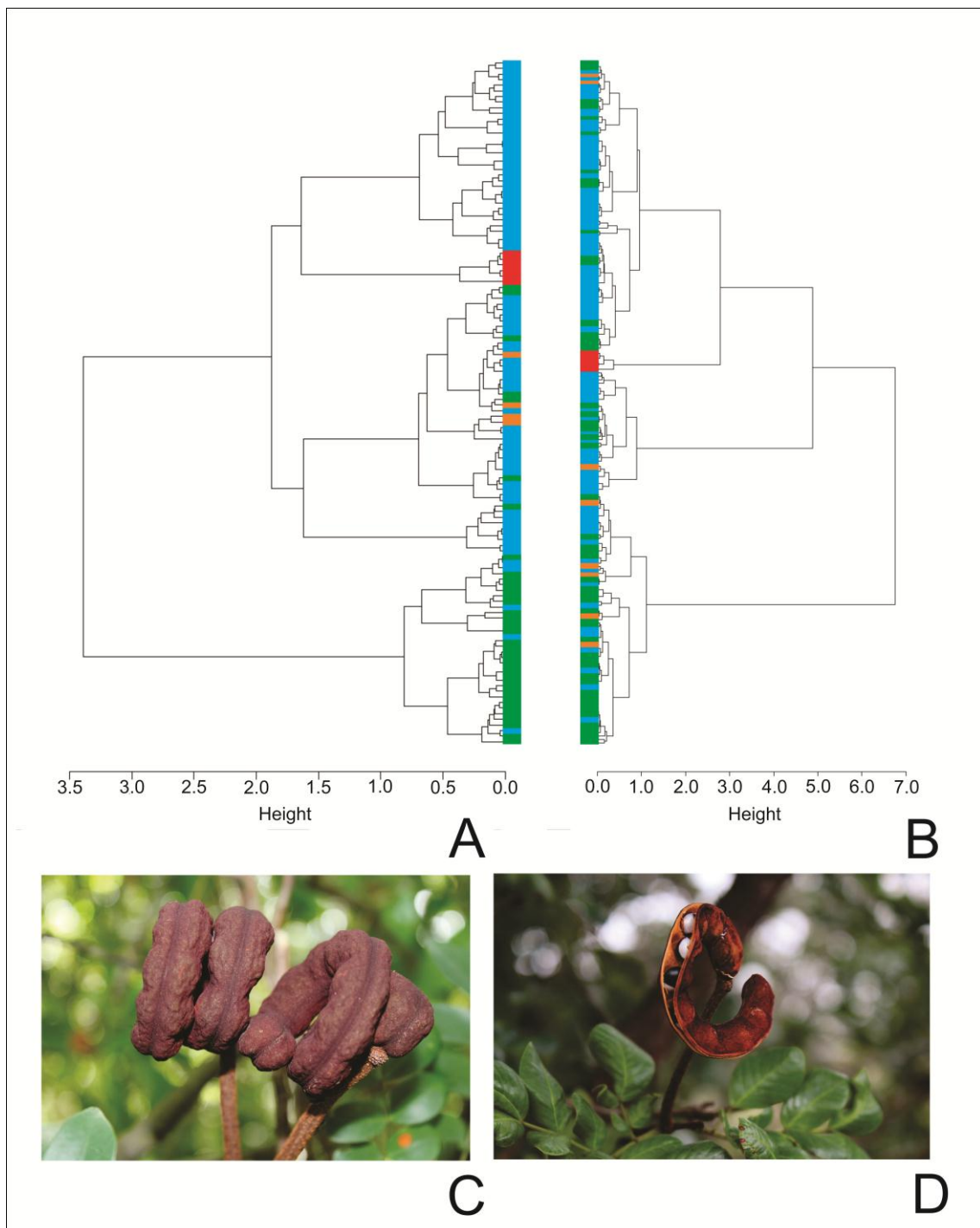
complex. **(a)** Morro do Chapéu municipality, in the Chapada Diamantina, Bahia state, Caatinga biome: habitat of the *Abarema diamantina* (photo: Guerra, E.); **(b)** habit of the *Abarema diamantina* (photo: Guerra, E.); **(c)** Cabo Frio Island, Rio de Janeiro state, dense ombrophilous forest, in Atlantic Forest biome: habitat of the Cabo Frio island morphotype (photo: Iganci, J.); **(d)** habit of the Cabo Frio island morphotype (photo: Iganci, J.); **(e)** Conde municipality, Paraíba state, restinga (coastal scrub) in Atlantic Forest biome: habitat of the upper northeast morphotype (photo: Guerra, E.); **(f)** habit of the upper northeast morphotype (photo: Guerra, E.); **(g)** Linhares municipality, Espírito Santo state, semi-deciduous forest in Atlantic Forest biome: habitat of the typical morphotype (photo: Morim, M.P.); **(h)** habit of the typical morphotype (photo: Morim, M.P.).



**Fig. 2** - The geographic distribution of the samples of *Abarema cochliacarpus* complex measured along the Atlantic Forest and Caatinga biomes, in Brazilian Southeast and Northeast. The pre-established morphological groups of the complex, *Abarema diamantina* species and the three morphotypes of the complex are differentiated by the

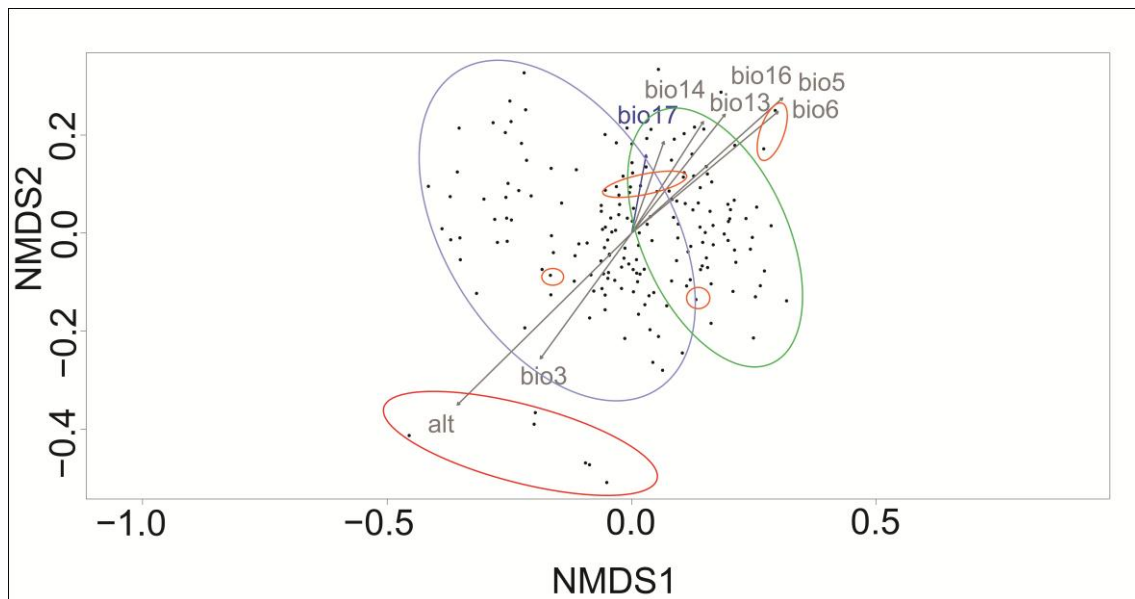


coloured dots. Groups di: *Abarema diamantina*; nt: upper northeast; cf: Cabo Frio island; and tp: typical.

