ALESSANDRA DOS SANTOS

Filogenia e Biogeografia de *Naucleopsis* Miq. (Moraceae)

Tese apresentada ao Instituto de Botânica da Secretaria de Estado do Meio Ambiente, como parte dos requisitos exigidos para a obtenção do título de DOUTOR em BIODIVERSIDADE VEGETAL E MEIO AMBIENTE, na Área de Concentração de Plantas Vasculares em Análises Ambientais.

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Orientador: Prof. Dr. SERGIO ROMANIUC NETO

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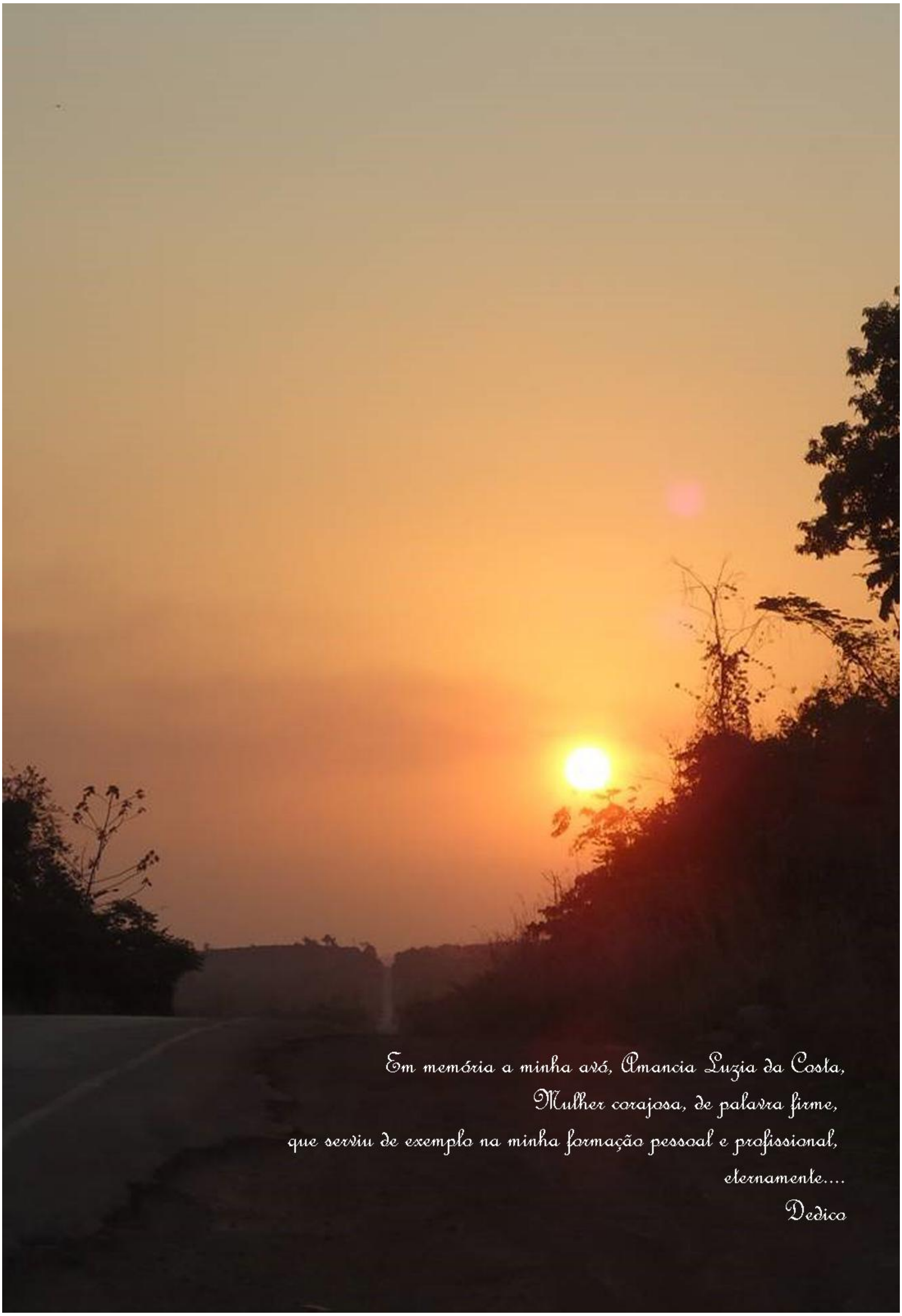

Em memória a minha avó, Amancia Luzia da Costa,
Mulher corajosa, de palavra firme,
que serviu de exemplo na minha formação pessoal e profissional,
eternamente....
Dedico

Sem a curiosidade que me move,

que me inquieta,

que me insere na busca,

não aprendo nem ensino"

Paulo Freire

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RESUMO

Naucleopsis é um gênero neotropical de Moraceae incluído na tribo Castilleae. O gênero inclui 31 espécies distribuídas nas florestas tropicais da América do Sul e Central, com a maioria das espécies na região Amazônica, principalmente em florestas úmidas e baixas. Ele é reconhecido por serem árvores, dioicas, raro monoicas. Folhas coriáceas a cartáceas, sempre inteiras, a maioria glabras. Estípulas totalmente amplexicaules, livres, caducas ou raro persistentes nos entrenós ao longo dos ramos foliares. Inflorescências estaminadas até 10, invólucro de brácteas internas cobrindo as flores antes da antese. As inflorescências pistiladas são na maioria solitárias, com ovário inteiramente imerso no receptáculo e flores com perianto indistinto a distinto. O gênero varia consideravelmente no tamanho das folhas, e principalmente nos caracteres das inflorescências pistiladas e infrutescências. O alto grau de polimorfismo do grupo criou problemas na história taxonômica do gênero. Esta tese representa um primeiro passo rumo ao entendimento da filogenia e biogeografia de Castilleae, mais especificamente de *Naucleopsis.* Além disso, uma sinopse de *Naucleopsis* é apresentada. Para inferir a filogenia DNA foram sequenciados a partir do gene plastidial *trnL-F* e nuclear FA03310 (EPIC). Nosso estudo incluiu 28 acessos (25 táxons) e sugeriram que *Naucleopsis* é monofilético, com uma linhagem específica para um grupo de espécies com perianto conato, partido no ápice, e outra linhagem específica para *Naucleopsis humilis* com pseudo-tépalas livres e ramos com entrenós curtos, suportadas por Máxima verossimilança e Inferência Bayesiana. A sinopse de *Naucleopsis* aqui apresentada resultou em 31 espécies: *N. acreana,* *N. caloneura*, *N. capirensis*, *N. chiguila*, *N. concinna*, *N. francisci*, *N. glabra*, *N. guianensis*, *N. herrerensis*, *N. humilis*, *N. imitans*, *N. inaequalis*, ***N. insculptula***, *N. jamariensis*, *N. krukovii*, *N. macrophylla*, *N. meridionalis*, *N. naga*, *N. oblongifolia*, ***N. pauciflora***, *N. pseudonaga*, *N. riparia*, *N. stipularis*, *N. straminea*, *N. ternstroemiiflora*, *N. ulei*, *N. velutina*, *N. sp1**, *N. sp2**, *N. sp3**, *N. sp4**, entre estas, quatro são novas para ciência (*), uma nova combinação e uma com novo status (sublinhado) e duas espécies foram restabelecidas (negrito). As análises biogeográficas focando *Naucleopsis* sugeriram que o gênero foi originado durante o Oligoceno (ca. 32.91 Mya), na região Boreal-Sul brasileira (Floresta Amazônica).

Palavras-chave: Análises moleculares, Castilleae, EPIC, estimativas de tempo de divergência, Floresta Amazônica

ABSTRACT

Naucleopsis is a neotropical genus of Moraceae included in tribe Castilleae. The genus includes 31 species distributed in the rainforest of South and Central America, with most species belong to the Amazon region, mainly in lowland moist forest. It is recognized by being usually trees, dioecious, rarely monoecious. Leaves coriaceous to chartaceous, always entire and mostly glabrous. Stipules fully amplexicaul, free, caducous or rare persistent in the internodes along leafy twigs. Staminate inflorescences up to 10 together, inner involucral bracts covering the flowers before anthesis. The pistillate inflorescences are mostly solitary, with ovary entirely immersed in the receptacle and flowers with distinct to indistinct perianth. The genus varies considerably in the size of the leaves, and mainly in the characters of the pistillate inflorescences and infructescences. The high degree of polymorphism of group created troubles along of the taxonomy history of the genus. This thesis represents a first step towards an understanding of the molecular phylogeny and biogeography of Castilleae, more specifically of *Naucleopsis.* In addition, a synopsis of *Naucleopsis* is presented. To infer the phylogeny was DNA sequence data from the plastidial *trnL-F* and nuclear FA03310 (EPIC) gene were sequenced. Our study included 28 accessions (25 taxa) and suggested that *Naucleopsis* is monophyletic, with one lineage specific for a group of species with connate perianth, parted at the apex, and other lineage specific for *Naucleopsis humilis* with free pseudo-tepals and branches with short internodes, supported by our maximum likelihood and Bayesian analyses. The synopsis of the *Naucleopsis* presented in this work resulted in 31 species: *N. acreana*, *N. caloneura*, *N. capirensis*, *N. chiguila*, *N. concinna*, *N. francisci*, *N. glabra*, *N.guianensis*, *N. herrerensis*, *N. humilis*, *N. imitans*, *N. inaequalis*, ***N. insculptula***, *N. jamariensis*, *N. krukovii*, *N. macrophylla*, *N. meridionalis*, *N. naga*, *N. oblongifolia*, ***N. pauciflora***, *N. pseudonaga*, *N. riparia*, *N. stipularis*, *N. straminea*, *N. ternstroemiiflora*, *N. ulei*, *N. velutina*, *N. sp1**, *N. sp2**, *N. sp3**, *N. sp4** among them, four are new for the science (*), one new combination and one with new status (underlined) and two species were reestablished (in bold). The analyses biogeographical focusing *Naucleopsis* suggest that the genus was originated during Oligocene (ca. 32.91 Mya), in Boreal-South Brazilian region (Amazon rainforest).

Keywords: Amazon rainforest, Castilleae, divergence time estimates, EPIC, molecular analyses

LISTA DE FIGURAS

Introdução Geral

Capítulo 1

Capítulo 2

Parte 1

Parte 2

Parte 3

Capítulo 3

LISTA DE TABELAS

Materiais e métodos geral

Capítulo 1

Capítulo 2

Parte 1

Parte 2

Parte 3

Capítulo 3

SUMÁRIO

I. Introdução geral e justificativa

1. Moraceae Gaudich.

A família apresenta distribuição predominantemente tropical e subtropical, com aproximadamente 1150 espécies, 37 gêneros e cinco tribos: Moreae Dumort., Artocarpeae Lam. & DC., Dorstenieae Dumort., Castilleae C.C. Berg e Ficeae Dumort. (Berg 2001). No Brasil ocorrem 19 gêneros com aproximadamente 200 espécies, sendo *Ficus* L. e *Dorstenia* L. os mais representativos em número de espécies (Romaniuc Neto *et al.* 2010). Suas espécies são reconhecidas por apresentarem estípulas terminais, livres ou unidas, presença de laticíferos, folhas simples e alternas. Apresenta espécies monoicas ou dioicas com inflorescências axilares, bissexuadas ou unissexuadas, racemosas ou cimosas, flores aclamídeas ou monoclamídeas e hábito arbóreo, arbustivo, herbáceo, hemiepífito ou trepador.

Moraceae está entre as nove famílias incluídas na ordem Rosales Bercht. & J. Presl (APG 1998, APG II 2003, APG III 2009, Weiblen 2000, Sytsma *et al.* 2002, Datwyler & Weiblen 2004, Chase & Reveal 2009), e difere das demais, principalmente, por apresentar látex abundante distribuído por todas as partes da planta, gineceu geralmente com dois carpelos evidentes, óvulos apicais e embriões frequentemente curvos (Judd *et al.* 1999, Romaniuc Neto 1999). Recentes estudos sobre a filogenética da ordem, usando dados moleculares, apontaram a monofilia de Rosales e reforçaram a estreita relação das famílias do clado "Urticalean-Rosides" proposto por Judd *et al.* (1999). Moraceae é apontado como grupo irmão de Urticaceae Juss. e Ulmaceae próximo à Cannabaceae Mirbel (Zhang *et al.* 2011). Esses resultados são condizentes com os trabalhos realizados por Sytsma *et al.* (2002), que obtiveram um cladograma corroborando a transferência de *Cecropia* Loefl. e gêneros afins para as Urticaceae, confirmando a monofilia de Moraceae. Judd *et al.* (2009)

apontaram a presença dos laticíferos distribuídos por todas as partes da planta, como caráter apomórfico em Moraceae. Além disso, Judd *et al.* (2009) também consideraram a presença de laticíferos como sinapomórfico entre Moraceae e Urticaceae.

O monofiletismo de Moraceae é fortemente corroborado pelas filogenias atuais, porém a delimitação infrafamiliar ainda não está totalmente elucidada, alguns de seus gêneros são facilmente reconhecidos, entretanto, existem outros como os inseridos atualmente em Castilleae, que tiveram seu histórico marcado por relações intrincadas e que ainda geram dúvidas com relação a sua delimitação (Romaniuc Neto 1999; Berg 1972, 2001, 2005; Datwyler & Weiblen 2004; Ribeiro 2007; Clement & Weiblen 2009).

A filogenética de Moraceae (Clement & Weiblen 2009), baseada nas sequências dos genes *ndh*F do cloroplasto e 26S DNA nuclear, resultou na proposta dos autores em organizar o grupo em seis tribos: Moreae, Artocarpeae, Dorstenieae, Castilleae, Ficeae e Maclureae W.L. Clement & Weiblen, sendo esta última monogenérica.

1.1. Tribo Castilleae C.C. Berg

Castilleae foi proposta por Berg (1977) principalmente pela anatomia da madeira, presença de um invólucro de brácteas imbricadas nas inflorescências (Fig. 1 D e F) e caducidade dos ramos (Fig. 1 C). A tribo apresenta predominantemente indivíduos arbóreos de médio a grande porte, sendo menos frequente arvoretas no sub-bosque e mais raro indivíduos arbustivos. Predominantemente dioicas mais raramente monoicas. O fuste tem geralmente base reta, sendo mais rara a presença de raiz tabular (*Castilla* Sessé) (Fig 1 A). O látex pode variar de branco amarelado oxidando rapidamente quando exposto, para amarronzado (Fig. 1 E). As folhas são sempre inteiras, nervação broquidódroma (Fig 1 B) e margem inteira ou dentada. Em alguns gêneros, mais frequente em *Pseudolmedia* Trécul, é comum a presença de perfurações nas folhas provavelmente causadas por fungos, podendo também ocorrer em outros gêneros da tribo, como em *Naucleopsis* Miq. e *Castilla* (Fig 1 B). As estípulas são terminais, podem ser amplexicaules ou não, e são frequentemente livres, com exceção de *Castilla*, onde estas são conadas. As inflorescências são unissexuadas, na grande maioria multiflora (Fig. D e F), com exceção de *Pseudolmedia* (uniflora), pedunculadas ou não, sendo mais frequentemente curto pedunculadas. O receptáculo da inflorescência estaminada pode ser discoide (Fig. 1 D) a globoide, mais raro cupuliforme, e em *Castilla*, este ainda é flabelado a bivalvado; o filete é frequentemente reto no botão, as anteras são base a dorsifixa e os conectivos espessos. O receptáculo da inflorescência pistilada pode ser discoide a globoide (Fig. 1 F). As flores estão dispostas superficialmente ou com o ovário imerso no receptáculo, são livres ou basalmente conadas. O invólucro de brácteas imbricadas é uma das características mais marcantes deste grupo (Fig. 1 D e F) presente em todos os gêneros, seguida pela caducidade de seus ramos secundários (Fig. 1 C), com exceção do gênero *Poulsenia* Eggers.

Castilleae foi proposta por Berg (1977) em substituição a Olmedieae Trécul, quando o mesmo autor observou que o gênero tipo da tribo, *Olmedia* descrito por Ruiz e Pavon (1794), de um material proveniente de *Olmedia aspera* Ruiz & Pav., não detinha todos os caracteres que a delimitavam. *Olmedia*, diferentemente dos outros gêneros da tribo, possuía flores estaminadas com tépalas valvadas, estames inflexos e algumas vezes pistilódios bem desenvolvidos, além disso, estudos anatômicos da madeira de Moraceae indicavam diferenças entre *Olmedia* e outras espécies do grupo e ainda, trabalhos de campo do mesmo autor indicavam também a ausência da caducidade dos ramos em *Olmedia*. Por estes motivos, Berg (1977) excluiu *Olmedia aspera* de Olmedieae sinonimizando-a em *Trophis caucana* (Pittier) C.C.Berg. Consequentemente, a tribo foi renomeada, Castilleae.

Desta forma, os gêneros atualmente inseridos em Castilleae anteriormente a sua proposição estavam inseridos em Olmedieae.

Um dos primeiros registros com citações para os gêneros de Olmedieae foi a proposição de *Perebea* e Maquira por Aublet (1775), que reiterou serem proximamente relacionados à *Ficus*.

Trécul (1847) estabeleceu Olmedieae que foi constituída por seis gêneros (*Olmedia* Ruiz & Pav., *Pseudolmedia* Trécul, *Perebea* Aubl., *Helicostylis* Trécul, *Noyera* Trécul e *Castilloa* Endl.)

Miquel (1853), no estudo para a ”*Flora Brasiliensis”,* propõe um novo gênero para Olmedieae, *Naucleopsis*.