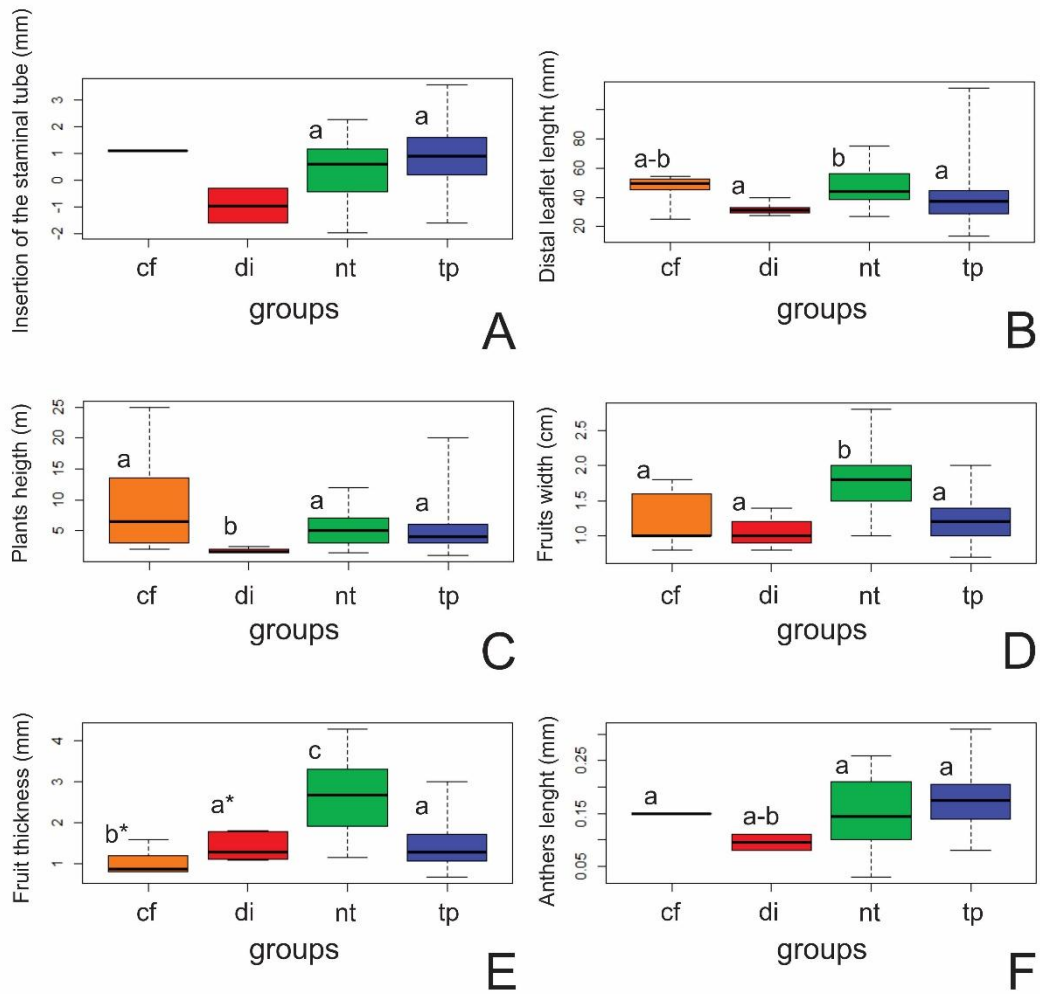


**Fig. 3** - (a) The cluster dendrogram of the morphotypes from the *Abarema cochliacarpus* complex obtained from the matrix composed by all the 194 samples and

eleven variables measured for each one; **(b)** The cluster dendrogram of the morphotypes from the *Abarema cochliacarpus* complex obtained from the reduced matrix of 122 samples and eight variables measured for each one; **(c)** the fruit of *Abarema cochliacarpus*, representing the morphotype of the upper northeast group (photo: Guerra, E.); **(d)** the fruit of *Abarema cochliacarpus*, representing the morphotype of the typical group (Guerra, E.).



**Fig. 4** - The nonmetric multidimensional scaling (NMDS) ordination realized with the matrix composed by all the 194 samples and eleven variables measured for each one, plus eight climatic/environmental variables measured along the *Abarema cochliacarpus* complex geographic distribution.



**Fig. 5** - Boxplots from the variance analyses applied for some morphological characters for each one of the four pre-established groups: cf: Cabo Frio island group; di: *Abarema diamantina* group; nt: upper northeast group; and tp: typical group. **(a)** the boxplots from the variance analysis of the insertion of the staminal tube character; **(b)** the boxplots from the variance analysis of the distal leaflet length character; **(c)** the boxplots from the variance analysis of the plant height character; **(d)** the boxplots from the variance analysis of the fruit width character; **(e)** the boxplots from the variance analysis of the fruit thickness character, \* = marginally significant ( $p = 0.065$ ); **(f)** the boxplots from the variance analysis of the anthers length character.

### Supporting Information

**Table S1** {Table of the analyzed herbaria material, voucher and pre-established group of each sample}

**Table S2** {Table of the variables measured, classified into vegetative or reproductive, and into quantitative or qualitative }

**Figure S3** {NMDS Ordination }

**Table S1**

Table of the material examined and measured for the morphometric study in the *Abarema cochliacarpos* complex. It is indicated the Herbarium and number of the exsiccate, plus the collector and the collection number. The pre-established group of each sample is also indicated. Groups: tp = typical; di = *Abarema diamantina*; cf = Cabo Frio island; nt = upper northeast.

<b>Grou p</b>	<b>Voucher</b>	<b>Collector</b>	<b>Number</b>
tp	HUEFS - 37406	F. França et al.	2749
tp	UEC - 063537 (doação MBM)	G. Hatschbach et al.	56880
tp	SPF - 77575 (UB, CTES, NY, HUEFS, MBM)	Arbo et al.	5789
tp	EAC - 44703	E. Silveira	s.n
tp	UB, NY - 32557	H.S. Irwin et al.	s.n
tp	UB, NY - 30882	H.S. Irwin et al.	s.n
tp	RB - 204938 (CEPEC - 10044)	S.A. Mori et al.	s.n
di	RB - 398762 (duplicata CEPEC, NY)	R.C. Forzza et al.	1397
tp	HUEFS - 37491	F. França et al.	2833
tp	SPF - 48799 (KEW, K,F)	J.R. Pirani et al.	2009
tp	RB - 288594 (ICN)	AH.C. de Lima et al.	3965
tp	RB - 388448 (CEPEC)	J.G. Jardim et al.	2528
tp	HUEFS - 77140	E.B. Miranda et al.	588
tp	SPF - 117110	A.M. Giulietti et al.	PCD 2277
tp	ALCB - 75668	Guedes et al.	13022
di	SPF - 130982	H.P. Bautista et al.	PCD 3220
tp	SPF - 115820	R. Atkinson et al.	PCD 2365
tp	SPF - 117111	R. Atkinson et al.	PCD 2458
tp	SPF - 163183	A.A. Conceição	974
tp	SPF - 151610 (ESA 74683)	V.C. Souza et al.	26432
tp	ALCB - 36411	T.R. Santos et al.	PCD 5785
tp	HUEFS - 18659	L.P. de Queiroz et al.	4230
tp	HUEFS - 90653	C. van den Berg et al.	1400
tp	HUEFS - 79759	L.S. Funch et al.	1531
tp	HUEFS - 79760	L.S. Funch et al.	1532
tp	HUEFS - 52225	A.A. Ribeiro-Filho	229
tp	HUEFS - 190290	E. Melo et al.	11627
tp	HUEFS - 14183	L.P. de Queiroz et al.	3541
tp	RB - 597309	E.P. Queiroz et al.	3913

tp	RB - 229858 (ICN, UEC 37660)	R.M. Harley	22516
tp	RB - 544530 (CEPEC 121714)	F.M. Ferreira et al.	1848
nt	UEC - 181398 (ASE 28984)	T. Carregosa et al.	386
tp	UB, HRB 23914 (RB 326861, ESA 11166)	G.C.G. Pinto	99a/85
tp	RB - 326861 (UB, HRB 23914,ESA 11166)	G.C.G. Pinto	99a/85
tp	UEC 40922 - NY 30882	H.S. Irwin et al.	s.n
tp	RB - 576537 (ESA 90618)	J.P. Souza et al.	5008
tp	RB - 271558	A.C. Sarmiento et al.	830
tp	RB - 129816 (ICN, K)	A.P. Duarte et al.	9202
tp	RB - 288600 (ICN)	H.C. de lima et al.	3902
tp	HUEFS - 164911	E. Melo et al.	8400
tp	HUEFS - 66883	M.E.R. Junqueira et al.	169
nt	HST - 2320	G. Teixeira	2967
tp	HUEFS - 149778	N.C.B. Albuquerque	9
tp	EAC - 24357	E. Nunes et al.	s.n
tp	CVRD - 8873 (ICN)	D.A. Folli	4931
tp	CVRD - 95 (ICN)	J. Spada	6/77
tp	CVRD - 8905 (ICN)	A.A. da Luz	235
tp	RB -168916 (ICN)	J. Almeida de Jesus	2036
tp	RB - 231434 (ICN)	H.C. de Lima	1787
tp	CVRD - 11249 (ICN)	G.S. Siqueira	412
nt	RB - 460694 (ICN)	A.J. Castro et al.	s.n
tp	RB - 204935 (CEPEC - 9431)	S.A. Mori et al.	s.n
tp	SPF - 82355(RB - 320166, HRBN - 30368)	H.P. Bautista et al.	1609
nt	HST - 1737	J.L.S. de Lima	10
nt	ALCB - 82532 (MAC 10111)	R.P.L. Lemos	4117
nt	RB - 460695 (ICN)	A. Fernandes et al.	s.n
nt	RB - 89267 (ICN)	J.L.A. Falcão et al.	1207
nt	RB - 460693 (EAC 11670, ICN)	A. Fernandes et al.	s.n
nt	HST - 2629	M.T. Monteiro	22746
nt	RB - 359282 (ICN)	S.M. de Faria et al.	1894
nt	HST - 3261	F. Paiva	3402
cf	RB - 422387	R.D. Ribeiro et al.	326
nt	RB - 460709 (doação EAC 19722)	Matos	s.n
nt	EAC - 11670	A. Fernandes et al.	s.n
tp	HUEFS - 55398 (doação HUNEB-A 453)	N.G. Jesus et al.	350
tp	RB	Hoehne	s.n
tp	RB - 422070 (ICN)	V.F. Gonçalves et al.	41
tp	RB - 298328	C.Farney et al.	2782
cf	RB - 393699 (K,MBM,SPF,US,ICN)	C. Farney et al.	4413
tp	ESA - 11166 (RB 326861, UB, HRB 23914)	G.C.G. Pinto	99a/85
nt	ESA - 10804	M.L. Guedes et al.	2262

nt	ESA - 10810	M.L. Guedes	2268
nt	ESA - 10900	M.L. Guedes	s.n
tp	SPF, CEPEC	R.M. Harley et al.	26500
tp	RB - 76099 (ICN)	O.X. de B. Machado	s.n
tp	HUEFS - 117811	R.M. Harley et al.	55611
tp	ALCB - 102537	M.C. Bellintani et al.	10
tp	HUEFS - 117484 (CEPEC 114901, NY, UEC, RB, SPFR, SP, SPF, MBM, ESA)	R.A.X. Borges et al.	380
tp	HUEFS - 80605	D.F. Gomes et al.	10
cf	RB - 414082 (ICN)	H.G. Dantas	408
tp	RB - 167674 (ICN)	D. Sucre et al.	10702
tp	RB - 401385 (ICN)	R.D. Ribeiro et al.	97
tp	RB - 284168 (ICN)	R.M. Araujo et al.	260
cf	RB - 417631 (ICN)	R.D. Ribeiro et al.	467
tp	RB - 496347	M.C.F. Santos et al.	908
tp	RB - 428260	J.M.A. Braga	1138
nt	RB - 491275 (IPA 78790)	N.A. Albuquerque	616
nt	RB - 76694 (instituto de pesquisas agrônômicas R.15599)	D.A. Lima	49319
nt	HST - 18588	L.V. Cunha	192
nt	HST - 2419 (R. 21495)	M. Tenório	21797
nt	UFPE - 65563	A. Alves-Araújo et al.	645
tp	UEC -24 391 (CEPEC 13006)	A.A. Mori et al.	s.n
nt	PEUFR - 25975	A. Laurênio	985
nt	PEUFR - 30896	A.C. Souza et al.	508
nt	PEUFR - 44125	S.S. Lira et al.	452
tp	CVRD - 13503 (ICN, RB 605689)	D.A. Folli	6801
nt	HST - 20287	L.R. Silva	406
nt	UEC - 7330	P. Montouchet	s.n
nt	UEC - 181435 (ASE 30706)	T. Carregosa et al.	468
nt	UFP - 76575	E. Córdula et al.	1077
nt	RB - 563687 (JPB 50139, NY)	P.C. Gadelha Neto	3197
tp	RB - 605689 (ICN, CVRD 13503)	D.A. Folli	6801
nt	RB - 563690 (JPB 50184, NY)	P.C. Gadelha Neto	3242
nt	RB - 607819 (JPB 48970)	L.A. Pereira et al.	303
nt	EAC - 19722	Matos	s.n
nt	HST - 1055	S. Tavares	1055
nt	EAC - 6900	A. Fernandes et al.	s.n
nt	EAC - 13622	C. Campelo et al.	2023
nt	EAC - 6935	A.J. Castro et al.	s.n
tp	UEC - 107281	S. Bridgewater et al.	S1051
tp	RB - 320166 (SPF 82355, HRBN 30368)	H.P. Bautista et al.	1609
nt	RB - 305749 (CEPEC)	S.C. Sant'Ana et al.	431
tp	RB - 365914	E.von S. Medeiros et al.	185
nt	HST - 18586	L.V. cunha	150