Posteriormente, Bureau (1873) posicionou Olmedieae em Artocarpaceae e considerou para a tribo dez gêneros (*Olmedia*, *Pseudolmedia*, *Antiaris* Lesch., *Maquira*, *Perebea*, *Noyera*, *Naucleopsis*, *Castilloa*, *Helicostylis* e *Ogcodeia*).

Benthan e Hooker (1880) reconheceram para Olmedieae sete gêneros, os mesmos usados na proposta de Trécul (1847) e *Antiaris*. Ainda, os mesmos autores transferiram *Naucleopsis* e *Ogcodeia* para *Noyera, Olmediopsis* H. Karst. para *Pseudolmedia* e *Maquira* para *Helicostylis*.

Pittier (1912) propôs uma primeira reorganização para Olmedieae com uma chave de identificação para os gêneros e espécies. Na proposta de Pittier (1912) *Noyera* e *Naucleopsis* foram considerados gêneros independentes.

Ducke (1922, 1925, 1932) apresentou a primeira sinopse para Olmedieae. Neste último trabalho, Ducke reconheceu para a tribo 13 gêneros (*Brosimopsis* S. Moore, *Pseudolmedia*, *Castilloa*, *Olmedia*, *Helicostylis*, *Perebea*, *Noyera*, *Olmediophaena* H. Karst., *Olmedioperebea* Ducke, *Naucleopsis*, *Ogcodeia*, *Palmolmedia* Ducke, *Acanthosphaera* Warb.).

No início de seus estudos relacionados à tribo Olmedieae, Berg (1969) publicou uma pré-organização do grupo, com novos táxons e novas importantes combinações para a tribo. Posteriormente, Berg (1972) apresentou uma revisão de Olmedieae, reiterando tratar-se de um grupo pouco compreendido, com delimitações genéricas pouco definidas.

Desta forma, desde a revisão de Olmedieae (Berg 1972) não houve outras revisões taxonômicas consistentes para o grupo. A partir deste ponto, posteriores estudos trouxeram nomes de novas espécies para Castilleae (*Perebea mennegae* (Berg 1978); *Naucleopsis capirensis*, *N. herrerensis*, *N. humilis*, *N. straminea*, *N. velutina*, *N. naga* subespécie *meridionalis*, *N. ulei* subespécie *puberula* (Berg & Franco 1996); *Pseudolmedia gentryi* e *P. manabiensis* (Berg 1998)).

Mais recentemente, Sytsma *et al.* (2002) realizaram uma análise das relações do clado "Urticalean Rosids" utilizando dados moleculares dos segmentos de *rbc*L, *trn*L-F e *ndh*F., entretanto Castilleae foi amostrada com apenas um gênero (*Castilla*). Neste estudo os autores obtiveram um cladograma confirmando a transferência de *Cecropia* e gêneros afins para Urticaceae e também corroboraram a monofilia de Moraceae. Além disso, o ramo que suporta as tribos Castilleae e Ficeae recebeu um suporte estatístico de 100%, reforçando a sugestão de que esses dois grupos são proximamente relacionados.

Datwyler & Weiblen (2004) apresentaram uma contribuição para delimitação das tribos em Moraceae, além de reforçar as fortes evidências da monofilia do grupo a partir de

Figura. 1. Morfologia geral Castilleae. **A.** *Castilla elastica* – raiz tabular. **B.** *Castilla ulei* – detalhe presença de fungos nas folhas; nervação broquidódroma. **C.** *Perebea guianensis* - cicatriz pela caducidade dos ramos secundários. **D.** *Perebea guianensis* – detalhe invólucro de brácteas imbricadas; inflorescência estaminada discoide**. E.** *Perebea mollis* – látex amarelado; F. *Naucleopsis inaequalis* (Foto: H. Medeiros) – detalhe invólucro de brácteas imbricadas; inflorescência pistilada globoide.

uma maior amostragem da família, com 83 táxons constituindo 33 gêneros. Os autores usaram o segmento *ndh*F para suas análises e propuseram a divisão do grupo em cinco tribos: Ficeae, Castilleae, Dorstenieae, Artocarpeae, Moreae, sendo que está última se mostrou parafilética e pendente de novas análises, com maior amostragem. Os resultados também indicavam a inclusão dos gêneros *Sparattosyce* Bureau, *Antiaropsis* K. Schum. e *Poulsenia* em Castilleae.

Clement & Weiblen (2009) baseados nas sequências dos genes *ndh*F plastidial e 26S DNA nuclear, propuseram a divisão de Castilleae em duas subtribos: Castillineae e Antiaropsineae. Este estudo teve como base, principalmente o trabalho de Datwyler & Weiblen (2004). Na proposta de Clemente & Weiblen (2009), a tribo Castilleae é alterada com a inclusão de *Antiaropsis*, *Poulsenia* e *Sparattosyce*, semelhantemente aos resultados obtidos por Datwyler & Weiblen (2004).

Todas as filogenias utilizando dados moleculares realizadas até o momento para Moraceae contribuíram principalmente para corroborar o monofiletismo da família (APG III 2003, Datwyler & Weiblen 2004, Sytsma *et al*. 2002, Zerega *et al*. 2005). Entretanto, as relações filogenéticas entre os gêneros de Castilleae continuam incertas. Embora a monofilia da tribo Castilleae tenha forte suporte estatístico (Datwyler & Weiblen 2004, Clement & Weiblen 2009), nenhum dos trabalhos realizados focou especificamente um gênero da tribo.

1.2. *Naucleopsis* Miq.

São árvores, raro arvoretas, dioicas, raro monoicas, com estípulas amplexicaules e látex espesso. As inflorescências são globoides a discoides, com invólucro de brácteas imbricadas, as flores possuem ovário ínfero, tépalas livres ou conadas e as infrutescências podem ser globoides, raramente discoides, com até 8(-10) cm de diâmetro. (Santos & Romaniuc Neto 2014).

O gênero foi estabelecido por Miquel (1853), quando descreveu *N. macrophylla* na "*Flora Brasiliensis*" a partir de uma coleta de Martius da região amazônica, apresentou uma breve descrição do gênero, seguida de uma descrição mais detalhada da espécie.

Posteriormente Bureau (1873) estabeleceu um novo gênero para Olmedieae, *Ogcodeia*, como base nas características do perianto da flor pistilada, a partir de *Naucleopsis glabra* Spruce ex Pittier.

Pittier (1912) no estudo das plantas da Colômbia e da América Central descreveu uma nova espécie, *N. naga*. Neste trabalho, Pittier (1912) considerou *Ogcodeia* como sinônimo *de Naucleopsis*.

Ducke (1922) transferiu *Acanthosphaera ulei*, de Warburg (1907), para *Naucleopsis*, entretanto, Macbride (1931) o transferiu para *Ogcodeia*. Ducke (1939) propõe uma sinopse para Olmediaeae e restabeleceu o gênero *Acanthosphaera*. Neste mesmo trabalho, Ducke (1939) publicou outras duas novas espécies para *Naucleopsis* (*N. insculptula* e *N. pauciflora*), além disso, propôs outro novo gênero *Palmolmedia*.

Berg (2001) listou 22 espécies de *Naucleopsis* para a Flora Neotropica e mais recentemente Berg & Homeier (2010) publicam outra nova espécie, *Naucleopsis. francisci*.

2. Justificativa

Castilleae é marcada por uma sistemática controversa, especificamente *Naucleopsis*, que apresenta um alto grau de polimorfismo de suas inflorescências pistiladas. Ao longo de sua história, importantes alterações na sua circunscrição foram propostas, sendo considerado como três outros gêneros independentes (*Ogcodeia*, *Palmolmedia* e *Acanthosfaera*). Das 23 espécies propostas (Berg 2001, 2010) para *Naucleopsis*, 15 ocorrem no Brasil (Romaniuc Neto *et al.* 2010) e estão concentradas principalmente na região Norte do país. Moraceae está entre as famílias mais ricas em espécies na composição da flora amazônica e o conhecimento da riqueza biológica das espécies de *Naucleopsis* é uma medida importante tanto para conservação dessas espécies quanto para a conservação do bioma local. O número de sinonímias (32 atualmente) propostas para *Naucleopsis* pode refletir de forma imprecisa o número total de táxons válidos. Além disso, um estudo mais detalhado dos binômios propostos em sinonímia e suas características morfológicas, associadas às análises dos respectivos protólogos e materiais tipos, poderão permitir o restabelecimento de alguns táxons. E por último, embora recentemente tenham sido publicadas diversas filogenias moleculares para as tribos de Moraceae verificou-se, ainda, a necessidade de corroborar uma proposta filogenética para o gênero aqui em estudo. A análise molecular do grupo fornecerá subsídios para fundamentar a delimitação genérica, especificamente em *Naucleopsis*, que já foi alterada em sua circunscrição por inúmeras vezes ao longo do seu histórico. Ainda, o presente estudo visa contribuir com dados que possam subsidiar programas de conservação dessas espécies.

II. Objetivos

A presente tese tem os seguintes objetivos centrais:

- Avaliar as relações moleculares dentro de Castilleae com foco em *Naucleopsis* e testar o seu monofiletismo.

- Apresentar uma sinopse das espécies de *Naucleopsis*;

- Estimar os tempos de divergência de linhagens em Castilleae, especialmente para *Naucleopsis*, a fim de propor hipóteses sobre a evolução espaço-temporal do gênero.

III. Organização da tese

A presente tese é composta de três capítulos, além destes, também é constituída de uma introdução geral, materiais e métodos gerais, referências bibliográficas gerais e considerações finais. As citações bibliográficas no texto da introdução geral, material e métodos gerais e das referências bibliográficas gerais seguiram as normas estabelecidas pelo periódico institucional Hoehnea, disponível em:http://www.ibot.sp.gov.br/publicacoes/hoehnea/Instru%E7%F5es%20aos%20autores.pdf. De acordo com código internacional de nomenclatura para algas, fungos e plantas (Mcneill, J. & Turland, N.J. 2011, McNeill *et al.* 2012), os nomes novos apresentados não são validamente publicados. Cada capítulo foi subdividido em partes quando se verificou a necessidade. Assim, cada uma das partes desta tese segue as normas para publicação das respectivas revistas às quais serão submetidas.

Capítulo 1 – Estudos moleculares

Molecular phylogenetics of Castilleae (Moraceae): an analysis of the species on *Naucleopsis* Miq.

Capítulo 2 – Estudos taxonômicos

Parte 1 - A new species of *Naucleopsis* (Moraceae) from Brazilian Amazon and the reestablishment of *Naucleopsis insculptula*

Parte 2 - Two new species of *Naucleopsis* (Castilleae, Moraceae) from South America

Parte 3 - Synopsis of species of *Naucleopsis* Miq. (Moraceae)

Capítulo 3 – Estudos biogeográficos

Patterns of biogeographic regionalization and biogeographical history of *Naucleopsis* (Moraceae) from Neotropics and comments from allied genera

IV. Material e Métodos Geral

4. Material e Métodos

4.1. Levantamento bibliográfico

Devido às questões históricas e à problemática sistemática entre os gêneros que compõem Castilleae, foi quase inevitável que se fizesse o estudo de *Naucleopsis* sem uma cuidadosa análise de todos os outros gêneros dentro da tribo.

O levantamento e o estudo de toda a bibliografia relacionada ao grupo Castilleae foi de suma importância para o entendimento da história de *Naucleopsis*, pois se trata de um grupo de difícil delimitação, que mostrou desde início uma circunscrição complexa, intrincada e controversa.

A busca do material bibliográfico foi realizada através de pesquisas nos principais portais de periódicos e referências disponíveis para consulta "on-line" de bibliotecas eletrônicas do Brasil e estrangeiras como: http://www.archive.org/; http://www.biodiversitylibrary.org/; http://www.botanicus.org./; http://gallica.bnf.fr/; http://www.ipni.org/; http://scielo.org/; http://www.tropicos.org/; http;//www.theplantlist.org/; http://www.jstor.org, entre outros. Além, da busca feita pela rede clássica de bibliotecas, principalmente, a do Instituto de Botânica de São Paulo, a biblioteca do Instituto de Biociências da Universidade de São Paulo e a biblioteca do Royal Botanic Gardens Kew, muito importante para algumas publicações não disponíveis on-line.

4.2. Coleta e processamento do material botânico

Expedições ao campo foram realizadas com o objetivo de complementar as coleções de Castilleae e observar as espécies em seu ambiente natural. No campo foram registrados dados gerais como altura dos indivíduos, coloração de flores e frutos, características do látex, entre outras características. As excursões de coleta foram realizadas em áreas onde o grupo estudado apresenta sua maior diversidade (Tab. 1).

Tab. 1. Expedições de campo para coleta de material botânico:

Período	**País. Estados e Municípios**
19/IX/2012	Brasil. Amazonas: Manaus, Campus do IFAM.
22-23/IX/2012	Brasil. Amazonas: Manaus, Reserva Florestal Ducke.
24/IX/2012	Brasil. Amazonas: Estrada para Presidente Figueiredo.
25-26/IX/2012	Brasil. Amazonas: Manaus, Campus do IFAM.
04/X/2012	Brasil. Pará: Santa Luzia do Pará.
05/X/2012	Brasil. Pará: Bosque Rodrigues Alves, Belém.
06/X/2012	Brasil. Pará: Tailândia.
07/X/2012	Brasil. Pará: Novo Repartimento.
08/X/2012	Brasil. Pará: Goianésia, Fazenda Suauma.
09/X/2012	Brasil. Pará: Benevides, Club Neópolis.
10/X/2012	Brasil. Pará: Capanema.
11/X/2012	Brasil. Pará: Belém, Bosque Municipal Rodrigues Alves.
21/I/2013	Brasil. Rio de Janeiro: Rio de Janeiro, Jacarepaguá.
18/II/2014	Brasil. Acre: Fazenda Catuaba.
22/II/2014	Peru. Santa Teresa-Mandor, trilha do trem.
23/II/2014	Peru. Mandor-Machu Picchu, trilha do trem.

A obtenção dos materiais botânicos e os procedimentos de herborização e processamento destes seguiram as recomendações de Peixoto & Maia (2013). Amostras suplementares foram acondicionadas em potes plásticos com fecho hermético, para conservação em sílica gel, no intuito de realizar os estudos moleculares.

4.3. Consultas aos herbários

O levantamento do material botânico e dos tipos nomenclaturais das espécies de Castilleae para análise de seus binômios foram feitos através de visitas e solicitações de empréstimos dos materiais mais representativos aos principais herbários que abrigam coleções importantes para o grupo, como: A. Ducke, A.B. Krukoff, J.F. Macbride, R. Spruce, P.C. Standley, H.F.Pittier, J.B.C.F. Aublet (Tab. 2).

Tab. 2. Acrônimos dos herbários visitados, Instituição, cidade e país.

B	Botanischer Garten und Botanisches Museum Berlin-Dahlem, Zentraleinrichtung der Freien Universität Berlin, Berlin (Alemanha).
BG	University of Bergen, Bergen (Noruega).
BM	The Natural History Museum, London (Reino Unido).
CUZ	Universidad Nacional de San Antonio Abad del Cusco. Cusco (Peru).
EAFM	Instituto Federal de Educação, Ciência e Tecnologia do Amazonas. Manaus. AM.
IAN	Embrapa Amazônia Oriental. Belém. PA.
INPA	Instituto Nacional de Pesquisas da Amazônia. Manaus. AM.

K	Royal Botanic Gardens, Kew, Richmond (Reino Unido).
L	Nationaal Herbarium Nederland, Leiden University branch, Leiden (Holanda).
LABEV	Laboratório de Botânica e Ecologia Vegetal, Universidade Federal do Acre. Rio Branco. AC.
MG	Museu Paraense Emílio Goeldi. Belém. PA.
NY	The New York Botanical Garden, New York.
P	Muséum National d’Histoire Naturelle, Paris (França).
RB	Jardim Botânico do Rio de Janeiro, Instituto de Pesquisas. Rio de Janeiro. RJ.
SP	Instituto de Botânica, Núcleo de Pesquisa Curadoria do Herbário SP, Herbário Maria Eneyda P. Kauffmann Fidalgo. São Paulo. SP.
SPF	Instituto de Biociências, Universidade de São Paulo. São Paulo. SP.
UFACPZ	Universidade Federal do Acre. Rio Branco. AC.
UEC	Universidade Estadual de Campinas. Campinas. SP.
US	Smithsonian Institution. Washington.

Os herbários cujas coleções foram examinadas constam listados na tabela acima (Tab. 2). Os acrônimos dos herbários listados seguem Thiers (2015). O acesso a estas coleções foi de suma importância para análise de alguns binômios e elucidação de questões taxonômicas do grupo.

4.4. Estudos moleculares

4.4.1. Amostragem para análises moleculares

A amostragem para as análises com os marcadores plastidial *trnL-F* e nuclear FA03310 (EPIC) compreendeu um total de 25 táxons, sendo que 20 destes são exemplares representativos da tribo Castilleae, três táxons são exemplares de *Ficus*, representando a tribo Ficeae, que foram utilizados com grupo irmão, outros dois exemplares representando Maclureae e Moreae, baseados em Sytsma *et al*. (2002), Datwyler & Weiblen (2004) e Clement & Weiblen (2009) (Apêndice 1, Capítulo 1).

Para as análises com marcador nuclear 26S a amostragem compreendeu 25 táxons, sendo que 23 destes são exemplares representativos da tribo Castilleae, um táxon é exemplar de *Ficus*, que foi utilizado com grupo irmão e outro de Cannabaceae (*Cannabis*) que foi utilizado como grupo externo (Apêndice 1, Capítulo 1).

4.4.2. Extração do DNA, amplificação e sequenciamento

Os procedimentos metodológicos foram realizados no laboratório de Biologia Molecular do Departamento de Fisiologia e Bioquímica de Plantas do Instituto de Botânica de São Paulo, sob a responsabilidade da Dra. Marília Gaspar.

As extrações de DNA foram feitas a partir de fragmentos de folhas desidratadas em sílica gel ou, quando necessário, removidas de fragmentos de material de herbário. Para a extração foi utilizado o método do protocolo CTAB modificado, de Doyle & Doyle (1987), com as modificações para plantas com látex de Weiblen (2000). Os fragmentos de folhas (15-20 mg) foram pesados e macerados com o auxílio de moinho de bola.

Foram usados como marcadores moleculares do DNA a região plastidial *trnL-F* por terem se mostrado informativos nos estudos de Weiblen (2000), Sytsma *et al.* (2002), e Zerega *et al*. (2010) e o de DNA nuclear FA03310 (EPIC) por se mostrar informativo neste estudo. Além disso, estudos cladísticos também foram operados com marcador molecular nr26S com dados previamente utilizados nos trabalhos de Clement & Weiblen (2009).

Sequências dos genes *trnL-F*, FA03310 e 26S para espécies de Castilleae publicadas no GenBank foram utilizadas na análise filogenética, juntamente com as novas sequências obtidas nesse estudo.

A amplificação foi realizada pela reação em cadeia da polimerase (PCR), em termocicladores. A região de DNA dos marcadores FA03310 e *trnL-F* foram amplificados com o uso de 25 µl volume ReadyMix^{TM} Taq PCR Reaction Mix with $MgCl_2$ (Sigma-Aldrich), 1mg/ml de BSA (bovine serum albumin), 20 µM de cada primer e ~50 ng of genomic DNA.

Os dados dos primers usados neste estudo constam detalhados no Capítulo 1 desta tese.

Os produtos da PCR foram quantificados e as amostras foram purificadas e sequenciadas pela Macrogen. Ambas as fitas foram sequenciadas para a determinação de bases com a utilização dos mesmos primers usados na amplificação, respectivamente.

4.4.3. Análises filogenéticas

As sequências foram alinhadas e estudos cladísticos foram operados em busca das relações filogenéticas dentro de Castilleae (Hennig 1966, 1969 e 1981). Estes foram realizados utilizando o método de máxima verossimilhança através da pesquisa heurística e teste de confiança por bootstrap com o programa Geneious® 6.1.8 (Kearse *et al.* 2012, Biomatters, 2015).

Com base em Posada & Buckley (2004) conjuntos dos dados individuais e combinados foram avaliados para o modelo apropriado de evolução molecular usando ModelTest v.3.7 (Posada & Crandall 1998).

Também foi realizada inferência bayesiana, com o programa MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003).

4.5. Estudos taxonômicos

As maiores dificuldades encontradas na separação dos materiais foram relacionadas ao alto grau de polimorfismo, principalmente nas inflorescências pistiladas de *Naucleopsis*.

Todos os espécimes foram agrupados de acordo com a semelhança morfológica, ecológica e biogeográfica, incluindo os tipos nomenclaturais de todos os binômios em estudo. A partir deste ponto, cada agrupamento foi analisado individualmente. A análise taxonômica foi baseada na caracterização dos agrupamentos encontrados, comparados com dados do grupo existentes na literatura (Berg 1972, 2001) e com os protólogos de cada binômio estudado, além dos tipos já previamente localizados nos respectivos agrupamentos. Somente para *Naucleopsis* foram analisadas aproximadamente 700 exsicatas. Após o término dos estudos e definida total coerência morfológica, geográfica e ecológica de cada agrupamento com os respectivos materiais tipos e protólogos foi possível fazer identificação dos materiais.

4.5.1. Estudos morfológicos

Para o levantamento e estudo dos caracteres morfológicos foi realizada a análise das estruturas vegetativas e reprodutivas das exsicatas dos acervos dos herbários visitados

(Tab. 2), devidamente hidratadas quando necessário. Adotaram-se Lawrence *et al.* (1968), Hickey (1973), Font-Quer (1985), Radford *et al.* (1974), Weberling (1989), Bell (1993) e Stearn (2004) como referências para a terminologia morfológica. Como complementação, utilizaram-se Corner (1962) e Berg (1972, 2001) para as estruturas reprodutivas. Os estudos morfológicos também serviram de base para definir os melhores caracteres diagnósticos para delimitação das espécies dentro do gênero. Para auxílio na visualização de algumas estruturas foi utilizado um microscópio estereoscópico.

O estudo dos tricomas foi realizado no Instituto de Botânica de São Paulo, sob a supervisão da Dra. Luciana B. Benatti. Para tal, foram obtidas amostras com cerca de 5mm^2 da porção mediana da face abaxial das folhas, brácteas e perianto de materiais de herbário da tribo Castilleae. As amostras foram montadas em stubs e posteriormente metalizadas. As elétron-micrografias foram feitas em microscópio eletrônico de varredura Philips v.5.21. Os termos morfológicos utilizados na classificação dos tipos de tricomas foram baseados em Payne (1978) e Stearn (1992).

4.5.2. Tratamento taxonômico

O tratamento e descrições taxonômicas das espécies seguiram as recomendações do Código Internacional de Nomenclatura Botânica (Mcneill & Turland 2011, Mcneill *et al.* 2012). A apresentação das espécies seguiu as normas para publicação da revista onde será publicado o respectivo capítulo. Comentários sobre ocorrência, estado fenológico e algumas vezes, variações morfológicas e aspectos ecológicos, de cada espécie foram apresentados após cada descrição.

A fim de melhor elucidar as estruturas morfológicas diagnósticas, foram elaboradas ilustrações, desenhadas por profissional (Klei Souza) a lápis, com auxílio do microscópio estereoscópico acoplado a uma câmara clara. Após revisão da conformidade necessária de cada ilustração, estas foram cobertas a nanquim em papel vegetal. Foram escolhidos os principais caracteres diagnósticos para os táxons e todos os materiais utilizados constam nas legendas das ilustrações.

4.6. Estudos biogeográficos

4.6.1. Elaboração de mapas de distribuição geográfica das espécies de *Naucleopsis*

Os dados de distribuição das espécies foram baseados em dados obtidos na literatura pesquisada e nos materiais analisados dos herbários visitados. Os mapas de distribuição geográfica das espécies de *Naucleopsis* foram elaborados somente com os dados obtidos nos rótulos de todos os materiais examinados. Para os materiais sem coordenadas geográficas o georreferenciamento foi realizado com o auxílio do programa Google Earth© e consultado a base geoLoc, ferramenta desenvolvida pelo CRIA, Centro de Referência em Informação Ambiental, com o objetivo de auxiliar o trabalho de coleções biológicas no georreferenciamento de seus acervos, disponível em http://splink.cria.org.br/geoloc?criaLANG=pt. Buscou-se georreferenciar as espécies de acordo com as coordenadas geográficas dos locais de ocorrência presentes nos rótulos, quando não encontrados foram utilizadas as coordenadas da sede do município citada no rótulo. Os pontos georreferenciados foram convertidos em graus decimais e exportados para um mapa base da região neotropical. Foi utilizado o software Quantum GIS, versão 2.12 para elaboração dos mapas de distribuição geográfica.

4.6.2. Padrões de distribuição geográfica

Os padrões de regionalização geográfica das espécies seguiram os conceitos propostos por Morrone (2014). As regiões correspondem aos domínios: Mesoamerican; Pacific; Boreal Brazilian; South Brazilian; Chacoan; Parana. As análises da abrangência da distribuição foram baseadas no levantamento das coleções dos herbários visitados (Tabela 2) e nos principais tratamentos taxonômicos recentes do grupo como Berg (1972, 2001) e Romaniuc Neto *et al.* (2010).

4.6.3. Análises biogeográficas

Este estudo utilizou a inferência bayesiana para estimar os tempos de divergência utilizando (BEAST) v.2.1.0 (Bouckaert *et al.*, 2013; Bouckaert *et al.*, 2014). Foram realizadas análises biogeográficas com RASP v 3.0 (Ancestral State in Phylogenies; Yu *et al.*, 2012). Utilizando a análise de dispersão-vicariance estatística (S-DIVA; Yu *et al*, 2010). Para isso foi utilizada uma filogenia molecular com bases nos seguimentos do DNA da região plastidial *trnL-F* e nuclear *FA03310* de *Naucleopsis*, já descritos nos capítulo 1 deste trabalho.

4.7. Conservação

As categorias de conservação foram determinadas com base nas disponibilizadas pela IUCN (2001), atualizadas por IUCN (2015). Além disso, foram consultados os principais livros vermelhos de espécies ameaçadas. Usou-se o software Quantum GIS, versão 2.12 com polígonos fechados, para as análises de área de extensão e área de ocorrência das espécies.

V. Capítulos

Capítulo 2 – Estudos moleculares

Molecular phylogenetics of Castilleae (Moraceae): an analysis of the species on *Naucleopsis* Miq.

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Abstract — DNA sequencing has transformed traditional taxonomy and has led to a robust new systematic classification for the family Moraceae. Particularly the Castilleae tribe has had largest difficulty with its circumscription and the delimitation its genera. Ours morphological studies indicated that the involucres with several series of imbricate bracts fully covering the outer surface of the receptacle may be considered the mainly common characteristic to all neotropical genera of the tribe. This study aimed to evaluate the phylogenetic relationships within of Castilleae with emphasis on *Naucleopsis.* To infer the phylogeny DNA sequence data from the plastidial *trnL-F* and nuclear FA03310 (EPIC) gene were sequenced in order to infer a preliminary phylogeny of *Naucleopsis*. Also a Bayesian analysis from the nuclear 26S used previously was performed. All neotropical genera of Castilleae were monophyletic, with the exception of *Perebea mollis*. The inferred phylogeny reveals two main lineages (I and II) in Castilleae. Lineage I included two clades with two genera: *Castilla* and *Poulsenia*. Lineage II included four clades with five genera: *Pseudolmedia*, *Perebea*, *Maquira*, *Helicostylis* and *Naucleopsis.* Ours phylogenetic analysis to the *Naucleopsis* also suggested that the genus is monophyletic, with one lineage specific for the group of species with connate perianth, parted at the apex, and other lineage specific for *Naucleopsis humilis* with free pseudo-tepals and branches with short internodes, supported by our maximum likelihood and Bayesian analyses.

Keywords: *Pseudolmedia, Perebea, Maquira*, *Helicostylis*, *Perebea mollis*, Amazonian forest, EPIC, 26S, *trnL-F*

Moraceae are well known by the presence of the milky latex in all plant, apical stipules, anatropous ovules and alternate leaves. These characteristics are strongly supported by molecular evidence (Sytsma et al. 2002; Datwyler & Weiblen 2004; Clement & Weiblen 2009). Recent phylogenetic analyses have shown that Moraceae have been suported into six tribes: Moreae Dumort., Artocarpeae Lam. & DC., Maclureae W.L. Clement & Weiblen, Dorstenieae Dumort., Castilleae C.C. Berg and Ficeae Dumort. (Clement & Weiblen 2009). DNA sequencing has transformed traditional taxonomy and has led to a robust new systematic classification for the family Moraceae. In particular, Castilleae tribe that stands out by its historical past characterized by circumscription controversies (Trécul 1847; Ducke 1939; Berg 1977). The tribe was described by Berg (1977) that used the presence of septate wood fibres and self-pruning branches as main criteria for its delimitation. Hence, *Olmedia* Ruiz & Pav. genus was excluded and Olmedieae tribe was renamed as Castilleae.

Olmedieae were established by Trécul (1847). The same author has circumscribed the tribe with six neotropical genera (*Olmedia*, *Pseudolmedia* Trécul, *Perebea* Aubl., *Helicostylis* Trécul, *Noyera* Trécul and Castilloa Endl.). The author showed an identification key for the tribe and used the involucre imbricate bracts as main criterion for the characterization of Olmedieae. Afterwards, Ducke (1939) published a synopse of Olmedieae with a view to facilitating the recognition of their genera. In this study, were considered thirteen genera for the tribe (*Brosimopsis* S. Moore, *Pseudolmedia*, *Castilloa*, *Olmedia*, *Helicostylis*, *Perebea*, *Noyera*, *Olmediophaena* H. Karst., *Olmedioperebea* Ducke, *Naucleopsis* Miq., *Ogcodeia* Bureau, *Palmolmedia* Ducke and *Acanthosphaera* Warb.), whereas *Palmolmedia*, proposed by Ducke (1939), was based in the specimens of *Naucleopsis stipularis.*

Berg (1969) maintained the name of the tribe and proposed new taxa and combinations in the neotropical Olmedieae. In this work, the author included *Noyera* in *Perebea*, *Olmediophaena* and *Olmedioperebea* in *Maquira* and *Ogcodeia* in *Naucleopsis*. Afterwards, Berg (1977) renamed and redefined the tribe with the exclusion of the type *Olmedia*.

Currently, Castilleae includes seven neotropical genera supported by molecular evidence. The tribe is distributed throughout the neotropics and to a limited extent in tropical Africa.

Naucleopsis Miq. is the largest genus of Castilleae. It is characterized mainly by dioecious, rarely monoecious, trees; stipules fully amplexicaul; staminate inflorescences often up to 10 together, inner involucral bracts covering the flowers before anthesis; pistilate inflorescences often solitary, ovary entirely immersed in the receptacle. Although recently has been published several molecular phylogeny for the tribes of Moraceae (Sytsma *et al.* 2002; Datwyler & Weiblen 2004; Clement & Weiblen 2009), it was also noted the need to corroborate a phylogenetic proposal for the genus.

Naucleopsis also has a history marked by several controversies and intricates circumscription proposals (Bureau 1873; Pittier 1912; Mildbraed 1927; Macbride 1931; Ducke 1922, 1939; Berg 1972, 2001).

Bureau (1873) established *Ogcodeia* genus, separating it of *Naucleopsis*. For Bureau (1873), *Naucleopsis* was characterized by tubular perianth, while *Ogcodeia* was characterized by ovoid-pyramidate. The same proposal was maintained in Pittier (1912) and Mildbraed (1927) recognized *Ogcodeia* as a distinct genus of *Naucleopsis.* In the opinion of Mildbraed in *Ogcodeia* the receptacle of the pistillate inflorescences was covered with processes, called “pseudo-bracteoles”. Significant differences in the inflorescences of *Naucleopsis* made Warburg (1907) propose a new genus, *Acanthosphaera.* Ducke (1922) recombines *Acanthosphaera* in *Naucleopsis* and Macbride (1931) recombines in *Ogcodeia.* The complexity of this group is so great that Ducke (1939) rethought and reestablished the genus *Acanthosphaera* based on characters of the staminate inflorescences. In the same publication, the author also reestablished the genus, *Palmolmedia* and published a synopsis for Olmedieae. In his view, *Palmolmedia* is an intermediate between *Naucleopsis* and *Acanthosphaera.*

The last taxonomic study for this genus was related to the revision of the tribe made by Berg (1972, 1977). Subsequently, Berg (2001) maintained the same organization proposal previously.

Based on the above, our aims in this research were: 1) test a new molecular markers of potential use to reconstruct a phylogeny of tribe with focus in *Naucleopsis*; 2) generate a preliminary phylogenetic tree of various species currently recognized in Castilleae neotropical with emphasis in *Naucleopsis*; 3) test the monophyly of the genus *Naucleopsis* and 4) clarify relationships of the tribe using all available data combined with phylogenetic methods.

MATERIAL AND METHODS

Taxon sampling — We included 28 accessions (25 taxa) in this study. The ingroup comprised all neotropical genera that have been placed in Castilleae in the most recent proposals (Datwyler & Weiblen 2004; Zerega *et al.* 2005; Clement 2008; Clement & Weiblen 2009; Zerega *et al.* 2010). Thus, the ingroup one accession of *Poulsenia* Eggers (1 taxon), two of *Castilla* (1), two of *Pseudolmedia* (2 taxa), five of *Perebea* (4), one of *Maquira* (1), three of *Helicostylis* (3), and nine of *Naucleopsis* (8).

Outgroup taxa belong to other tribes of Moraceae, such as Ficeae (3 taxa of *Ficus*), Maclureae (1 taxon of *Maclura*) and Moreae (1 taxon of *Sorocea*) as recognized in the most recent accounts of the tribes of Moraceae (Clement & Weiblen 2009). The nuclear 26S DNA sequences were obtained from GenBank of Clement and Weiblen (2009) and included 25 accessions (25 taxa). Taxa sampled, voucher information, and GenBank accession numbers for the three data sets are listed in Appendix 1.

DNA Extraction, PCR Amplification, and Sequencing — Leaf samples were collected either in silica gel or from herbarium sheets (Appendix 1). Genomic DNA was extracted with approximately 20 mg of dried leaf tissue using a modified CTAB (cetyltrimethylammonium bromide) method (Weiblen, 2000). Amplification of the *trnL-F* region utilized external primers “c” and “f,” and the internal primers “d” and “e” were also employed for amplification from herbarium specimens (Taberlet et al., 1991). Thermal cycling conditions for amplification of the *trnL-F* region were: 94°C for 10 min followed by 32 cycles of 94°C for 45 sec, 57°C for 30 sec, 72°C for 1 min 30 sec, and a final extension of 74°C for 7 min.

PCR amplification of the nr FA03310 DNA region was achieved in one fragment using FA03310 forward (5’-GCGGGTATAAGAAGGGAACC-3’) and FA03310 reverse (5’- GGTGCATTGACCACCTTGAT-3’) an exon-primed intron-crossing (EPIC) marker designed specifically for *Ficus* from Yao et al. (2013). Amplification of FA03310 included about 25 μl volume ReadyMixTM Taq PCR Reaction Mix with MgCl2 (Sigma-Aldrich), 1mg/ml de BSA (bovine serum albumin), 20 μM of each primer and ~50 ng of genomic DNA. Thermal cycling conditions for amplification of the FA03310 region were: 94°C for 10 min followed by 36 cycles of 94°C for 45 sec, 54°C for 30 sec, 72°C for 1 min 30 sec, and a final extension of 74°C for 7 min.