nt	HST - 17042	L.R. Silva	205
nt	HST - 2858	M.T. Monteiro	21697
nt	UFP - 70167	D. Cavalcanti et al.	514
tp	SPF - 118169 (ALC 26179)	J.A.R. Jesus et al.	s.n
nt	PEUFR - 46932	A.D.C. Cavalcanti	207
tp	ALCB - 93576	N. Roque et al.	2496
tp	SPF - 146755 (HUEFS 15388)	L.P. de Queiroz et al.	3773
tp	ALCB - 75915	M.L. Guedes et al.	13270
tp	ALCB - 50458	G. Carvalho et al.	32
tp	HUEFS - 94691	D. Cardoso et al.	455
tp	ALCB - 58341	M.L. Guedes et al.	9574
tp	HUEFS - 14155	L.P. de Queiroz et al.	3513
tp	RB - 544498 (CEPEC 121747)	F.M. Ferreira et al.	1881
tp	RB - 460697 (ICN)	A. Fernandes et al.	s.n
tp	EAC - 20480	A. Fernandes et al.	s.n
tp	HUEFS - 183868	A.F.P. Machado et al.	1014
tp	HUEFS - 55408	N.G. Jesus et al.	498
tp	HUEFS - 123119	R.Funch	598
tp	HUEFS - 163096	R.Funch	26
tp	EAC - 11391	A. Fernandes et al.	s.n
tp	UEC - 41801	G. Hatschbach	48345
nt	HST - 2931	M.T. Monteiro	22713
tp	RB - 264569	R.P. Orlandi et al.	755
nt	RB - 607782 (JPB 45495)	A.A.M. Araújo et al.	169
tp	HUEFS - 190308	E. Melo et al.	11690
tp	HUEFS - 180528	E.N. de Matos et al.	817
tp	HUEFS - 59535	K.R.B. Leite et al.	191
nt	RB - 89266 (ICN)	J.I.A. Falcão et al.	1188
tp	HUEFS - 168792	V.S. Almeida et al.	83
tp	RB - 288593 (ICN)	H.C. de Lima et al.	3894
tp	ALCB - 83559	M.L. Guedes et al.	14319
tp	RB - 597702 (HUEFS 193578)	L.P. de Queiroz et al.	15538
tp	RB - 460712 (ICN)	E. Nunes et al.	s.n
nt	RB - 608273 (ICN)	G.B. Freitas et al.	187
tp	RB - 328091 (ICN)	M.C.L. Ramos	1112
di	ICN, RB	E. Guerra	147
di	ICN, RB	E. Guerra	148
di	ICN, RB	E. Guerra	149
di	ICN, RB	E. Guerra	150
tp	ICN, RB	E. Guerra	151
tp	ICN, RB	E. Guerra, Filipe Torres, Cristiana Torres	152
tp	ICN, RB	E. Guerra	140
tp	ICN, RB	E. Guerra	141
tp	ICN, RB	E. Guerra	142
tp	ICN, RB	E. Guerra	143

tp	ICN, RB	E. Guerra	144
tp	ICN, RB	E. Guerra	145
tp	ICN, RB	E. Guerra	146
nt	ICN, RB	E. Guerra, J.R. Lima, I.B. de Lima	115
nt	ICN, RB	E. Guerra, J.R. Lima, I.B. de Lima, R. Queiroz	116
nt	ICN, RB	E. Guerra, J.R. Lima, I.B. de Lima, R. Queiroz	117
nt	ICN, RB	E. Guerra, J.R. Lima, I.B. de Lima, R. Queiroz	118
nt	ICN, RB	E. Guerra, J.R. Lima, I.B. de Lima, R. Queiroz	119
nt	ICN, RB	E. Guerra, J.R. Lima	120
nt	ICN, RB	E. Guerra, J.R. Lima	121
nt	ICN, RB	E. Guerra, J.R. Lima	122
nt	ICN, RB	E. Guerra, J.R. Lima	123
nt	ICN, RB	E. Guerra, J.R. Lima	125
nt	ICN, RB	E. Guerra, E. Córdoba, M.J.C. Pereira, C. Alcântara	126
nt	ICN, RB	E. Guerra, E. Córdoba, M.J.C. Pereira, C. Alcântara	127
nt	ICN, RB	E. Guerra, E. Córdoba, M.J.C. Pereira, C. Alcântara	128
nt	ICN, RB	E. Guerra, E. Córdoba, M.J.C. Pereira, C. Alcântara	129
nt	ICN, RB	E. Guerra, E. Córdoba, M.J.C. Pereira, C. Alcântara	130
nt	ICN, RB	E. Guerra, E. Córdoba, M.J.C. Pereira, C. Alcântara	131
nt	ICN, RB	E. Guerra, W.T.C.C. Santos	133
nt	ICN, RB	E. Guerra, W.T.C.C. Santos	134
nt	ICN, RB	E. Guerra, L.R. Lima	137
nt	ICN, RB	E. Guerra, L.R. Lima	138
nt	ICN, RB	E. Guerra, L.R. Lima	139
tp	ICN, RB	E. Guerra, M.P. Morim, J. Iganci	104
cf	ICN, RB	E. Guerra, J. Iganci	105
cf	ICN, RB	E. Guerra, J. Iganci	106
cf	ICN, RB	E. Guerra, J. Iganci	107
cf	ICN, RB	E. Guerra, J. Iganci	108
tp	ICN, RB	E. Guerra, M.P. Morim	109
tp	ICN, RB	E. Guerra, P. Viany	110



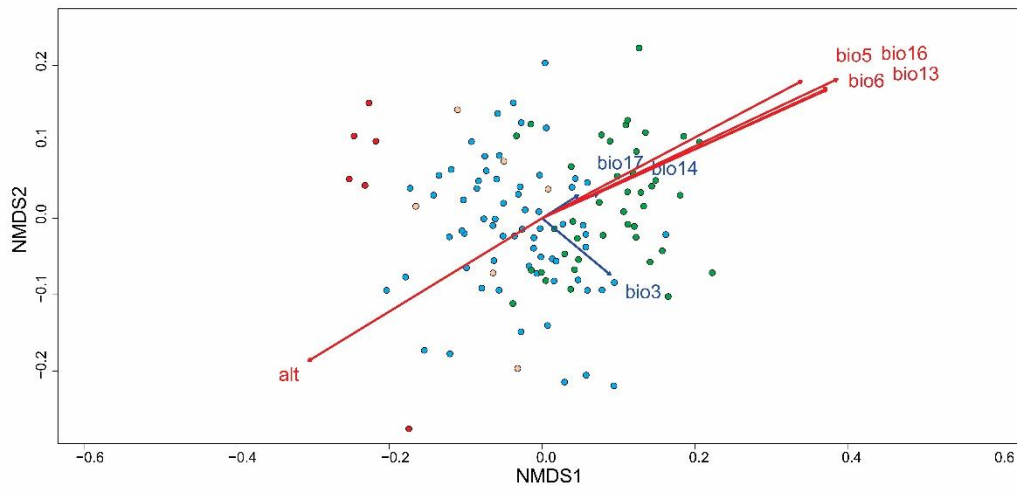
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tp	ICN, RB	E. Guerra, P. Viany	111
tp	ICN, RB	E. Guerra, P. Viany	112
tp	ICN, RB	E. Guerra, P. Viany	113
tp	ICN, RB	E. Guerra, P. Viany	114

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**Table S2** Table of the variables measured, classified into vegetative or reproductive, and into quantitative or qualitative.

<b>VARIABLES</b>	<b>REPRODUCTIVE/VEGETATIVE</b>	<b>QUANTITATIVE/QUALITATIVE</b>
Height (m)	Vegetative	Quantitative
Leaflet form	Vegetative	Qualitative
Leaflet apex	Vegetative	Qualitative
Venation	Vegetative	Qualitative
Leaflet consistency	Vegetative	Qualitative
Length of the distal leaflet (mm)	Vegetative	Quantitative
Length of the proximal leaflet (mm)	Vegetative	Quantitative
Width of the distal leaflet (mm)	Vegetative	Quantitative
Width of the proximal leaflet (mm)	Vegetative	Quantitative
Peduncle (mm)	Reproductive (inflorescence)	Quantitative
Bract (mm)	Reproductive (inflorescence)	Quantitative
Pedicel (mm)	Reproductive (flower)	Quantitative
Bracteole (mm)	Reproductive (flower)	Quantitative
Calyx (mm)	Reproductive (flower)	Quantitative
Corolla (mm)	Reproductive (flower)	Quantitative
Filets (mm)	Reproductive (flower)	Quantitative
Staminal tube insertion	Reproductive (flower)	Qualitative
Staminal tube (mm)	Reproductive (flower)	Quantitative
Anthers (mm)	Reproductive (flower)	Quantitative
Ovary (mm)	Reproductive (flower)	Quantitative
Ovary apex	Reproductive (flower)	Qualitative
Fruit ligneous	Reproductive (fruit)	Qualitative
Fruit length (cm)	Reproductive (fruit)	Quantitative
Fruit width (cm)	Reproductive (fruit)	Quantitative
Fruit thickness (mm)	Reproductive (fruit)	Quantitative
Fruit turns	Reproductive (fruit)	Qualitative
Fruit apex	Reproductive (fruit)	Qualitative
Fruit adpression	Reproductive (fruit)	Qualitative
Peduncles (cm)	Reproductive (fruit)	Quantitative
Seed testa	Reproductive (fruit)	Qualitative



**Figure S3** – The NMDS ordination realized with the reduced matrix composed by 122 samples and eight variables measured for each one, plus eight climatic/environmental variables measured along the *Abarema cochliacarpus* complex geographic distribution.

## CONSIDERAÇÕES FINAIS

A nova circunscrição de *Abarema* Pittier apresentou caracteres morfológicos robustos para a identificação do gênero. Foi possível o reconhecimento de duas espécies distinguíveis por caracteres morfológicos reprodutivos. *Abarema* está proxivamente relacionado aos gêneros que compõem a Aliança *Inga*, sobretudo *Macrosamanea*. Comentários acerca das afinidades morfológicas de *Abarema* s.s. e os gêneros filogeneticamente afins ainda requerem mais estudos. Apesar de apresentarem grande semelhança nas estruturas vegetativas, os gêneros da Aliança são muito distintos quando se trata de caracteres reprodutivos, sobretudo os frutos. Esta reorganização sistemática em *Abarema* implica na necessidade de futuros estudos para circunscrever as demais espécies que faziam parte do gênero. Estes estudos estão sendo desenvolvidos no grupo de pesquisa.

Os conceitos de espécie utilizados associados ao estudo morfológico para formular a nova circunscrição de *Abarema* foram o morfológico e o ecológico. Durante o estudo morfométrico, levamos em consideração características ambientais e climáticas das regiões onde os morfotipos conhecidos para o então gênero monoespecífico, *Abarema*, composto pela espécie *Abarema cochliacarpus* (Gomes) Barneby & J.W.Grimes ocorrem. A partir da análise dos dados morfológicos, associada a observações de campo, reconhecimento da área de ocorrência e do hábito dos morfotipos em cada habitat, foi possível o reconhecimento de uma nova espécie, *Abarema diamantina* E.Guerra, Iganci & M.P.Morim. *Abarema diamantina* teve sua descrição baseada na morfologia. Apresenta distribuição restrita, ocupando uma área com características ambientais extremas no bioma Caatinga, o que deu suporte à sua descrição com base nos conceitos morfológico e ecológico de espécie.

O estudo morfométrico do complexo *Abarema cochliacarpus*, composto pela espécie *A. diamantina* e os morfotipos reconhecidos para *A. cochliacarpus*, corroborou a segregação de *A. diamantina*, confirmando a espécie descrita durante a realização dos estudos desta dissertação. Além disso, as análises indicaram a segregação do morfotipo do Nordeste, que é caracterizado principalmente pelo fruto lenhoso e espesso.

Durante a revisão de literatura, análise das exsicatas e viagens a campo, foi possível reconhecer algumas características de *Abarema* que nos sugeriram possíveis futuros estudos. Uma delas é o uso medicinal da casca de *Abarema cochliacarpus*, amplamente reconhecido nos estados do Nordeste. A entrecasca é avermelhada nas duas

espécies do gênero, sendo inclusive, uma característica importante para o reconhecimento em campo quando os caracteres reprodutivos não estão presentes. Entre as duas espécies, esta estrutura é diferenciada pela profundidade da coloração, sendo superficial em *A. diamantina* e profunda em *A. cochliacarpus*. Esse aspecto nos chamou atenção a partir de alguns comentários em exsicatas sobre o uso medicinal e de estudos químicos voltados à área farmacêutica analisando propriedades químicas com potenciais usos medicinais e propriedades tóxicas de *A. cochliacarpus*. Aqui apontamos que os estudos realizados não levam em consideração as diferenças morfológicas da espécie ao longo da distribuição e nem mesmo a existência de morfotipos. Em apenas um dos estudos é citado o voucher do espécime analisado. Após a reflexão sobre a importância desta estrutura, não apenas para a taxonomia, mas também para a etnobotânica, química e farmácia, nós coletamos amostras de cascas de todos os morfotipos durante as saídas a campo. Temos o intuito de realizar um futuro estudo sobre as propriedades químicas presentes na casca, que será utilizado para reconhecimento quimiotaxonômico das espécies e auxiliará na diferenciação entre os morfotipos. Esse estudo é promissor principalmente pelo motivo das propriedades medicinais serem amplamente reconhecidas somente no morfotipo do Nordeste. A partir do reconhecimento de uma nova espécie para a Caatinga e do morfotipo Nordeste indicado como potencial unidade taxonômica, torna-se imprescindível compreender o comportamento químico de cada morfotipo/espécie.

As sementes das duas espécies reconhecidas para o gênero apresentam uma importante diferença morfológica. A testa da semente de *A. cochliacarpus* é lisa, enquanto a testa da semente de *A. diamantina* é foveolada, um estado de caractere incomum nas leguminosas mimosoidas. A partir da diferença na morfologia externa da semente, o processo de germinação das sementes das espécies e morfotipos de *Abarema* despertou nosso interesse. A germinação inicial e as plântulas são pouco conhecidas e estudadas em *Abarema*. Acreditamos que estas sejam possíveis fontes de novas diferenças morfológicas e ecológicas, apresentando características distintas no seu desenvolvimento. Essas características possivelmente refletirão as diferenças ambientais extremas ocorrentes na ampla abrangência geográfica do gênero, que já confirmamos influenciar na morfologia através da ordenação realizada no estudo morfométrico.

Dos morfotipos reconhecidos inicialmente para o gênero, apenas *A. diamantina* já teve sua delimitação confirmada através da morfologia e segregação realizada através da descrição como um novo táxon. No estudo morfométrico o morfotipo do extremo

Nordeste forma um agrupamento consistente. O morfotipo típico também forma um grupo consistente, porém apresenta uma distribuição geográfica mais ampla e, dessa maneira, uma maior variação morfológica entre os indivíduos analisados. O morfotipo da ilha de Cabo Frio encontra-se agrupado com o típico, por apresentar uma variação morfológica que é contemplada na variação do morfotipo típico. Para a descrição do morfotipo do extremo Nordeste como um táxon distinto, consideramos necessário analisar de maneira mais aprofundada e entender melhor alguns caracteres morfológicos que demonstraram ser importantes para a delimitação das espécies do gênero, como as flores.

Além disso, consideramos que uma análise molecular, baseada em marcadores comprovadamente eficientes para testar relações de táxons próximos, seja uma ferramenta chave para continuarmos respondendo aos nossos questionamentos sobre a diversidade de táxons pertencentes ao gênero *Abarema*. Sendo assim, o nosso próximo passo é acrescentar ao nosso estudo taxonômico o uso do conceito filogenético de espécie, utilizando uma taxonomia mais integrativa do que a que apresentamos até aqui. Uma abordagem filogeográfica do gênero, associada a modelagem de nicho, possibilitará a elucidação de questões sobre a diversificação do gênero, relações entre os morfotipos existentes nos diferentes biomas e entendimento sobre os processos de migração ou dispersão entre as diferentes formações vegetacionais. Assim, a identificação de padrões ecológicos que atuaram na diversificação das linhagens de *Abarema* entre a Mata Atlântica e a Caatinga, contribuirá para o conhecimento dos processos que condicionaram a atual distribuição geográfica dos táxons e dos processos evolutivos que propiciaram a diversificação do grupo. Além disso, estes estudos trarão luz à questões sobre os eventos de especiação em *Abarema* estarem ligados a evolução de nicho ecológico, sugerida durante a realização dos estudos desenvolvidos nesta dissertação.