PCR products were sent to Magrogen Inc. South Korea (Seoul), where they were purified and subsequently sequenced in both directions using the same PCR primers.

Sequence Alignment and Phylogenetic Analysis — Complementary DNA sequences were assembled for each accession using Geneious® 8.0.2 (Kearse et al. 2012; Biomatters 2014). Multiple-sequence alignment was performed using Clustal W (Chenna et al. 2003) followed by manual optimization. Manual alignment and optimization were performed in Geneious® 8.0.2.

Trees obtained for each region were examined for high (bootstrap of 70% or higher) or low (bootstrap below 70%) incongruences based on bootstrap support for nodes in both of the separate analyses.

The incongruence length difference (ILD) test between FA03310 and *trnL-F* results were conducted to assess data congruence (Farris et al. 1995; Barker & Lutzoni 2002). The ILD test was performed using PAUP* v.4.0b10 (Swofford, 2002) and 1000 heuristic search replications after the removal of all invariant positions from the data set (Cunningham 1997). The consistency index (CI; Kluge & Farris, 1969) and retention index (RI; Farris, 1989) were calculated to measure the amount of homoplasy in the dataset.

Phylogenetic analyses of FA03310 and *trnL-F* combined data set were performed using maximum likelihood (ML), and Bayesian inference (BI). Phylogenetic analyses of 26S data set were performed using BI for the taxa from Clement and Weiblen (2009), appendix 1.

Combined data sets (FA03310 and *trnL-F*) were evaluated based on the hierarchical likelihood ratio tests – hLRT, for the appropriate model of molecular evolution using ModelTest v. 3.7 (Posada & Buckley 2004) (Table 1).

The clade support for ML phylogenies was assessed with a bootstrap analysis using 1,000 replicates with 100 random addition sequence replicates, and tree bisection and reconnection (TBR) branch swapping as implemented in PAUP* 4.01b10 (Swofford 2002). Bootstrap analyses (1000 pseudo replicates) were conducted with the same parameters to examine the relative level of support for clades on the cladograms (Felsenstein 1985).

The BI tree was constructed using MrBayes v.3.1.2 (Ronquist & Huelsenbeck 2003). Four Markov Chain Monte Carlo simulations were run simultaneously and sampled every 1000 generations for a total of 10 000 000 generations until the average deviation of split frequencies was well below 0.01. A Bayesian posterior probability (PP) and Bootstrap (BP) were showed in the figure 1. The analyses were performed in the Physiology and Biochemistry and Urticineae Laboratory of Instituto de Botânica.

RESULTS

nr 26S and FA03310 analyses — Data sequences of high quality were obtained of 22 specimens from the nuclear FA03310 marker. Yao et al. (2013) suggested that these markers should therefore be extremely useful for phylogenetic analysis at the family level and potentially beyond. The marker shows a level of intron divergence that is of similar magnitude as ITS, which is one of the most informative and broadly used markers in plant molecular systematics. The use of this marker is inedited for this group. In this study, the EPIC alignment for 24 accessions from 20 ingroups (Castilleae) and four outgroups (sister tribe of Castilleae), contained 701 characters.

The nuclear 26S DNA was aligned for 25 accessions from 23 ingroups (Castilleae) and two outgroups (sister of tribe Castilleae and family Cannabaceae), contained 1031 characters. The BI tree showed that *Naucleopsis* was supported as monophyletic (PP = 1.00). This result was similar to Clement and Weiblen (2009).

The BI 26S topology showed a strong cohesion to the clade of *Naucleopsis* (Fig. 2). Besides the topology of 26S corroborated the phylogeny previously proposed for Castilleae (Datwyler & Weiblen 2004; Clement & Weiblen 2009).

Plastid gene trnL-F analyses — Data sequences of high quality of 26 specimens also were obtained from the nuclear *trnL-F* marker. This marker was used by Sytsma et al. (2002) that obtained a strong support in the analysis for the individual families Ulmaceae, Cannabaceae, Moraceae, and Urticaceae (with Cecropiaceae), each of which strongly monophyletic (89%). The *trnL-F* alignment for 26 accessions from 23 ingroups (Castilleae) and three outgroups (other tribe of Castilleae), contained 689 characters.

Combined Analyses— Comparing the phylogenies based on the separate analyses of 26S the most parts of the clades suggest the genera within Castilleae are monophyletics, with the exception of *Perebea mollis* (Fig. 1).

The combined strict consensus tree was better resolved than the separate analysis. This showed one specific lineage of *Naucleopsis* with connate perianth, parted at the apex, and other lineage specific for *Naucleopsis humilis* with free pseudo-tepals and branches with short internodes, supported by our maximum likelihood and Bayesian analyses.

Analysis of the combined data set resulted in 2002 trees, variable sites (35.5%) and CI = 0.4944, RI = 0.8409 (Table 2). Also, the BI topology for combined data was strongly supported for *Naucleopsis*. All ML and BI combined FA03310 and *trn*L-F suggested that *Naucleopsis* is monophyletic (BP = 100, PP = 1.00; Fig. 1). However the analysis combined (FA03310 and *trn*L-F) showed lineages specific for the group of species with

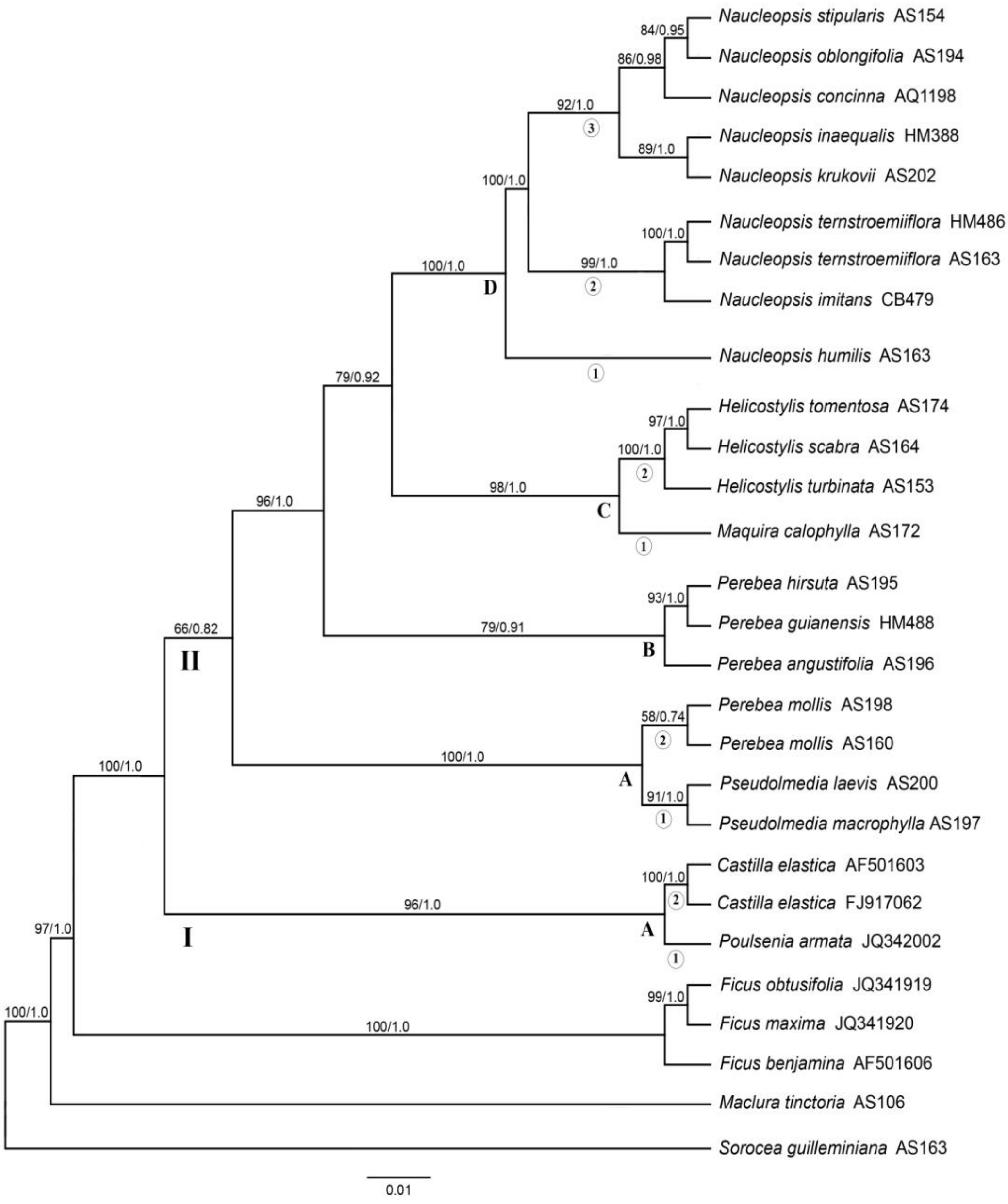

Figure 1. Bayesian consensus tree for Castilleae based on combined molecular data (FA03310-EPIC and *trnL-F*). The numbers along the branches indicate support (maximum likelihood bootstrap [BP] / Bayesian posterior probability [PP]). The two lineages [I (A,1), II (A, 1-2), (B, 1), (C, 1-2) and (D, 1-3)], within Castilleae are indicated.

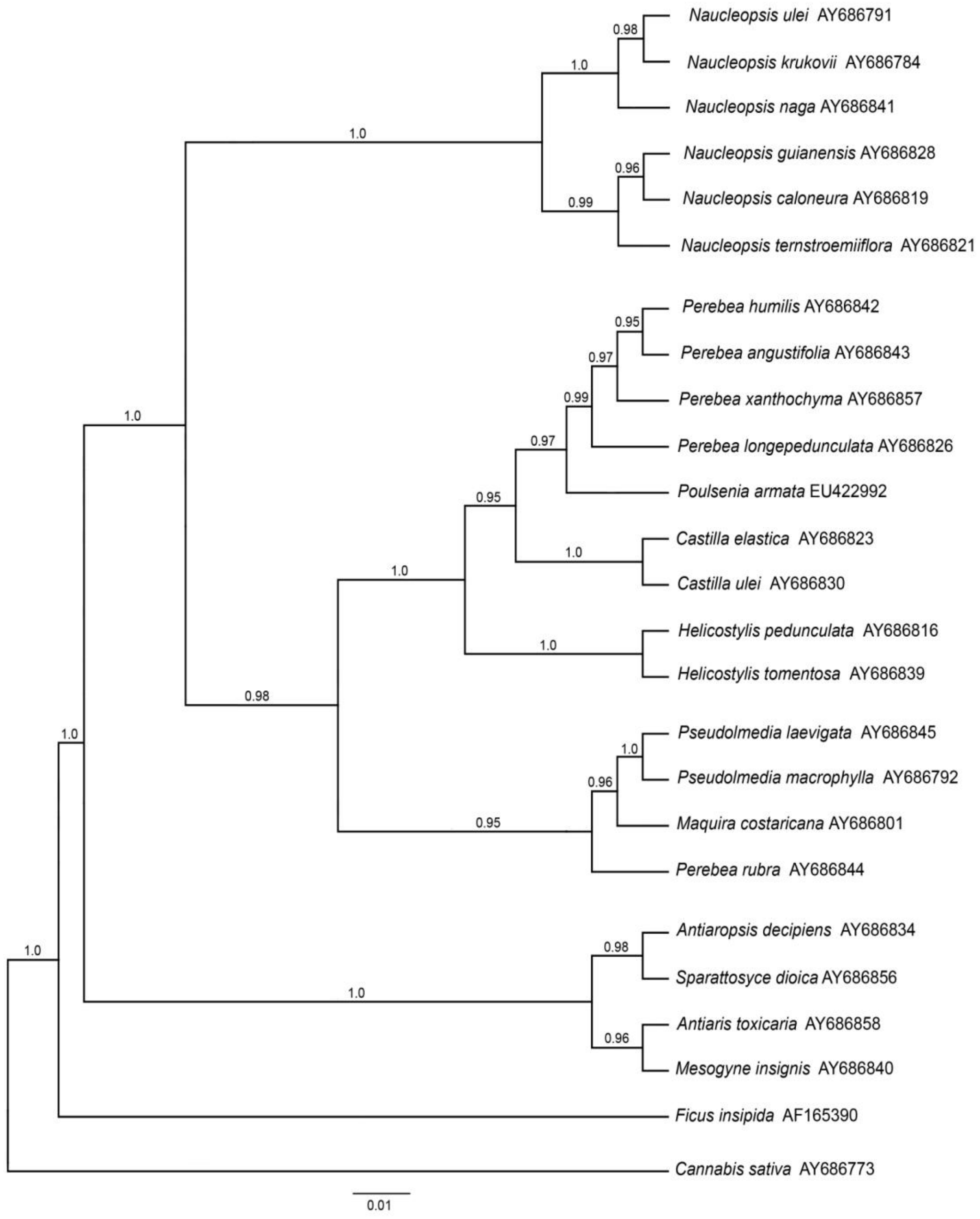

Figure 2. Bayesian consensus tree for Castilleae based on separate molecular data (26S). The numbers along the branches indicate support Bayesian posterior probability [PP].

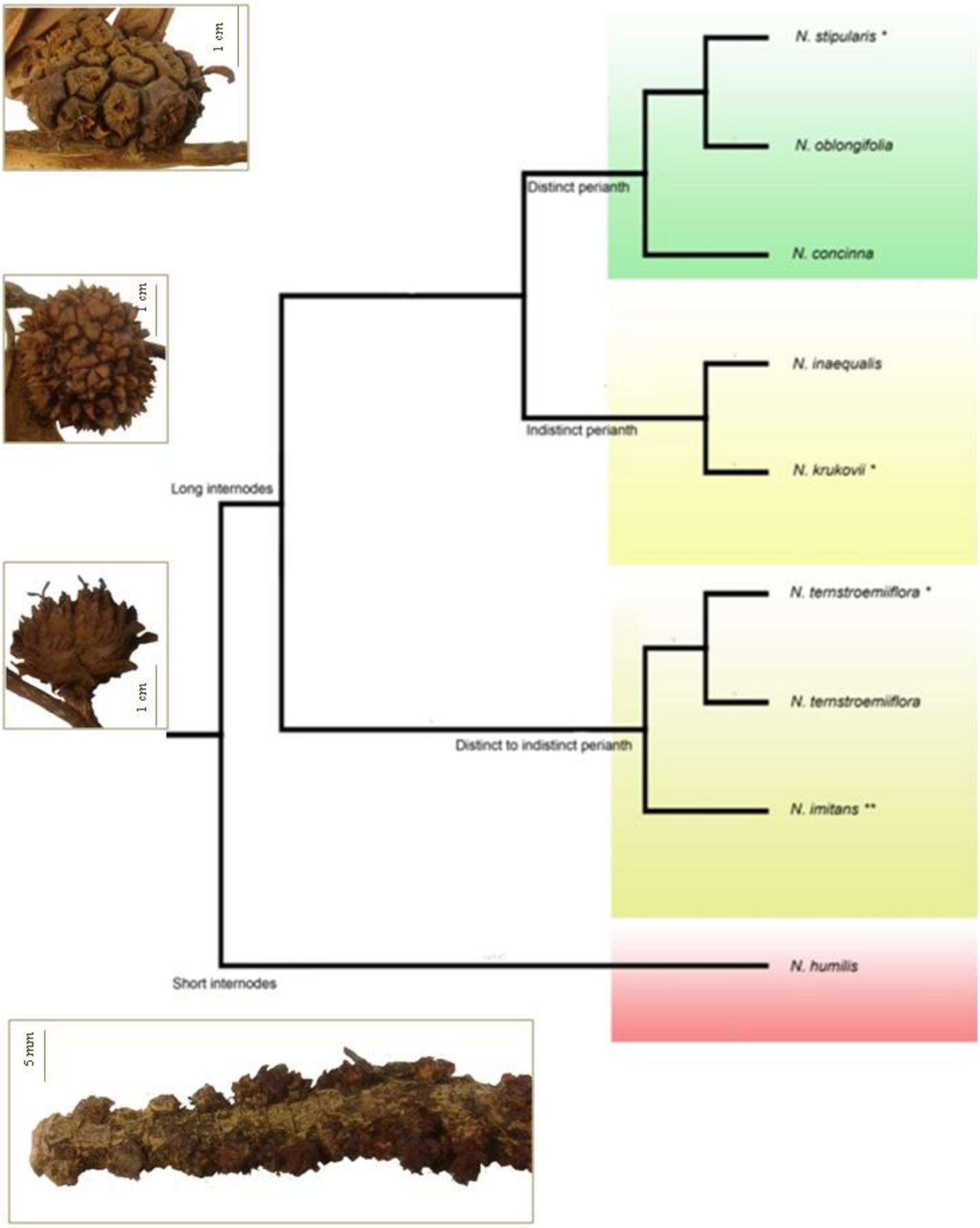

Figure 3. Bayesian consensus tree for Castilleae with focus on *Naucleopsis*. The pictures represent some of the main keys characters of group (* Image of the species are indicated).

connate perianth, parted at the apex and with free pseudo-tepals and branches with short internodes.

As well as in the combined analysis with marker FA03310 and *trnL-F*, both ML and BI corroborate with previous analyses performed by Clement & Weiblen (2009), including the uncertain position of *Perebea mollis* subsp. *mollis*.