## APÊNDICE

A new species of *Abarema* (Fabaceae) from Brazil

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## A new species of *Abarema* (Fabaceae) from Brazil

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### Abstract

A new species of *Abarema* from Brazil is described and illustrated. The new species is endemic to Morro do Chapéu, Chapada Diamantina, in the state of Bahia. *Abarema diamantina* shares morphological affinities with *A. cochliacarpus* by having a capitate raceme, strongly lenticelate branches, and median-basal pleurogram. However, there are remarkable vegetative and reproductive morphological characters which distinguish the two taxa. Here a description of the new species and illustrations are presented; a distribution map, and comments highlighting the differences between the closely related species are discussed.

**Keywords:** Chapada Diamantina, Ingeae, Mimosoideae, Morphology, Northeast Brazil, Taxonomy

### Resumo

Uma nova espécie de *Abarema* do Brasil é descrita e ilustrada. A nova espécie é endêmica do Morro do Chapéu, na Chapada Diamantina, estado da Bahia. *Abarema diamantina* compartilha afinidades morfológicas com *Abarema cochliacarpus*, apresentando racemo capitado, ramos fortemente lenticelados e pleurograma mediano-basal. Porém, importantes caracteres morfológicos vegetativos e reprodutivos distinguem os dois táxons. Aqui a descrição da nova espécie e ilustrações são apresentadas; mapa de distribuição e comentários evidenciando as diferenças entre espécies relacionadas são discutidos.

**Palavras-chave:** Chapada Diamantina, Ingeae, Mimosoideae, Morfologia, Nordeste do Brasil, Taxonomia

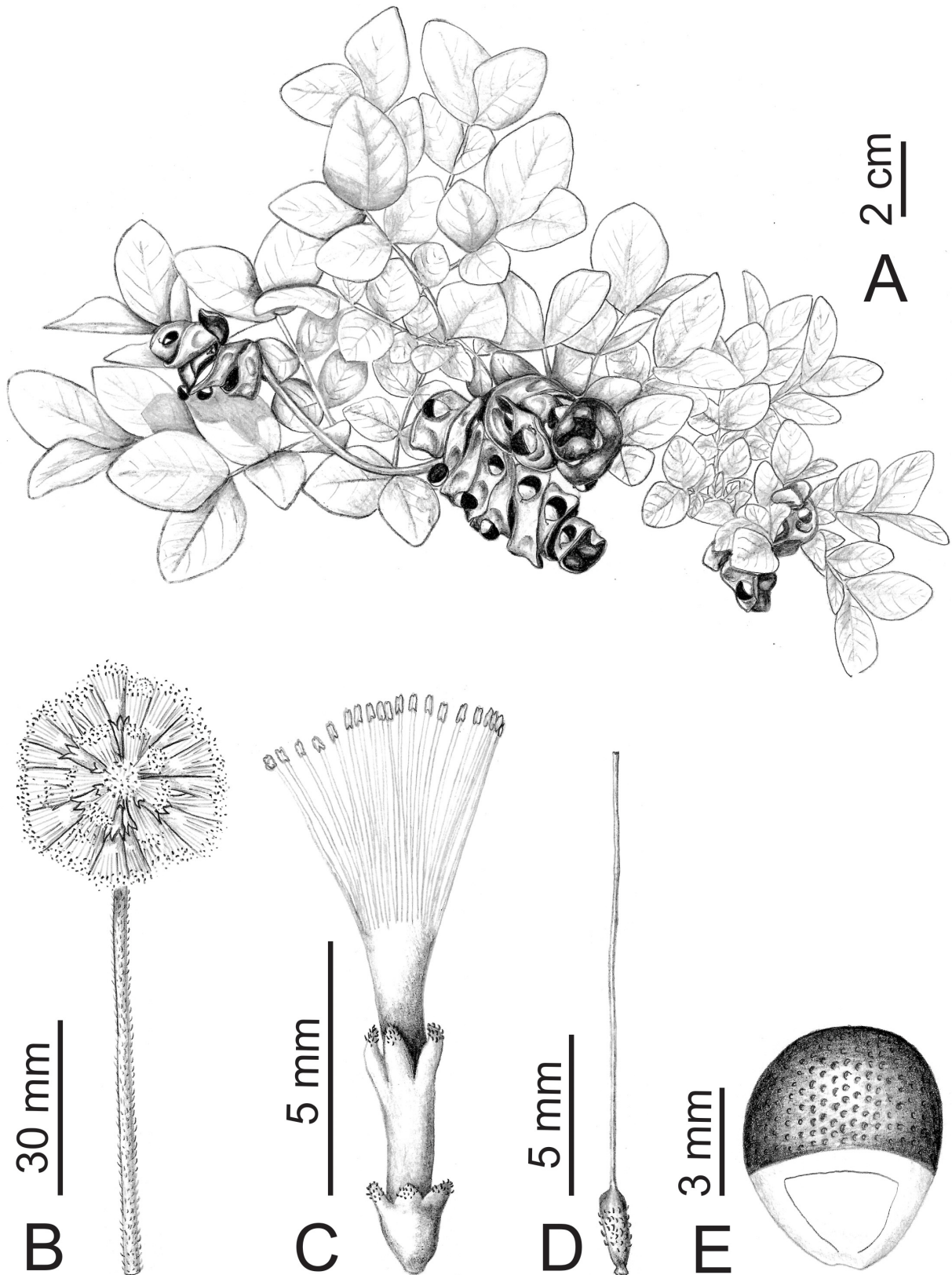
### Introduction

*Abarema* Pittier (1927: 86) is a Neotropical genus of Fabaceae and comprises around 50 species (Barneby & Grimes 1996, Iganci & Morim 2012a). *Abarema* is widespread over forests and coastal scrubs from Southern Brazil up to Mexico. The richest areas in number of species are the Atlantic Forest and the Amazonia in Brazil, the Venezuelan Amazonia, the Andean valleys in Colombia and Ecuador, Mexico and the Caribbean islands (Barneby & Grimes 1996, Iganci & Morim 2012b).

The species of *Abarema* are unarmed trees or shrubs, with bipinnate leaves and extra-floral nectaries; the inflorescences are racemes or spikes, the flowers have the characteristic androecium of the tribe Ingeae, with numerous stamens partially fused forming a tube; the fruits are legumes, curved to spiraled, generally with a reddish endocarp; and the seeds have a persistent funicle, open or closed pleurogram and translucent testa with usually bicolored white and dark portions partially showing the inner dark green embryo (Iganci & Morim 2009).

The genus was described based on the *Pithecolobium* sect. *Abaremotemon* Bentham (1844). It is currently part of the tribe Ingeae and the *Abarema* Alliance (Barneby & Grimes 1996, Lewis *et al.* 2005). Recent molecular phylogenetic studies showed that *Abarema* is polyphyletic (Iganci *et al.* 2016), and a new classification is in progress. However, our studies reveal that a remarkable new species occurs in the Chapada Diamantina region in Bahia state. The new species here presented is related to *Abarema cochliacarpus* (Gomes) Barneby & J.W.Grimes (1996: 94), the type species of the genus.





João Iganci  
2016

**FIGURE 1.** Illustration of *Abarema diamantina* E.Guerra, Iganci & M.P.Morim. A. Branch with fruits; B. Inflorescence; C. Flower; D. Ovary; E. Seed. (Vouchers: A, C, D—E. Guerra 147; B—M.E.R. Junqueira 169; E—E. Guerra 150). Drawn by João Iganci.

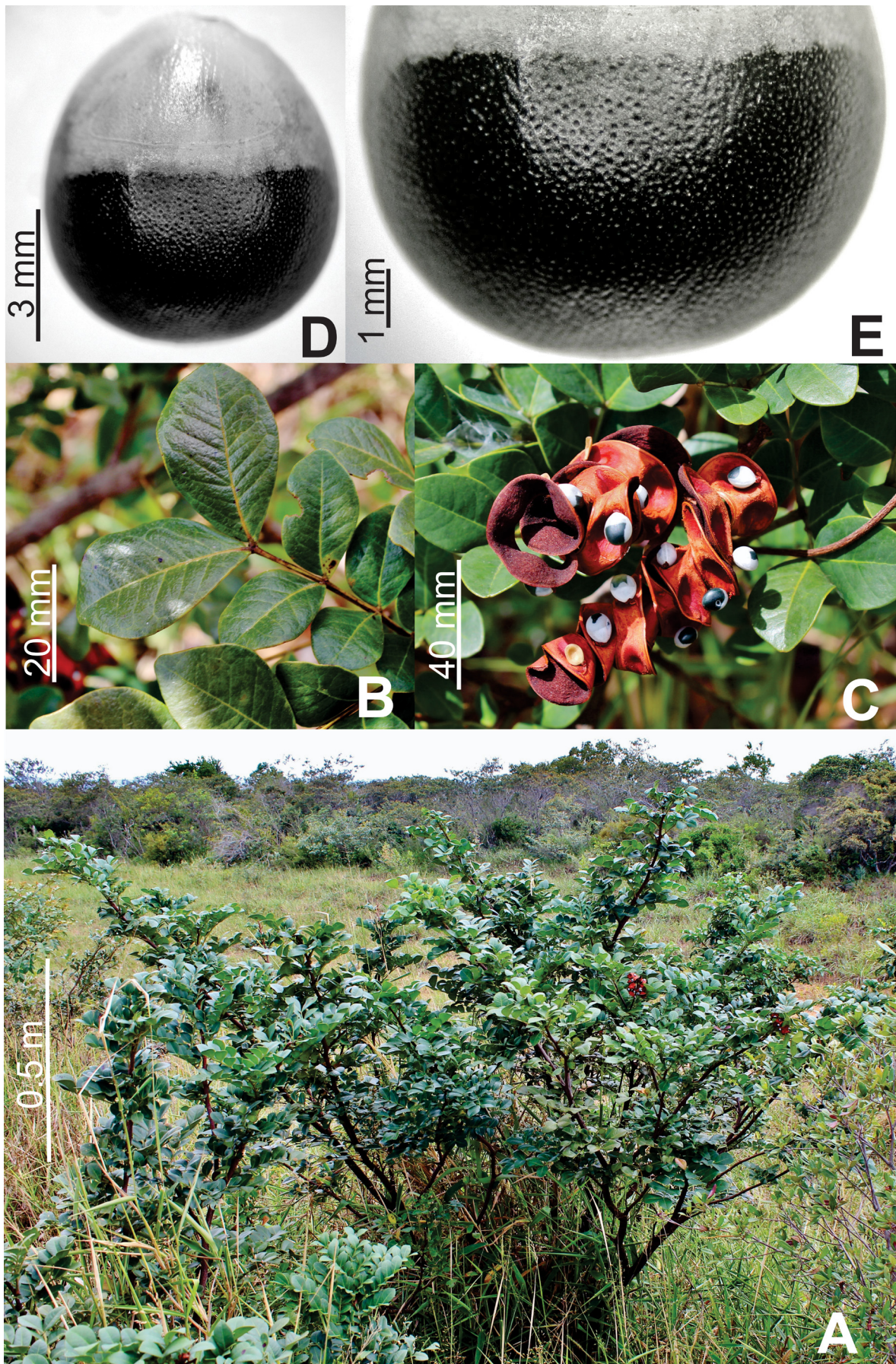


FIGURE 2. *Abarema diamantina* E.Guerra, Iganci & M.P.Morim. A. Habit; B. Leaflets; C. Pod; D-E. Seed.

## Description and comments about the new species

*Abarema diamantina* E. Guerra, Iganci & M.P. Morim *sp. nov.* (Figs. 1, 2 and 3)

*Abarema diamantina* is closely related to *A. cochliacarpus*, but it is distinguished by its leaflets consistency (chartaceous in the first versus membranaceous); the length of staminal tube in relation to the corolla (exserted in the first versus inserted); and the seed testa (foveolate in the first versus smooth).

**Type**:—BRAZIL. Bahia: Morro do Chapéu, Estrada do Feijão, trecho da estrada conhecido como Coreia, 9 a 10 km de Morro do Chapéu [BA 052] km 259 até km 260, 11°35'44,18"S 41°04'11,10"W, 982 m elev., 21 March 2016, *E. Guerra 149* (holotype ICN, isotypes RB, HUEFS).

**Shrub** ca. 1–2.5 m. Branches with conspicuous lenticels; petiole, rachis and rachilla with pubescent and ferruginous pulverulent indumentum. **Stipules** deciduous. **Leaves** alternate, bipinnate, 1–4 pairs of pinnae; petiole canaliculate, 5–25 mm long; rachis 13–70 mm, canaliculate; foliar nectaries sessile, orbicular and patelliform on the rachis (1–1.4 mm in diameter), and sessile, patelliform (0.4 mm in diameter) on the rachilla; **Leaflets** 2–4 pairs per pinnae, opposite, sessile, chartaceous and discolorous, light green in adaxial surface, dark green in abaxial surface, obovate to oblanceolate, the proximal (8–9) 14–19 (28) × (5–9) 10–14 (17–19) mm, and the distal (20–25) 27–37 (38–42) × (12–14) 19–23 (24–25) mm, the apex rounded, sometimes emarginated, usually glabrous, sometimes puberulous on the primary veins of the abaxial surface, venation brochidodromous, secondary veins prominent on both surfaces. **Inflorescences** in capitate racemes, homomorphic, axillary; peduncle 65–85 mm long, with pubescent and ferruginous pulverulent indumentum; **Bracteole** spatuliform, 0.6 mm, pubescent. **Flowers** sessile; calyx campanulate 2–2.5 mm long, apex acute and puberulous; corolla campanulate 4.7–5.6 mm long, infundibuliform, apex acute and puberulous; stamens 12.3–12.6 mm, staminal tube 5.5–6 mm, exserted; anthers 0.1 mm long, with rimose apertures; ovary puberulous, 1.3 mm, truncate at the apex. **Legumes** with spiralled valves, 170–250 × 8–14 mm, epicarp brown, with ferruginous pulverulent indumentum, endocarp brown-orange, apex acute. **Seeds** 7–8 × 5–6 mm, bicoloured, white and dark bluish, foveolate mostly on the distal portion, obovate; pleurogram opened, median-basal.