DISCUSSION

The molecular analyses presented here constitute the first study with specific focus for *Naucleopsis*. In addition, this study also brought well-supported combined analyses with use of a new marker for this group. The EPIC marker specifically developed for the studies with *Ficus*, in this study, showed extremely useful for phylogenetic analysis at the generic level with the group studied here.

Our results strongly supported monophyly of *Naucleopsis* in all analyses. The inferred phylogeny combined reveals two main lineages (I and II) in Castilleae. Lineage I included two clades with two genera: *Castilla* and *Poulsenia*. Lineage II included four clades with five genera: *Pseudolmedia*, *Perebea*, *Maquira*, *Helicostylis* and *Naucleopsis.*

Lineage I, group A: *Poulsenia armata* clade (Fig. 1 - I, A, 1). This species was strongly supported (BP = 96, PP = 1.00) in an isolate clade with stipules and often also other parts aculeate. The genus *Poulsenia* was included previously in tribe Artocarpeae. Only after the phylogenetics analyses performed by Datwyler & Weiblen (2004) and Clement & Weiblen (2009) the genus was included in Castilleae. However, the genus *Poulsenia* shares a common characteristic to the other genera in Castilleae. *Poulsenia* also can be recognized by involucres with several series of imbricate bracts fully covering the outer receptacle surface.

Lineage I, group A: *Castilla elastica* clade (Fig. 1 - I, A, 2). This clade was strongly supported (BP = 100, PP = 1.00) in a isolate clade with stipules connate and a involucre with several series of imbricate bracts. *Castilla* genus differently from *Poulsenia* has always had a position in tribe and shares with a majority of the genera of this lineage the presence of septate wood fibres and self-pruning branches.

Lineage II, group A: *Pseudolmedia laevis* clade (Fig. 1 - II, A, 1). This clade is divided in two lineages one diversifying in *Pseudolmedia* itself with staminate flowers enclosed by involucral bracts until anthesis and pistillate inflorescences uniflorous.

Lineage II, group A: *Perebea mollis* clade (Fig. 1 - II, A, 2). This clade present staminate flowers not enclosed by involucral bracts until anthesis; pistillate inflorescences usually with more than 1 flower. Both lineages were strongly supported (BP = 100, PP = 1.00) and form groups coherent within Castilleae, both lineages also share the presence of septate wood fibres, self-pruning branches and inflorescences involucrate, but the *Perebea mollis* was paraphyletic due to the position of other species of genus. Particularly, *Perebea mollis* and *Perebea rubra* were considered within *Noyera* by several other authors (Trécul 1847; Bureau 1873; Ducke 1939). Differently than the other genus of group, *Noyera* was characterized mainly by position of ovary in relation to the receptacle. *Perebea mollis* and less often *Perebea rubra* present also leaves bullate different of the other of the genus *Perebea*. However, Berg (1969) in an attempt to reorganize the group includes *Noyera* in *Perebea*.

Lineage II, group B: *Perebea guianensis* clade (Fig. 1 - II, B). This species was hardly supported (BP = 79, PP = 0.91) in a group with staminate flowers not enclosed by involucral bracts until anthesis and pistillate inflorescences, usually, with more than one flower. This genus has always had a position in tribe and also shares with a majority of the genera of this lineage the presence of septate wood fibres, self-pruning branches and inflorescences involucrate.

Lineage II, group C: *Maquira calophylla* clade (Fig. 1 - II, C, 1). This clade is divided in two strong lineages. The first diversifying in *Maquira* with stamens straight and pistillate inflorescences with more than one flower, or if only one flower, then with free tepals.

Lineage II, group C: The second lineage (Fig. 1 - II, C, 2). diversifying in *Helicostylis* with lamina and sometimes other parts with distinctly hairy and leaf margin often denticulate. These two lineages also share the presence of septate wood fibres, self-pruning branches and inflorescences involucrate with several series of imbricate bracts fully covering the outer surface of the receptacle.

Lineage II, clade D: *Naucleopsis humilis* clade This clade was strongly supported (BP = 100, PP = 1.00) in staminate inflorescences with inner involucral bracts covering the flowers before anthesis, pistilate inflorescences with ovary entirely immersed in the receptacle and flowers with free pseudo-tepals aculeate to subulate and/or connate perinath, parted at the apex. This clade is divided in three lineages. The first lineage includes one species (Fig. 1 - II, D, 1). *Naucleopsis humilis* is treelet with pistillate flower with indistinct perianth, free pseudo-tepals subulate, branches with short internodes and stipules persistent along branches. The second lineage includes two species *Naucleopsis imitans* and *Naucleopsis ternstroemiiflora* (Fig. 1 - II, D, 2). These lineages present distinct to indistinct perianth; free pseudo-tepals acuminate to subulate or ovate, connate perianth, 4-6 parted in apex (Fig. 3). *Naucleopsis ternstroemiiflora* present perianth connate, parted at the apex and free pseudo-tepals peripherical. *Naucleopsis imitans* can present distinct to indistinct perianth, this species was considered by Berg (2001) as intermediate condition between free and connate perianth. The third lineage *Naucleopsis eucore* clade (Fig. 1 - II, D, 3) was diversified in two groups. The first group includes *Naucleopsis inaequalis* e *Naucleopsis krukovii* that presents indistinct perianth, free pseudo-tepals, acuminate to subulate. The other group in this lineage includes three species, *Naucleopsis stipularis, Naucleopsis oblongifolia* and *Naucleopsis concinna* with connate perianth, parted at the apex.

The high level of polymorphism in *Naucleopsis* led various authors to propose different classifications for the group. *Naucleopsis* has a historic of classifications marked by several controversal circumscription proposals (Bureau 1873; Pittier 1912; Mildbraed 1927; Macbride 1931; Ducke 1922, 1939; Berg 1972, 2001). Among the main proposals as the *Ogcodeia* (represented by *N. humilis*, *N. imitans*, *N. ternstroemiiflora* and *N. krukovii*) and *Palmolmedia* (represented by *N. stipularis*), are not supported by molecular analyses. The species in this group varies considerably in the size of the leaves, and the mainly characters of the pistillate inflorescences and infructescences.

Because of these issues, *Naucleopsis* has been regarded as a difficult taxonomically genus, however, all the separate or combined analyses corroborate with a clade strongly supported.

CONCLUSION

It is very important and sometimes extremely difficult to find a molecular marker, which would meet with easy and fast assay combined to good results. Our analyses represent a first step towards an understanding of the molecular phylogeny of Castilleae, more specifically of *Naucleopsis.* Ours morphological studies and the analyses prepared here indicated that the involucre with several series of imbricate bracts fully covering the outer surface of the receptacle is considered the mainly common characteristic to all neotropical genus of the tribe. However, we consider that a global review of the tribe results in a better understanding of Castilleae and of the need of reestablishing *Noyera.*

We also believe that the use of new markers EPIC to this group could be used for excellent effect in other future analysis in Castilleae.

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Appendix I. Specimens, voucher and GenBank accession number for taxa included in this study.

Species, voucher specimen (Herbarium), GenBank accession for nuclear FA03310 and 26S / plastid *trnL-F*. (GenBank numbers will be added after acceptance of manuscript)

Taxa	**Voucher/ GenBank accession**	**Markers**
Ingroup		
Naucleopsis caloneura (Huber) Ducke	AY686819	26S
Naucleopsis concinna (Standl.) C.C. Berg	A. Quinet 1198	FA03310 and *trnL-F*
Naucleopsis guianensis (Mildbr.) C.C. Berg	AY686828	26S
Naucleopsis humilis C.C. Berg	A. Santos 163	FA03310 and *trnL-F*
Naucleopsis imitans (Ducke) C.C. Berg	C. C. Berg 479	FA03310 and *trnL-F*
Naucleopsis inaequalis (Ducke) C.C. Berg	H. Medeiros 388	FA03310 and *trnL-F*
Naucleopsis krukovii (Standl.) C.C. Berg	A. Santos 202	FA03310 and *trnL-F*
Naucleopsis krukovii (Standl.) C.C. Berg	AY686784	26S
Naucleopsis naga Pittier	AY686841	26S
Naucleopsis oblongifolia (Kuhlm.) Carauta	A. Santos 194	FA03310 and *trnL-F*
Naucleopsis ternstroemiiflora (Mildbr.) C.C. Berg	A. Santos 163	FA03310 and *trnL-F*
Naucleopsis ternstroemiiflora (Mildbr.) C.C. Berg	H. Medeiros 486	FA03310 and *trnL-F*
Naucleopsis ternstroemiiflora (Mildbr.) C.C. Berg	AY686821	26S

Naucleopsis stipularis Ducke	A. Santos 154	FA03310 and *trnL-F*
Naucleopsis ulei subsp. *ulei* (Warb.) Ducke	AY686791	26S
Castilla elastica Sessé	AF501603	*trnL-F*
Castilla elastica Sessé	FJ917062	*trnL-F*
Castilla elastica Sessé	AY686823	26S
Castilla elastica Sessé	AY686830	26S
Antiaris toxicaria Lesch.	AY686858	26S
Antiaropsis decipiens K. Schum.	AY686834	26S
Helicostylis scabra (J.F. Macbr.) C.C. Berg	A. Santos 164	FA03310 and *trnL-F*
Helicostylis pedunculata Benoist	AY686816	26S
Helicostylis tomentosa (Poepp. & Endl.) Rusby	AY686839	26S
Helicostylis tomentosa (Poepp. & Endl.) Rusby	A. Santos 174	FA03310 and *trnL-F*
Helicostylis turbinata C.C. Berg	A. Santos 153	FA03310 and *trnL-F*
Maquira calophylla (Poepp. & Endl.) C.C. Berg	A. Santos 172	FA03310 and *trnL-F*
Maquira costaricana (Standl.) C.C. Berg	AY686801	26S
Mesogyne insignis Engl.	AY686840	26S
Perebea angustifolia (Poepp. & Endl.) C.C. Berg	A. Santos 198	FA03310 and *trnL-F*
Perebea angustifolia (Poepp. & Endl.) C.C. Berg	AY686843	26S
Perebea guianensis subsp. *guianensis* Aubl.	H. Medeiros 488	FA03310 and *trnL-F*

Perebea guianensis subsp. *hirsuta* C.C. Berg	A. Santos 195	FA03310 and *trnL-F*
Perebea humilis C.C. Berg	AY686842	26S
Perebea longipedunculata C.C. Berg	AY686826	26S
Perebea mollis (Poepp. & Endl.) Huber	A. Santos 198	FA03310 and *trnL-F*
Perebea mollis (Poepp. & Endl.) Huber	A. Santos 160	FA03310 and *trnL-F*
Perebea rubra (Trécul) C.C. Berg	AY686844	26S
Perebea xanthochyma H. karst.	AY686857	26S
Pseudolmedia laevis (Ruiz & Pav.) J.F. Macbr.	A. Santos 200	FA03310 and *trnL-F*
Pseudolmedia laevigata Trécul	AY686845	26S
Pseudolmedia macrophylla Trécul	AY686792	26S
Pseudolmedia macrophylla Trécul	A. Santos 197	FA03310 and *trnL-F*
Poulsenia armata (Miq.) Standl.	JQ341920	*trnL-F*
Poulsenia armata (Miq.) Standl.	EU422992	26S
Sparattosyce dioica Bureau	AY686856	26S
Outgroup		
Ficus benjamina L.	AF501606	*trnL-F*
Ficus insipid Willd.	AF165390	26S
Ficus maxima Mill.	JQ341920	FA03310
Ficus obtusifolia Kunth	JQ341919	FA03310
Maclura tinctoria (L.) D.Don ex Steud.	A. Santos 106	FA03310 and *trnL-F*
Sorocea guilleminiana Gaudich.	A. Santos 163	FA03310 and *trnL-F*
Cannabis sativa L.	AY686773	26S

Table 1. Best-fitting models and parameter values for combined plastid (pt) + nuclear (nr) markers datasets in this study.

Base frequencies	Combined pt trnL-F + nr FA03310
A	0.2673
C	0.2203
G	0.2235
T	0.2889
Model selected (hLRT)	HKY + G

Table 2. Number of accessions sequenced for each marker and combined plastid (pt) + nuclear (nr) markers, character statistics, tree statistics for the maximum likelihood (ML) analyses.

Parameters	Markers	pt*trnL-F*	nrFA03310	nr*26S*	Combined pt*trnL-F*+ nrFA03310
Number of accessions (ingroup/outgroup)		26 (23/3)	24 (20/4)	27 (24/3)	28 (23/5)
Number of characters (bp)		729	741	1031	1470
Consistency index		not show	not show	not show	0.4944
Retention índex		not show	not show	not show	0.8409

Capítulo 2 – Estudos taxonômicos

Parte 1

A new species of *Naucleopsis* (Moraceae) from Brazilian Amazon and the reinstatement of *Naucleopsis insculptula*

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Abstract

Naucleopsis sp1 (Moraceae), a new species, endemic to the Brazilian Amazon is described and illustrated in this paper. This species has been identified incorrectly as *N. caloneura* for a long time. The tubular shape of the perianth of pistillate flower and fruit, the narrowly oblong shape of the leaves and the filament connate at the base, differs from other species. This new species shows morphological similarities with *N. caloneura* and *N. insculptula*, the latter previously treated as a synonym of *N. caloneura* is reestablished in this paper.

Resumo

Naucleopsis sp1 (Moraceae), uma nova espécie, endêmica da Amazônia brasileira é descrita e ilustrada neste trabalho. Esta espécie tem sido identificada incorretamente como *N. caloneura* por um longo tempo. A forma tubular do perianto da flor pistilada e fruto, a forma da folha estreitamente oblonga e o filete conado na base, difere *N. sp1* de outras espécies. Esta nova espécie mostra similaridades morfológicas com *N. caloneura* e *N. insculptula*, esta última anteriormente tratada como sinônimo de *N. caloneura* é restabelecida neste trabalho.

Key words: Brazilian Amazon, Castilleae, Conservation, Diversity, Taxonomy

Introduction

Naucleopsis Miq., is the largest genus of the tribe Castilleae C.C.Berg. The genus was established by Miquel (1853), who described *N. macrophylla* in *Flora Brasiliensis. Naucleopsis* is a Neotropical genus and ranges from Honduras to the State of Rio de Janeiro, in Brazil. One of the greatest diversity of Brazilian species occurs within the Amazon region, mainly in “Terra Firme” forest at low altitudes. In Brazil, occur 15 species (Romaniuc Neto *et al.* 2015).

The genus is characterized by dioecious, rarely monoecious, trees. Leaves coriaceous to chartaceous, always entire and mostly glabrous. Stipules fully amplexicaul, free, caducous or persistent on apex of stems. Staminate inflorescences often 4-10 together, inner involucral bracts covering the flowers before anthesis; pistilate inflorescences solitary, ovary entirely immersed in the receptacle.

Twenty three species have been described within this group of genera (Berg 2001, Berg & Homeier 2010). Some of them have been transferred one or more times owing to the different opinions about the delimitation of the genera (Bureau 1873, Pittier 1912, Mildbraed 1927, Ducke 1939, Berg 1969, 1972, 1977, 2001). The genus is rather poorly represented in herbaria. Several species are only known by one or a few collections and, furthermore, the last taxonomic study for the group is related to the revision of the tribe made by Berg (1972, 1977).

As part of a taxonomic revision of the genus, this new species was discovered. It was possible too, after the analyzes of all the type materials to reestablish *Naucleopsis insculptula* Ducke. The new species shows morphological similarities with *N. caloneura* and *N. insculptula*, these three species are morphologically very close and not easy to distinguish. These conclusions have been drawn after morphological analysis of specimens of *Naucleopsis* from 16 herbaria (B, BG, BM, CUZ, EAFM, IAN, INPA, K, L, LABEV, MG, NY, P, RB, SP, SPF, UFACPZ, UEC and US), as well as voucher samples acquired from multiple field trips within Brazil.

Taxonomic Treatment

Naucleopsis sp1 Al.Santos & Romaniuc, *sp nov*. Fig. 1

Type:—BRAZIL. Amazonas: Manaus, Estação Experimental de Silvicultura Tropical, 1997, *M. C. Lemos 174* (holotype INPA!).

Diagnosis:—Folia oblonga; lamina supra glabra, subtus scabra. Stamina filamentis basi connatis; perianthum et fructum tubiforme.

Tree (6-)10-22 m tall; latex white to yellow. Leafy twigs 4-5(-9) mm thick, brownish puberulous to velutinous; lenticels conspicuous. Leaves narrowly oblong, 19-39 cm long, (5.5-)6.5-9.5 cm broad, coriaceous, glabrous above, scabrous beneath, acute to obtuse at the base; acute-acuminate apex; margin mostly semi-revolute; secondary veins 20-28 pairs, prominent beneath, often straight to the margin; petioles 1.5-3 cm long, 3-4 cm broad, brown puberulous to velutinous, canaliculated; stipules 1-1.5 cm long, brown-velutinous. Staminate inflorescences 4-10 together, 4-8 mm in diam.; peduncle 3-6 mm long, puberulous to pubescent; involucre with ovate puberulent to pubescent bracts. in 3 series; perianth 1-2 mm high; tepals 3-5, free; stamens 3-4; filaments 0.5-0.8 mm long, connate at the base; anthers 0.5-0.8 mm long. Pistilate inflorescences 1-3 together, up to 10 mm diam.; sessile; involucre with ovate puberulous to pubescent, smooth bracts, in 4-6 series; perianth 2-4 mm high, connate, 4-6 parted at the apex, pubescent to velutinous; style 0.5-1.5 cm long, stigma filiform. Infructescences globoid, 1.8-3 cm diam.; fruiting perianth 0.5-1.5 cm high, tubular.

Distribution and Ecology:—It is known only from Brazilian Amazon, in the states of Amazonas and Pará, in terra firme forest, at low elevation up to 125 m.