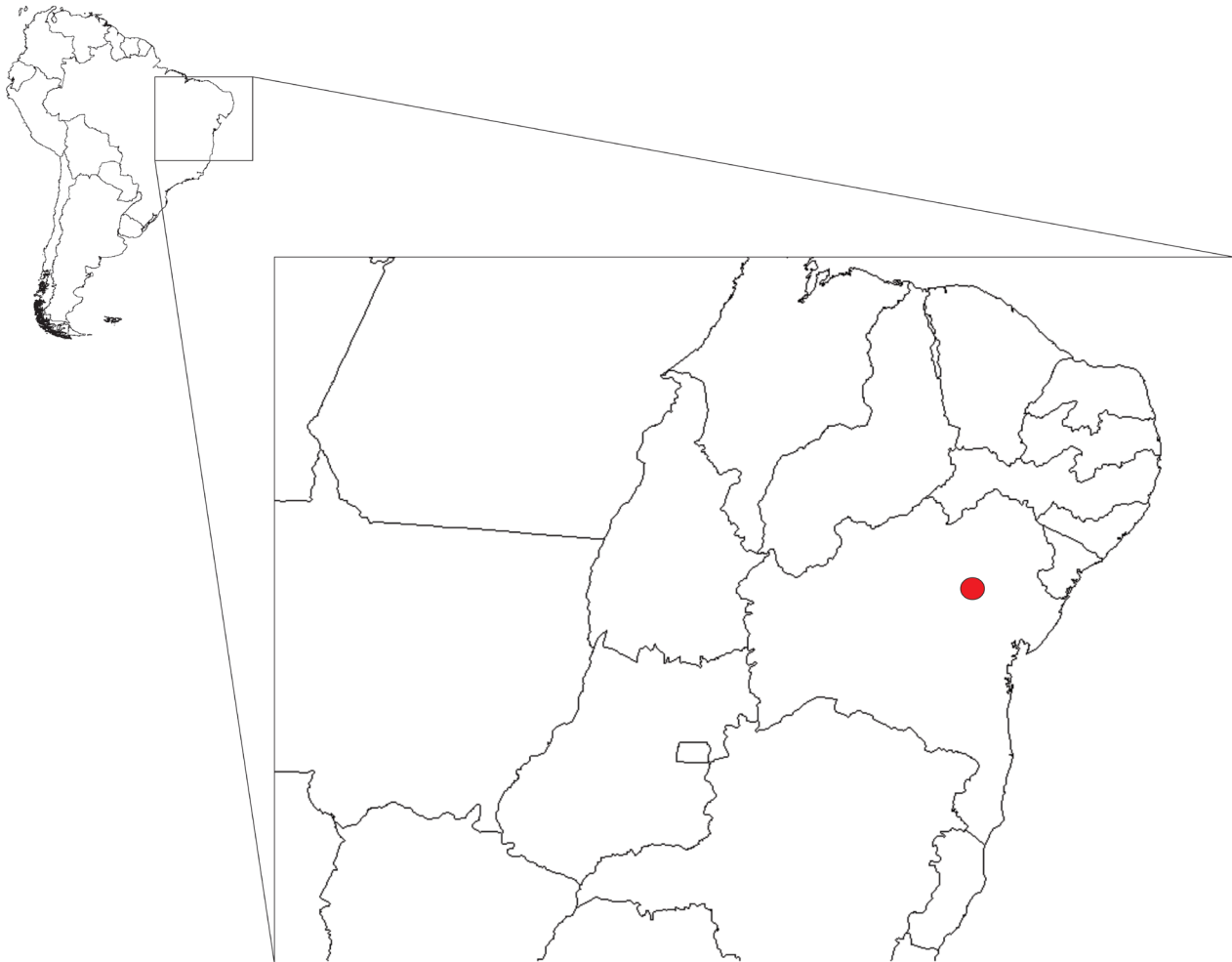
**Distribution and habitat**:—*Abarema diamantina* occurs in Brazil, until now it has been found only in the state of Bahia; it is restricted to the Chapada Diamantina, and it is found, up to this moment, only in the municipality of Morro do Chapéu (Fig. 3).

**Etymology**:—The specific epithet refers to the region where the species occurs, the Chapada Diamantina, a species rich area within the Caatinga domain.

**Phenology**:—Old flowers and mature fruits observed in March.

**Specimens examined (paratypes)**:—BRAZIL. Bahia: Morro do Chapéu, Distrito de Palmeiras, 11°55'S 41°15'W, 04 December 2002, *M.E.R. Junqueira 169* (HUEFS 66883!); Estrada do Feijão, trecho da estrada conhecido como Coreia, 9 a 10 km de Morro do Chapéu [BA 052] km 259 até km 260, 11°35'44,18"S 41°04'11,10"W, 982 m elev., 21 March 2016, *E. Guerra 147* (ICN!); Estrada do Feijão, trecho da estrada conhecido como Coreia, 9 a 10 km de Morro do Chapéu [BA 052] km 259 até km 260, 11°35'44,18"S 41°04'11,10"W, 982 m elev., 21 March 2016, *E. Guerra 148* (ICN!); Estrada do Feijão, trecho da estrada conhecido como Coreia, 9 a 10 km de Morro do Chapéu [BA 052] km 259 até km 260, 11°35'44,18"S 41°04'11,10"W, 982 m elev., 21 March 2016, *E. Guerra 150* (ICN!); Estrada para Torre, 27 April 1999, *R.C. Forzza, A.M. Amorim, S.C. de Sant'ana 1397* (SPF 136620!); Serra Pé do Morro, 11°35'27S 41°12'24"W, 1293 m elev., 29 June 1996, *H.P. Bautista, N. Hind, A.M. Giuliatti, R. Harley, S. Smith s.n.* (SPF 130982!).

**Comments**:—*Abarema diamantina* shares morphological characters with *A. cochliacarpus*, and remarkable differences to distinguish them are shown at Table 1. *Abarema cochliacarpus* has wider morphological variation and geographical distribution, from Ceará state to São Paulo state. Lewis (1987) indicated the necessity of detailed studies focused on *A. cochliacarpus* after signaling the existence of recognizable morphotypes in Bahia state. The morphotypes cited by Lewis (1987) were distinguished mainly by the habit height: one is restricted to the coast of Bahia (a tree of 10 m or taller), and an extreme inland form as a shrub up to 2 m, with leaflets rounded, apically emarginated, and prominent venation in both leaflet surfaces (Harley 22900). Barneby & Grimes (1996), agreed with Lewis (1987), mentioned the occurrence of a diminute morphotype, similar to those of Chapada Diamantina, in Rio de Janeiro state. Iganci & Morim (2012), recognized the morphotypes cited by Lewis (1987), and highlighted the existence of another smaller morphotype occurring in the island of Cabo Frio, in Rio de Janeiro state.



**FIGURE 3.** Distribution map of *Abarema diamantina* E.Guerra, Iganci & M.P.Morim showing the unique location where the species is found until now, in the Bahia state.

**TABLE 1:** Diagnostic morphological characteristics to distinguish between *Abarema diamantina* from *Abarema cochliacarpus*.

	<i>A. diamantina</i>	<i>A. cochliacarpus</i>
Leaflets consistency	Chartaceous	Membranaceous
Staminal tube in relation to the corolla	Exsert	Insert
Testa seed	Foveolate	Smooth
Geographic distribution	Bahia	Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Sergipe, Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo

The morphological plasticity that follows *Abarema cochliacarpus* distribution range is noteworthy on the leaf. Characters such as number of pinnae, leaflet size, consistency and form widely vary within inland populations and when comparing inland and coastal populations. However, reproductive characters are fairly stable along its geographical range. The flowers in *A. cochliacarpus* have included staminal tube and the seeds have smooth testa, while the new species presents exserted staminal tube and foveolate testa. Besides the clear differences on leaf morphology of the material examined by Lewis (1987), which are more membranous (Mori 9431, from Vitória da Conquista) or coriaceous with prominent nerves (Harley 22990, from Morro do Chapéu), none of these samples present flowers with exserted staminal tubes and the seeds are not available. Thus, it is not possible to say for sure if they belong to *A. diamantina*. Both species do occur in the Chapada Diamantina, being the new species restrict to the Morro do Chapéu until now.

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