Etymology:—The epithet refers to the tubular format of the perianth of the pistillate flower and fruit.

Additional specimens examined:—BRAZIL. Amazonas: Manaus, ca. 90 km NNE Manaus, Distrito Agropecuário da Suframa, 02º24’26”-02º25’31”S, 59º43’40”-59º45’50”W, 10 November 1989, *P. Kukle 18* (K, SP, INPA), 21 November 1990, *M. A. Freitas et al. 455* (INPA), *A. A. Oliveira et al. 225* (INPA, SPF), BR 174, Fazenda Dimona, 02º19’S 60º05’W, *P.A.C.L. Assunção s.n*. (INPA), Estrada Manaus-Caracaraí km 39, Reserva Experimental de Silvicultura Tropical, 14 November 1977, *J. Ribamar & J. Ramos 212* (INPA), Estrada Itacoatiara-Manaus km 31, 09 November 1963, *E. Oliveira 2933* (IAN), Estrada Manaus-Itacoatiara km 99, 19 September 1965, *W. Rodrigues & Loureiro 7132* (INPA). Pará: Oriximiná, Área de Mineração Rio Norte, Platô da Serra Sacazinho, 40 km ao Sul da vila de mineração, 01º45’S 56º30’W, *C. A. Cid Ferreira 9506* (INPA, K, MG, RB, UFACPZ), BR 163, Cuiabá-Santarém, km 1221, 20. November. 1997, *G.T. Prance et al. P 25594* (MG, RB).

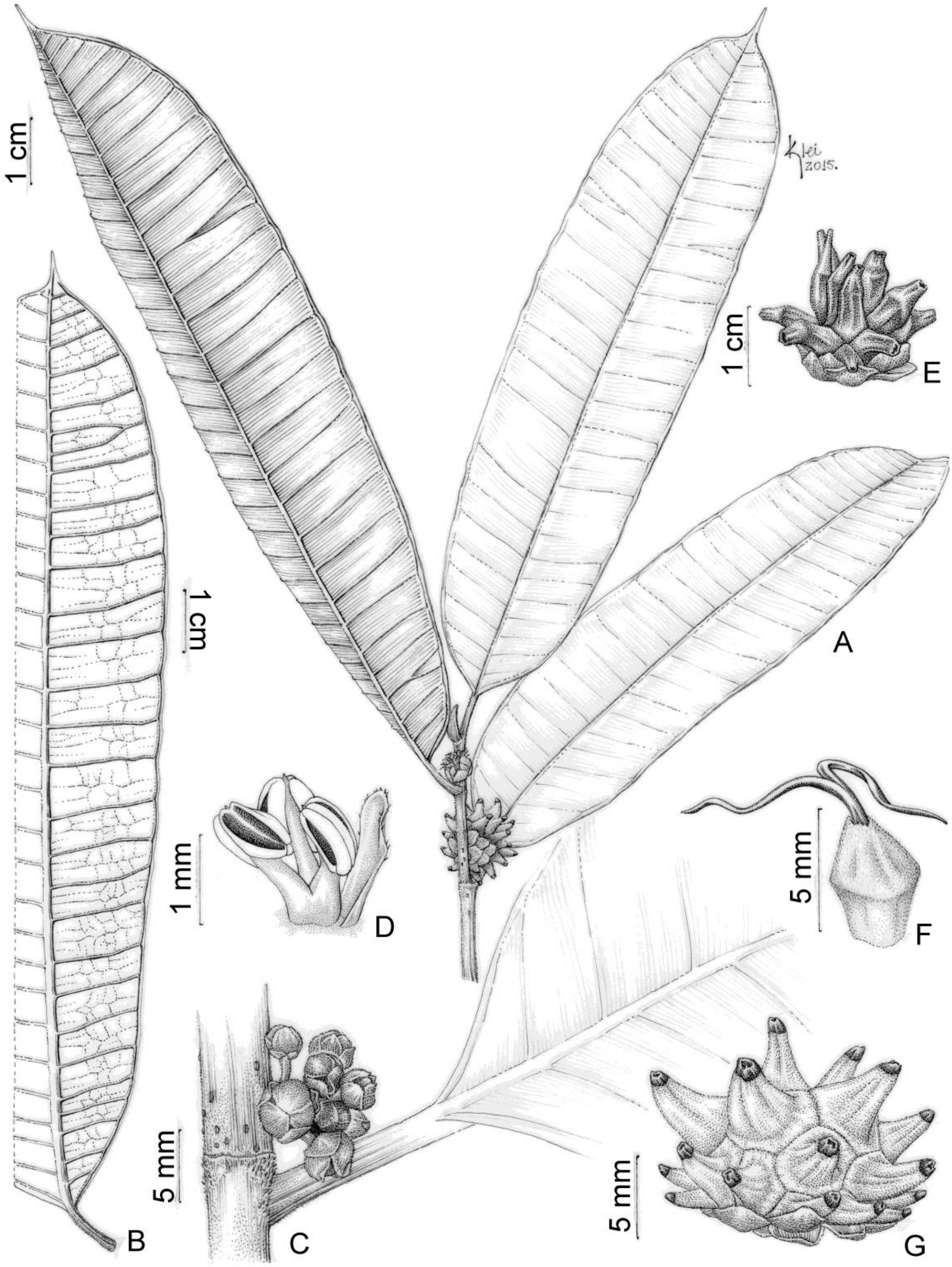

FIGURE 1. *Naucleopsis sp1.* **A.** Habit. **B.** Detail of the lower surface of the lamina. *M. C. Lemos 174* (INPA 202218) **C.** Staminate inflorescences 4-10 together. *M. A. Freitas 455* (INPA 190596) **D.** Staminate flower. *W. Rodrigues 7132* (INPA 15794) **E.** Young infructescence. *P. Kukle 18* (SP 319446) **F.** Pistillate flower. *C. A. Cid Ferreira 9506* (K) **G.** Ripe infructescence. *M. C. Lemos 174* (INPA 202218).

TABLE 1. The major characters separating *N. sp1*, *N. caloneura* and *N. insculptula*

	N. sp1	*N. caloneura*	*N. insculptula*
Leaf form	narrowly oblong	lanceolate	lanceolate
Leaf indument	scabrous beneath	glabrous beneath	scabrous beneath
Filaments	connate at the base	connate at the base	free
Perianth pistillate flower	tubular	Deltoid	ovate

Discussion and reinstatement of *Naucleopsis insculptula*:— In Flora Neotropical Monograph, Berg (1972) treated *N. insculptula* as synonym of *N. caloneura* (Huber) Ducke arguing that the species varies considerably in the indument of the twings, the size of the leaves, and the characters of the pistillate inflorescences and infructescences. However, the analyzes of both type materials enabled us to reestablish *N. insculpula* as distinct species from *N. caloneura.* The main characteristics that distinguish them are related to the structure of the pistillate flower and infructescence and form, texture, indument leaf. *Naucleopsis caloneura* has lanceolate, glabrous beneath leaves and ovate fruiting perianth. To contrast, leaves in *N. insculptula* are scabrous beneath and ovate fruiting perianth. Both species, *N. caloneura* and *N. insculptula*, are sympatric with the new species, *N. sp1*.

For these characteristics we reestablish *N. insculptula* in this paper. Both species, *N. caloneura* and *N. insculptula*, showed affinities with *N. sp1*. However, the morphology of the new species showed deviates distinctly those and others in the genus mainly by the tubular shape of the perianth of pistillate flower and fruit.

Conservation:—According to the IUCN red list categories (IUCN 2015), *N. sp1* is considered endangered, EN B1a,b(iii), because of the limited occurence, known only from Brazilian Amazon, in the states of Amazonas and Pará.

Acknowledgements

This study was financially supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). We are grateful to the graduation program on Plant Biodiversity and Environment from Instituto de Botânica of São Paulo.

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Parte 2

Two new species of *Naucleopsis* (Moraceae: Castilleae) from South America

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Abstract—Two new species of *Naucleopsis* (Moraceae: Castilleae) from South America are described, illustrated and compared with closely related species. *Naucleopsis oblata* and *N. tomentosa* are presumably closely related to *N. krukovii* (Standl.) C.C.Berg. Both new species were found exclusively in Amazon rainforest. Comments on taxonomy and an identification key to the related species were provided.

Resumo—Duas novas espécies de *Naucleopsis* (Moraceae: Castilleae) da América do Sul são descritas, ilustradas e comparadas com espécies proximamente relacionadas. *Naucleopsis oblata* e *N. tomentosa* são presumivelmente proximamente relacionadas à *N. krukovii*. Ambas novas espécies foram encontradas na floresta Amazônica. Comentários taxonômicos e uma chave de identificação para as espécies foram apresentados.

Keywords—Amazon rainforest, Castilleae, Conservation, Diversity, Neotropics, Taxonomy.

INTRODUCTION

Molecular phylogenies (Sytsma et al., 2002, Datwyler & Weiblen; 2004; Clement & Weiblen, 2009), have indicated the taxonomic affiliation of the genus within the Castilleae and Moraceae. The tribe differs from most other Moraceae by unisexual involucrate inflorescences with discoid to globoid receptacles, self-pruning branches, septate wood fibers, and Cook's model of tree architecture (Berg 1977). *Naucleopsis* Miq. is the largest genus of Castilleae. Since the most recent revision on the group (Berg 1972, 1977) others studies followed this one showed the discovery of new species (Berg 2001, Berg & Homeier 2010). Currently, twenty three species have been described within this genus.

Naucleopsis is a Neotropical genus and ranges from Honduras to the State of Rio de Janeiro, in Brazil. The greatest diversity of species occurs within the Amazon region, mainly in lowland tropical moist forest. It is recognized by being usually trees, dioecious, rarely monoecious. Leaves coriaceous to chartaceous, always entire and mostly glabrous. Stipules fully amplexicaul, free, caducous or persistent on apex of stems. Staminate inflorescences often up to 4 together, inner involucral bracts covering the flowers before anthesis. Pistillate inflorescence mostly solitary, ovary entirely immersed in the receptacle.

As part of a taxonomic revision of the genus and after intensive and systematic studies about the group the authors establish here these two new species, *Naucleopsis oblata* and *N. tomentosa*. Both new species are similar to *N. krukovii*.

In this study, we describe the two new species of *Naucleopsis* native to the Amazon region: *N. oblata* and *N. tomentosa* and we also provide comments on taxonomy and conservation for both new species.

.

MATERIAL AND METHODS

The new species were identified and proposed after morphological analysis of specimens of *Naucleopsis* from 16 herbaria: B, BG, BM, CUZ, EAFM, IAN, INPA, K, L, LABEV, MG, NY, P, RB, SP, SPF, UFACPZ, UEC and US (Herbarium abbreviations follow Thiers, 2015). All collections and type specimens were examined using a stereomicroscope and the specialized literature on the family was consulted. The terminology on the shapes of leaves and other organs follows Hickey (1979) and Radford et al. (1974) and for inflorescences follows Weberling (1989), Bell (1993) or terminology adopted by Berg (1972, 2001).

Naucleopsis sp2 Al. Santos & Romaniuc, sp. nov. —TYPE: BRAZIL. Amazonas, Manaus, BR 174, km 159, Manaus-Caracaraí Road, 20 Sept 1974, *G.T. Prance et al. 22716* (holotype: INPA!).

Diagnosis— *Naucleopsis sp2* is similar to *Naucleopsis krukovii*. However, this new species presents the pistillate flower with connate perianth, oblate.

Tree (06-)10-16 m tall; latex colorless. Leafy twigs peeling to ridged, 3-4 mm thick, brownish glabrous to puberulous; lenticels conspicuous. Leaves lanceolate, 15-19 cm long, 4-5.5 cm broad, coriaceous, both faces glabrous; acute to attenuate at the base; acute-acuminate apex; margin entire; secondary veins 13-15 pairs, prominent beneath, curved-arched to the margin; petioles 0.6-1 cm long, brown glabrous to pubescent, canaliculated; stipules 0.5-1.0 cm long, brownish puberulent to pubescent. Pistillate inflorescences solitary, up to 2 cm diam.; sessile; involucre with ovate, puberulous to pubescent bracts, the inner oblong apex, in 4-5 series; perianth 1-2 mm high, connate, puberulous to pubescent, stigma not seen. Infructescences globoid, 4-5 cm diam.; fruiting perianth 2-3 mm high, oblate.

Additional specimens examined—BRAZIL: Amazonas, Estrada Manaus-Caracarí, BR174, km 159, Manaus-Caracaraí Road, 20 Sept 1974, *G.T. Prance et al. 22713* (K). PERU. Cusco, Distrito Echarate, Kepashiato, 12º41’00”S, 73º15’45”W, 20 March 2007, *L. Valenzuela et al. 9295* (BG, MO).

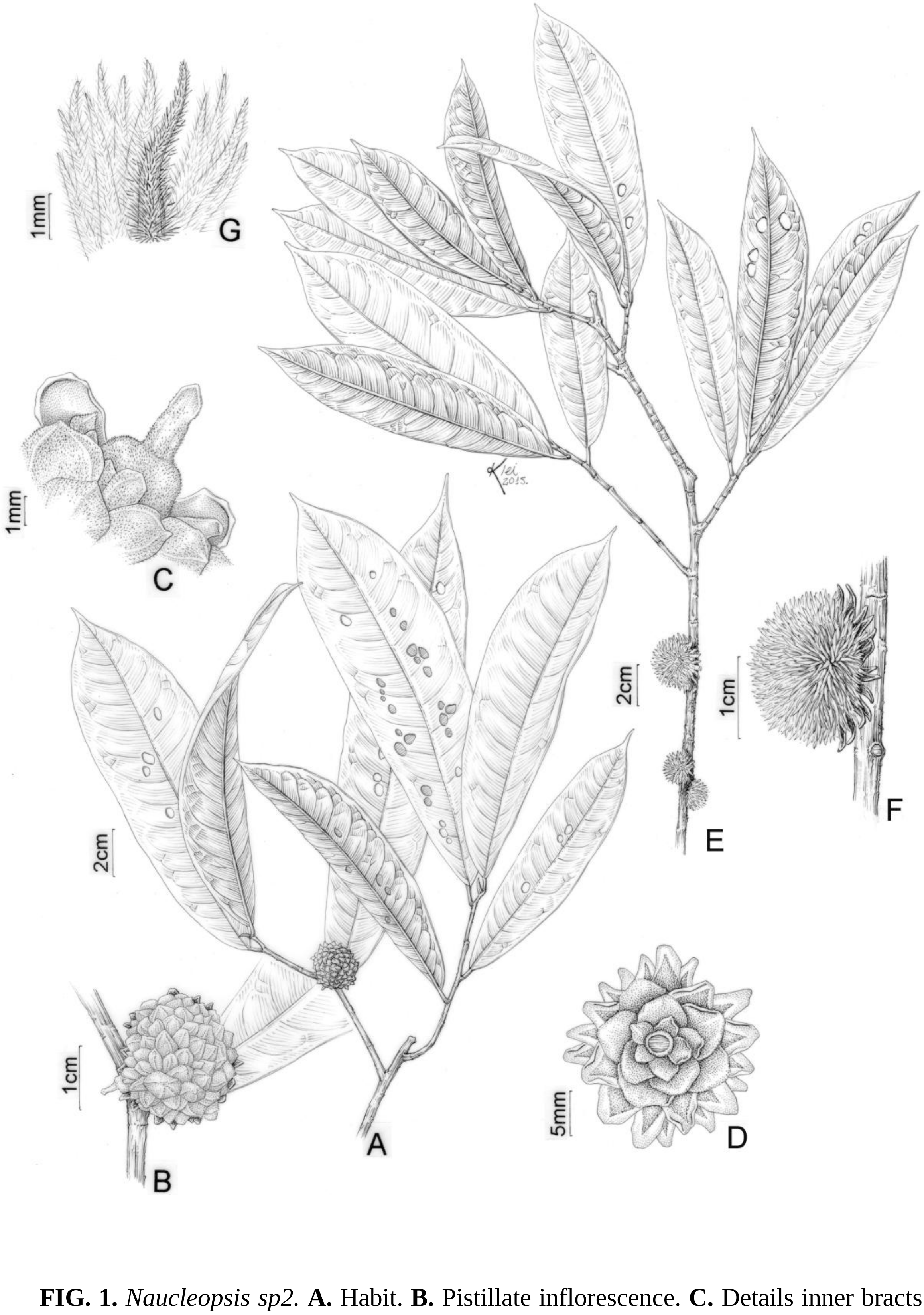

FIG. 1. *Naucleopsis sp2.* **A.** Habit. **B.** Pistillate inflorescence. **C.** Details inner bracts. *Naucleopsis sp3.* **D.** Details involucre of imbricate bracts. **E.** Habit. **F.** Pistillate inflorescence. **G.** Details free pseudo-tepals.

***Distribution*—** It is known only from Brazilian Amazon and Peru, in terra firme forest, at an elevation up to 1200 m.

Phenology—Specimens of *Naucleopsis sp2* were collected with flower in September and with fruit in March and September.

***Etymology*—**The epithet refers to morphological of fruiting perianth, oblate.

***Notes*—** Morphologically, this species shows similarities with *N. krukovii* due to the leaves greenish, veins green-yellowish beneath when dried and lamina with perforations, but *N. sp2* is distinguished especially by structure of its pistillate flower. In *N. sp2* the perianth is oblate and the tepals are connate, differently than in *N. krukovii*, which presents the perianth with free pseudo-tepals.

The lamina with perforations, probably by being infected by a fungus causing circular warty spots becoming holes can also be seen in other groups of Moraceae, such as *Pseudolmedia*. However, others species of *Naucleopsis* can present lamina with perforations, such as *N. francisci* C.C. Berg & Homeier

Naucleopsis sp3 Al.Santos & Romaniuc, sp. nov. TYPE—: ECUADOR. Morona Santiago, Puerto Morona, rio Morona, 02º52’00”S, 77º41’00”W, 30 Sept 1975, *E.L. Little et al. 501* (holotype: US!)

***Diagnosis*—** *Naucleopsis sp3* is similar to *Naucleopsis krukovii*. However, this new species presents the pistillate flower with tomentose free pseudo-tepals.

Tree (8-)10-20 m tall; latex white. Leafy twigs peeling, 3-4 mm thick, greyish to brownish glabrous; lenticels conspicuous. Leaves lanceolate, 12-21 cm long, 3-6.5 cm broad, coriaceous, both faces glabrous, puberulent, acute to obtuse at the base; acute-acuminate apex; margin entire; secondary veins 10-13 pairs, prominent beneath, curved to the margin; petioles 0.6-1 cm long, brown, pubescent, canaliculated; stipules 0.5-0.6 cm long, brownish, tomentose. Pistillate inflorescences solitary, up to 1.5 cm diam.; sessile; involucre with ovate to deltoid, puberulous tomentose to velutinous bracts, in ca 4-5 series; indistinct perianth, free pseudo-tepals 0.4-0.6 cm high, subulate, tomentose to velutinous; stigma not seen. Infructescences globoid, 2-2.5 cm diam.; indistinct fruiting perianth, fruiting pseudo-tepals 2-3 mm high, subulate.

***Additional specimens examined*—** BRAZIL: Rondonia, Rio Jamari, Cachoeira de Santa Cruz, 28 Jun 1965, *J.M. Pires 9955* (IAN), *J.M. Pires 9956* (IAN).

***Distribution*—**Brazil and Ecuador, in terra firme forests, at an elevation up to 120 m.

***Phenology*—**Specimens of *Naucleopsis sp3* were collected in flower and fruit June and September.

***Etymology*—** The epithet refers to the tomentose indument of the fruiting free perianth.

TABLE 1. The major characters separating *N. sp2*, *N. sp3*, *N. krukovii* and *N. humilis*.

Species Character	*N. sp2*	*N. sp3*	*N. krukovii*	*N. humilis*
Fruiting perianth	Connate, oblate	Free pseudo-tepals, subulate	Free pseudo-tepals, subulate	Free pseudo-tepals, subulate
Perianth indument	Puberulous to pubescent	Tomentose to velutinous	Glabrous to puberulent	Glabrous to puberulent
Leaf form	Lanceolate	Lanceolate	Oblong to lanceolate	Obovate

Notes—As with *N. sp2*, morphologically this new species also shows similarities with *N. krukovii* due to the leaves greenish, veins green-yellowish beneath when dried and lamina with perforations, but *N. sp2* is distinguished mainly by indument tomentose of indistinct perianth with free pseudo-tepals.

Acknowledgments. The authors would like to thank the following herbaria for use of their collections and facilities: BG, K. This study was financially supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). We are grateful to the graduation program on Plant Biodiversity and Environment from Instituto de Botânica SP.

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Parte 3

Synopsis of *Naucleopsis* Miq. (Moraceae)

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Manuscript to be submitted for publication in the Phytotaxa Monograph

Table of contents

Abstract

A synopsis of the genus _Naucleopsis_ (Moraceae) is presented in this work. The genus is the largest in number of species of the tribe Castilleae and ranges from Honduras to the State of Rio de Janeiro, in Brazil. Our work was based in the analysis of taxonomic literature, herbarium specimens and fieldwork. This work resulted in 31 species: _N. acreana,_ _N. caloneura, N. capirensis, N. chiguila, N. concinna, N. francisci, N. glabra, N.guianensis, N. herrerensis, N. humilis, N. imitans, N. inaequalis,_ **_N. insculptula,_** _N. jamariensis, N. krukovii, N. macrophylla, N. meridionalis, N. naga, N. oblongifolia,_ **_N. pauciflora_**, _N. pseudonaga, N. riparia, N. stipularis, N. straminea, N. ternstroemiiflora, N. ulei, N. velutina, N. sp1*, N. sp2*, N. sp3*, N. sp4*_ among them, four are new for the science (*), one new combination and one with new status (underlined) and two species were reestablished (in bold). This paper presents a key to the species, descriptions, synonyms, illustrations diagnostic characters, as well as comments on the geographic distribution and ecology of each species are presented.

Key words: Castilleae, Diversity**,** Neotropics, New species, Taxonomy

Resumo

Uma sinopse do gênero *Naucleopsis* é apresentada neste trabalho. O gênero é o maior em número de espécies da tribo Castilleae e ocorre de Honduras até o estado do Rio de Janeiro, no Brasil. Nosso trabalho foi baseado na análise da literatura taxonômica, espécimes de herbários e trabalho de campo. Este trabalho resultou em 31 espécies: *N. acreana*, *N. caloneura*, *N. capirensis*, *N. chiguila*, *N. concinna*, *N. francisci*, *N. glabra*, *N.guianensis*, *N. herrerensis*, *N. humilis*, *N. imitans*, *N. inaequalis*, ***N. insculptula***, *N. jamariensis*, *N. krukovii*, *N. macrophylla*, *N. meridionalis*, *N. naga*, *N. oblongifolia*, ***N. pauciflora***, *N. pseudonaga*, *N. riparia*, *N. stipularis*, *N. straminea*, *N. ternstroemiiflora*, *N. ulei*, *N. velutina*, *N. sp1**, *N. sp2**, *N. sp3**, *N. sp4** dentre estas, quatro são novas para a ciência (*), uma nova combinação e um novo status (sublinhado) e duas reestabelecidas (em negrito). Apresentamos uma chave de identificação das espécies, descrições, sinônimos, ilustrações, bem como comentários de distribuição geográfica e ecologia de cada espécie.

Palavras chave: Castilleae, Diversidade, Neotropico, Nova espécie, Taxonomia

Introduction

Naucleopsis Miq. is a neotropical genus of Moraceae included in tribe Castilleae C.C. Berg subtribe Castillineae W.L. Clement & Weiblen (Berg 1977, Clement & Weiblen 2009). Recognized by stipules fully amplexicaul, leaves always entire, mostly glabrous, staminate inflorescences with involucral bracts covering the flowers before anthesis, presence of pseudo-tepals in the perianth of pistilate flowers and ovary entirely immersed in the receptacle; flowers with distinct to indistinct perianth. The genus ranges from Honduras to the State of Rio de Janeiro, in Brazil (Berg 1977, 2001).

Naucleopsis was established by Miquel (1853), who described *N. macrophylla* in the *Flora Brasiliensis.* Bureau (1873) recognized a group of specimens morphologically different of the *Naucleopsis* species described by Miquel. Bureau, based on the pistillate inflorescences of Spruce 2793, proposed a new genus - *Ogcodeia*. Afterwards, Bentham (1880) does not agree with Bureau concept and proposed to essemble *Ogcodeia* and *Naucleopis* with *Noyera* Trécul. Later, Pittier (1909) complemented the Miquel's description of *N. macrophylla* with details obtained from *Ogcodeia* and described a new species - *N. naga*. Only in 1927, Mildbraed recognized *Ogcodeia* as a distinct genus of *Naucleopsis.* According to him, *Ogcodeia* presents processes, called pseudo-bracteoles, which do not show any distinct correlation with the pistils, in contrast to *Naucleopsis*.

At the same time, Warburg (1907) established the genus *Acanthosphaera* with *A. ulei*. Ducke (1922) does not agree with Warburg (1907) and united *Acanthosphaera* with *Naucleopsis.* In 1931, Macbride transferred this genus to *Ogcodeia.*

Ducke (1939) published a synopse to tribe Olmedieae Trécul. In this study, the author organized the tribe in 13 genera (*Brosimopsis*, *Pseudolmedia*, *Castilla*, *Olmedia*, *Helicostylis*, *Perebea*, *Noyera*, *Olmediophaena*, *Olmedioperebea*, *Naucleopsis*, *Ogcodeia*, *Palmolmedia* and *Acanthosphaera*). The author also considered *Ogcodeia* as independent genus of *Naucleopsis*, similarly to Bureau (1873) and Mildbraed (1927). Ducke (1939), recognized that the similarities between *Naucleopsis* and *Ogcodeia* were restricted to characteristics of the inflorescence pistillate. In addition, Ducke proposed a new genus for the group (*Palmolmedia*) based in the specimens of *Naucleopsis stipularis*, transferring it to the new genus and reestablished the genus *Acanthosphaera*.

After Ducke (1939), only Berg (1969, 1972, 1977, 2001) published studies in Moraceae were included, in same of this, the Castilleae tribe.

Just the present, because all of these issues, Castilleae has been regarded as a taxonomically difficult tribe, and this has led to great variation in the number of species recognized within each genus over time. Especially in the case of *Naucleopsis*, that varies considerably in the size of the leaves, and mainly in the characters of the pistillate inflorescences and infructescences, was divided into others three genera (*Acanthosphaera*, *Ogcodeia* and *Palmolmedia*) creating troubles among the taxonomy history of the genus.

Twenty three species have been described within of *Naucleopsis* (Berg 2001, Berg & Homeier 2010). Some of them have been transferred one or more times owing to the different opinions about the delimitation of the genera (Bureau 1873, Pittier 1912, Mildbraed 1927, Ducke 1939, Berg 1969, 1972, 1977, 2001).

Naucleopsis is rather poorly represented in herbaria. Several species are only known by one or a few collections and, furthermore, the last taxonomic study for the group is related to the revision of the tribe made by Berg (1972, 1977, 2001). Recently has been published several molecular phylogenies for the tribes of Moraceae (Sytsma *et al.* 2002, Datwyler & Weiblen 2004, Clement & Weiblen 2009), but the genus is poorly represented too. It was also noted the need to intensive taxonomic studies to contribute to the phylogenetics researches for the genus.

Material and Methods

The revision was based on a survey of specimens deposited in the following herbaria (Thiers 2015): B, BG, BM, CUZ, EAFM, IAN, INPA, K, L, LABEV, MG, NY, P, RB, SP, SPF, UFACPZ, UEC and US. Fieldwork was realized in several Brazilian municipalities (AC: Rio Branco; AM: Manaus, Presidente Figueiredo; PA: Belém, Benevides, Capanema, Goianésia, Novo Repartimento, Santa Luzia do Pará, Tailândia; RJ: Rio de Janeiro) and Peru (Machu Picchu, Mandor, Santa Teresa). The terminology on the shapes of leaves and other organs follows Hickey (1979) and Radford *et al.* (1974) and for inflorescences follows Weberling (1989), Bell (1993) or terminology adopted by Berg (1972, 2001). Species delimitation was based on the comparison of type material, including digital images and original descriptions with specimens analyzed. For each species, arranged in alphabetical order, complete synonymy is given. Most specimens types have been examined for this study and these are followed by a “!”.For better understand of the morphological variation within the genus, illustrations of some specimens were performed using a stereomicroscope with attached camera lucida.

Scanning electron micrographs (SEM) were obtained from the herbaria voucher for the preparation of this work. We selected parts of the leaves, bracts and flowers of representatives of all neotropical tribe. These samples were coated with gold in a Balzers SCD050 sputter-coater and examined using a Philips v.5.21 scanning electron microscope at the Electronic Microscopy Laboratory of the Instituto de Botanica de São Paulo, Brazil.

The geographic distribution maps of the *Naucleopsis* species were georeferenced using the softwares QuantumGIS, version 2.12 ©. Moreover, the collection points were obtained from herbaria collections and software Google Earth©

Conservation status assessments have been assigned to individual species using the categories defined by the IUCN Species Survival Commission (IUCN 2015): endangered (EN), vulnerable (VU), data deficient (DD) can be applied if necessary.

A list of specimens examined, ordered by collector, is given in Appendix I. An index to all names is given in Appendix II.

Results

For better comprehension of *Naucleopsis*, we present morphological details, key for determination, illustrations of the main diagnostic characters, distribution maps, taxonomic and morphological comments for 31 taxa recognized.

The classification adopted in this study follows the proposal made by Clement & Weiblen (2009). Where Moraceae is divided in six tribes (Moreae Dumort., Artocarpeae Lam. & DC., Dorstenieae Dumort., Castilleae C.C. Berg, Ficeae Dumort and Maclureae W.L. Clement & Weiblen) and Castilleae is organized in two subtribes: Castillineae e Antiaropsineae. *Naucleopsis* is classified in Castillineae.

Of the species recognized for the genus 17 (3 subsp.), almost 50%, were assigned an IUCN threatened status Endagered and the results are summarized in the Table 1.

Table 1. Sumary of IUCN conservation status ratings for species of *Naucleopsis*. Ratings were determinated using Guidelines for IUCN Red List Categories and Criteria, version 11 (IUCN 2015).

Conservation Status	Species	Number of species
Endangered (EN)	*N. acreana, N. capirensis, N. chiguila, N.guianensis, N. herrerensis, N. humilis, N. inaequalis, N. insculptula, N. macrophylla, N. meridionalis, N. naga, N. riparia, N. straminea, N. ulei* subsp. *amara, N. ulei* subsp. *puberula, N. ulei* subsp. *subandina, N. sp1,*	17
Vulnerable (VU)	*N. caloneura, N. concinna, N. glabra, N. imitans, N. krukovii, N. oblongifolia, N. pauciflora, N. pseudonaga, N. stipularis, N. ternstroemiiflora, N. ulei* subsp. *ulei,*	11
Near Threatened (NT)	*N. velutina*	1
Data Deficient (DD)	*N. francisci, N. jamariensis, N. sp2, N. sp3, N. sp4*	5

Morphology

Habit – Most of the species are medium-large trees size (8-20 m tall) dioecious, rarely monoecious. However, it may reach a height of up to 30 m, as *Naucleopsis oblongifolia* (Fig. 1 A). Distinctly, *Naucleopsis humilis* and *Naucleopsis stipularis* are strictly treelets

(3-6 m tall). Architectural patterns of *Naucleopsis* follow the model of Cook (Hallé & Oldeman 1970, Hallé *et al.* 1978) with the occurrence of cladoptosis. Trees with cladoptosis are characterized by a monopodial orthotropous trunk bearing the leaves and the branches in spirals, limited growth and shedding. Branches shed also were observed in *Naucleopsis humilis* by scars left on trunk (Fig. 1 B). The leafy twigs often show long internodes distinctly different in length, but it also can be conspicuous short (2-10 mm long). The internodes conspicuous short can be found noted in two species *Naucleopsis humilis* and *N. ulei* (Fig. 1 C). In contrast, leafy twigs usually are absent in *Naucleopsis stipularis*. This species is unbranched or litte branched treelets and its leaves are concentrated at the apex of the trunk (Fig. 1 E).

The periderm of leafy twigs of most of species is irregularly peeling to ridged (Fig. 1 D).

Latex – The latex is present mainly in the bark, in the leaves, and in the inflorescences and infructescences. It is abundant, milky aspect (Fig. 1 D, F) and usually is white to yellowish or cream, rare colorless, turning darkened if exposed to the air.

Stipule – These are fully amplexicaul, free (Fig. 4 C). These are terminals, but in some species it is persistent in the internodes along leafy twigs (Fig. 1 C). They are varied, ranging 0,3 cm (e.g., *N. krukovii*) to 3,5 cm long. (e.g., *N. ulei*, *N. stipularis* and *N. imitans*).

Leaves – The leaves are alternate and always entire. They can be very large and reach 60 even 80 cm long, as in *Naucleopsis stipularis* (Fig 1 E) or small, reaching 7,5 to 13 cm long., as in *N. straminea* (Fig 2 A). Usually, in *Naucleopsis* lamina is mostly glabrous, but can be puberulent or pubescent (Fig 2 F-G); coriaceous to chartaceous.

Some species present most of the leaves with perforations probably caused by fungal infection (Fig. 29 H).

Abaxial lamina surface often is smooth, with trichomes simple and long. These also can be scabrous, with simple and short trichomes. This characteristic is important for distinguishing some species, such as *N. insculptula*, *N. meridionalis, N. ulei* subsp *puberula*, *N. sp1*.

Less often the margin is revolute. The secondary veins are often conspicuously prominent beneath. Often, the primary veins are brown-reddish beneath, but some groups present primary veins yellow-greenish or orange-yellowish beneath (Fig. 2 A). Furthermore, the secondary veins are often curved to arched to the margin (Fig. 2 A) or less often are straight to the margin (Fig. 1, chapter 1 – part 1 B).

The petioles may vary between slender with ca. of 1 mm broad (Fig. 2 B) or thickened with ca. of 4 to 6 mm broad (Fig. 2 C). Also, in *Naucleopsis imitans* the petioles presented the upper portion smooth and the lower portion distinctly thickened base (Fig. 2 C).

<u>Staminate inflorescences</u> – These are globoid to cupuliform, rare discoid, solitary to 10 together. It is often peduncled, in *Naucleopsis ulei* subsp *ulei* and *N. ulei* subsp *amara,* the peduncle is sessile to short (to 2 mm long). In contrast, *Naucleopsis stipularis* presents a peduncle larger (1,5-)2-4 mm long.

Before the process of anthesis, the filaments and anthers are covered by tepals and the flowers are covered by an involucral imbricate bracts. The inner bracts usually are large and cover the anthers. During the anthesis the flowers are exposed with the opening of the involucral bracts and then the filaments are exposed with the opening of the tepals (Fig. 4 C, Fig. 22 F,N).

Staminate flower – The staminate flowers are very similar in all species of *Naucleopsis*. In general, the tepals can be free or basally connate, often inflexed (Fig. 15 G, L, Q, Fig. 22 D, J, M, Fig 29 G). The number of tepals and stames is variable, even in the same inflorescence; 2-7, most frequently 3-4. The number of stames is often 3-4 and the filaments are free or basally connate (Fig. 4 D).

Pistillate inflorescences – These are globoid (Fig. 3 D, Fig. 4 A-B), rare discoid (Fig 9 D), are often solitary, rare 2(-10) together, sessile or shortly peduncled (1,5-6 mm long.). These can be varied, in some cases the receptacles are covered by free processes, among which the style are scattered (Fig 3 D, Fig. 4 A, Fig. 15 A,B, M, Fig. 22 A,B, C, Fig. 29 A, H). In this case, the perianth is indistinct on the receptacle. In others species these free processes are in periphery of receptacle or rare absent (*e.g. N. concinna*), in this case, the perianth is distinct on the receptacle (Fig. 4 B, Fig. 15 H).

Pistillate flower –the pistillate flowers present the ovaries completely immersed in the receptacle (Fig. 3 A). Basically, the pistillate flowers can be organized on the receptacle of two forms: with the distinct perianth and tepals connate, 4-8 parted at the apex with free pseudo-tepals mostly peripherical (Fig. 2 E, Fig. 3 C, Fig. 4 B, F, Fig. 15 H, Fig 29 D), or rare absent. In this case, the distinct perianth is varied in deltoid, tubular (Fig. 4 F), oblate (Fig. 2 E) and ovate forms. Or even: In those cases where the styles together with the free processes are scattered on the receptacle (Fig. 3 D, Fig. 4 A, Fig. 22 C, Fig. 29 B). In this case, it is called free pseudo-tepals in this work. The free pseudo-tepals can be subulate or acuminate (Fig. 3 C-D, Fig. 15 E, Fig. 22 C, Fig. 29 B).

Bracts–The involucre in pistillate and staminate inflorescences consists in a series of imbricate bracts covering the outer surface of the receptacle (Fig. 4 C, Fig. 15 C, I, N, Fig. 22 F, N, Fig. 29 C, F, I). The external involucral bracts are smaller than the internal, often coriaceous and ovate. In contrast, the internal involucral bracts of the pistillate inflorescences are often larger than the external, chartaceous or membranaceous and deltoid, lanceolate, ovate or cucullate. During the maturation sometimes the bracts will become thicker (Fig. 3 F).

Infructescences, fruits and seeds – The Infructescences are globoid, rare discoid (Fig. 3 A-F, Fig. 4 A-B, Fig. 15 B, H, Fig. 22 K, Fig. 29 D). The tepals and less frequently the free pseudo-tepals become more enlarge (Fig 3 F, Fig. 42 G). The fruits are drupes, immersed in the receptacle. Often, they are quite large (ca. 1-1,5 cm diam.), globoid to ellipsoid, sometimes fleshy in the maturation. The seeds are ellipsoid to globoide, smooth; testa thin, equal cotyledons and short radical.

FIGURE 1. General morphology. **A.** *Naucleopsis oblongifolia* – Fuste of an adult plant. *A. Santos 194*. **B.** *N. humilis* – Details scars made by shed branche, *A. Santos 163*. **C.** *Naucleopsis ulei* subsp *ulei*, *A Ducke 1045* (RB). **D.** *N. krukovii* – Details of the periderm irregularly peeling to ridged, *A. Santos 202*. **E.** *N. stipularis* - Detail of leaves concentrated at the apex of the stem, *A. Santos 154*. **F.** *N. imitans** – Detail of cream latex in the pistillate inflorescence and involucre of imbricate bracts, *H. Medeiros 479*. *(Foto: H. Medeiros).

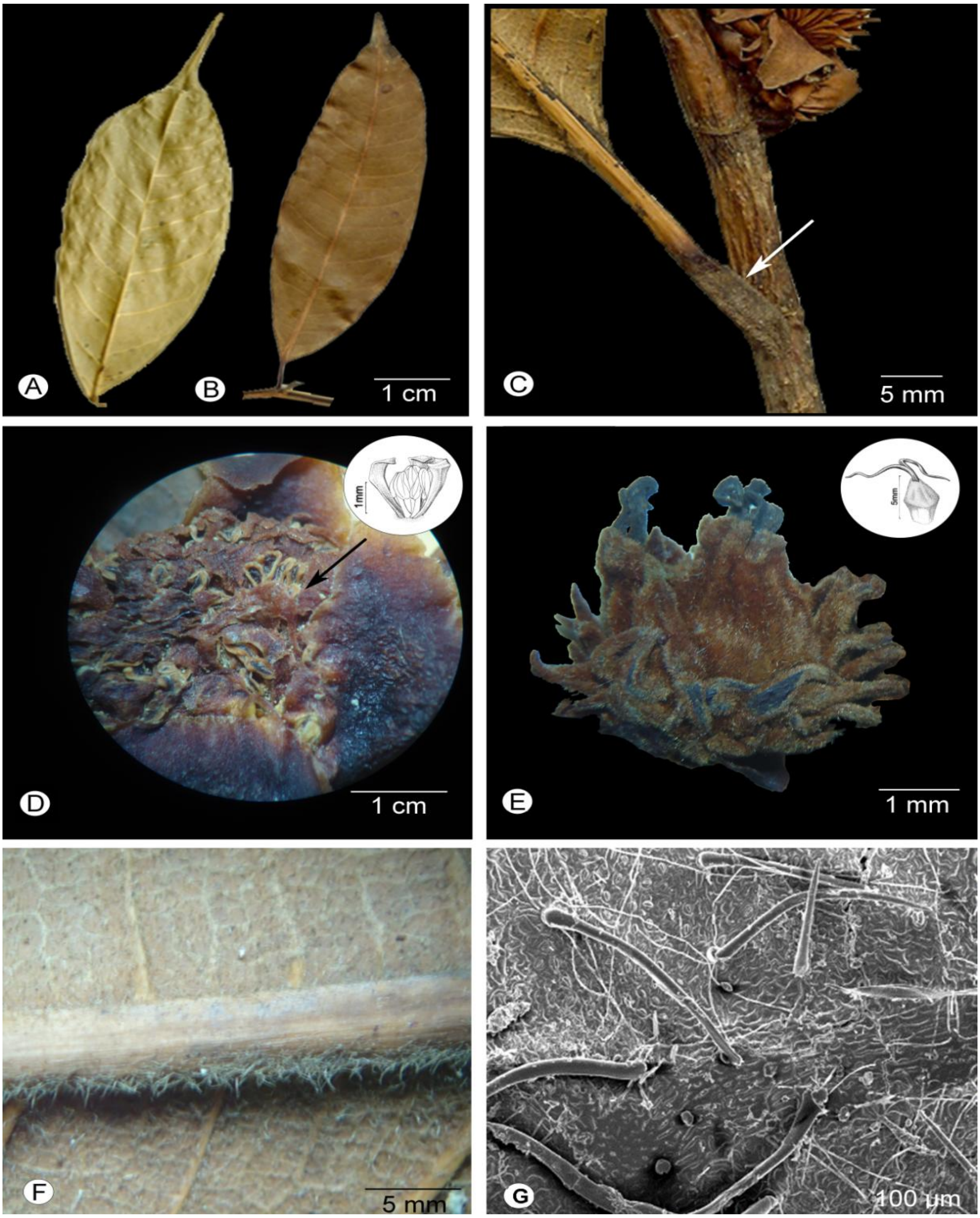

FIGURE 2. General morphology. **A.** *Naucleopsis straminea* **-** Details of the size of lamina 7,5 cm long.; primary veins yellow-greenish beneath, *A. Gentry & J. Brandy 36924* (BG). **B.** *N. oblongifolia* **-** Details of petioles slender with ca. of 1 mm broad; primary veins brown-reddish beneath, *P. Fiaschi et al. 3460* (SP). **C.** *N. imitans* **-** Details of petioles with the upper portion smooth and the lower portion distinctly thickened base, *C.A. Cid et al. 8391* (INPA). **D.** *N. inaequalis* **-** Details of the staminate flowers, *H.F. Paulino Filho 61* (RB). **E.** *N. pauciflora* **-** Details of the pistillate flowers, *L.S. Coelho et al. 90* (INPA). **F.** *N. macrophylla* - Details of the abaxial lamina surface, puberulous to pubescent, *W. Thomas et al. 4950*. **G.** Details of the abaxial lamina surface on MEV, *W. Thomas et al. 4950*.

FIGURE 3. General morphology. **A.** *Naucleopsis imitans** - Details of infructescences globoid; fruit immersed in the receptacle. **B.** *N. stramine* - Details infructescences globoid; indistinct perianth; free pseudo-tepals sparse, *A. Gentry & J. Brandy 36924* (BG). **C.** *N. caloneura* - Details infructescences globoid; distinct perianth, free pseudo-tepals peripherical; involucres of imbricate bracts. **D.** *N. inaequalis** - Infructescences globoid; indistinct perianth; free pseudo-tepals sparse. **E.** *N. imitans** - Details infructescences globoid; distinct perianth, free pseudo-tepals peripherical. **F.** *N. oblongifolia* - Details infructescences globoid; thickened bracts; Details of petioles with the upper portion smooth and the lower portion distinctly thickened base. (*Photo: H. Medeiros).

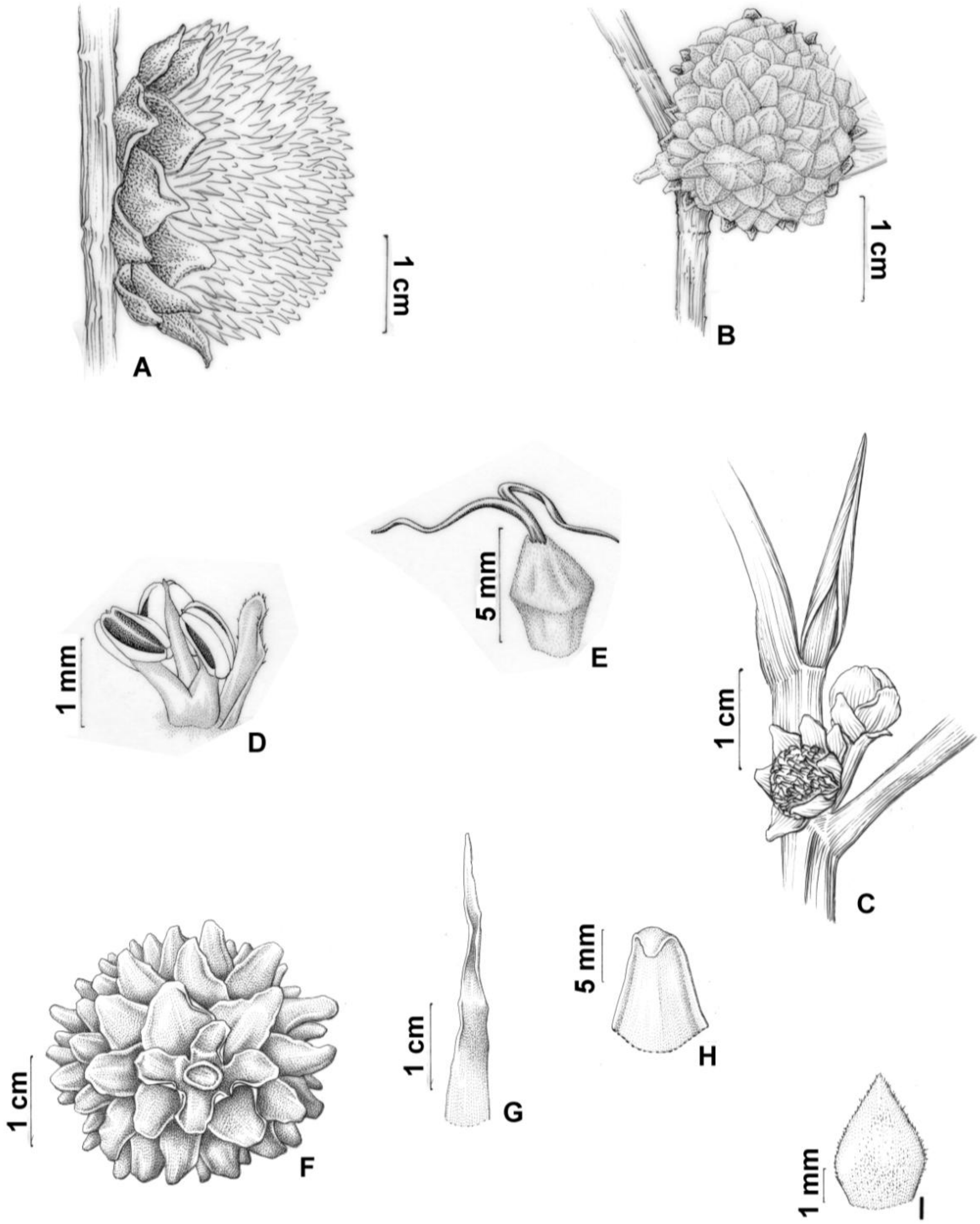

FIGURE 4. General morphology. **A.** *Naucleopsis capirensis* **-** Details infructescences globoid; indistinct perianth, free pseudo-tepals sparse. **B.** *N. sp2* **-** Details infructescences globoid; distinct perianth, free pseudo-tepals peripherical. **C.** *N. imitans* – Details staminate inflorescence globoid; after and before of the process of anthesis, the filaments and anthers are covered by an involucral imbricate bracts. **D.** *N.sp1* – Details staminate flower. **E.** *N.sp1* – Details pistillate flower, perianth tubular. **F.** *N. pseudonaga* – Details involucre imbricate bracts. **G.** *N. chiguila* – Details lanceolate bracts. **H.** *N.sp2*– Details deltoid bracts. **I.** *N. inaequalis* – Details ovate bracts. (Illustrations: Klei R. Sousa).

Taxonomic treatment

Tribe **Castilleae C.C. Berg (1977: 78).**

Subtribe **Castillineae W.L. Clement & Weiblen (2009: 545).**

Type:—*Castilla elastica* Sessé in Cerv.

Olmedieae Trécul (1847: 126). Type:—*Olmedia aspera* Ruiz & Pav.

Naucleopsis Miq. (1853: 120).

Type:—*Naucleopsis macrophylla* Miq.

Ogcodeia Bureau (1873: 286). *Oncodeia* Bentham in Bentham & Hooker (1880: 373). Type:—*Naucleopsis glabra* Spruce ex Baill.

Uleodendron Rauschert (1982: 560). Type:—*Acanthosphaera ulei* Warb.

Palmolmedia Ducke (1939: 20). Type:—*Naucleopsis stipularis* Ducke

Dioecious, rarely monoecious trees, rare treelets. Leaves entire, coriaceous rare chartaceous mostly glabrous, stipules fully amplexicaul, free, caducous or rare persistent along of the branches, in the internodes. Staminate inflorescences solitary or to 10 together, globoid to discoid, or cupuliform, mostly pedunculate; involucral bracts covering the flowers before anthesis; flowers free or basally connate; tepals free or basally connate; stamens 1-4(-6), straight in the bud; filaments free or basally connate; connectives broad. Pistillate inflorescences solitary or to 10 together, often globoid, rare discoid; ovary immersed in the receptacle; distinct to indistinct perianth; distinct perianth with tepals connate, mostly 4-8 parted at the apex; indistinct perianth with free pseudo tepals sparse on receptacle; stigmas filiform to linguiform. Infructescences globoid to discoid; seed ellipsoid to globoid, hilum terminal, orbiculate, large.

Key to the species of *Naucleopsis*

1. Leaves larger (57-)60-80 cm long.; peduncle of staminate inflorescence larger than (15-) 20-40 mm long. ….. *N. stipularis*

1’. Leaves smaller 56 cm long.; peduncle of staminate inflorescence smaller than 14 mm long.

2. Leaves often wrinkled; petioles with upper portion smooth and distinctly thickened base, often (2-)4-6 mm broad …………………..……………….……………………. *N. imitans*

2’. Leaves rarely wrinkled; petioles with both upper and lower portion equal

3. Leaves pubescent beneath.

4. Stipules 0,5-1 cm long.; infructescence with indistinct fruiting perianth, fruiting pseudo-tepals tomentose-velutinous, subulate…………..…………………….……... *N. velutina*

4’. Stipules (1,2-)1,5-2 cm long.; infructescence with disctint fruiting perianth; fruiting perianth connate, parted at the apex

5. Leaf base acute-attenuate; pistillate inflorescences with brownish pubescent bracts, fruiting perianth ovate .... *N. macrophylla*

5’. Leaf base obtuse; pistillate inflorescences with yellowish dense-velutionous bracts; fruiting perianth oblate ………………..…………………..…………………. *N. riparia*

3’. Leaves glabrous to puberulent beneath

6. Leaf twigs with conspicuous short internodes; stipules persistent in the internodes

7. Leaves lanceolate to oblong; leaf base cordate to truncate, rare acute to obtuse…. *N. ulei*

7’. Leaves obovate; leaf base attenuate ………………..……..………..……….. *N. humilis*

6’. Leaf twigs with long internodes distinctly different in length; stipules terminals

8. Leaves scabrous beneath

9. Leaves oblong; filaments connate at the base; distinct fruiting perianth tubular ... *N. sp1*

9’. Leaves lanceolate to elliptic; filaments free; distinct fruiting perianth ovate or fruiting pseudo-tepals subulate

10. Leaves with veins plane beneath; pistillate flowers with distinct perianth, fruiting perianth ovate ………………………………………………………….. *N. insculptula*

10’. Leaves with veins prominent beneath; pistillate flowers with indistinct perianth, fruiting pseudo-tepals subulate ...…………..…………………………..… *N. meridionalis*

8’. Leaves smooth beneath

11. Leaves distinctly inequilateral, one side with obtuse and other attenuate base

12. Filaments basally connate; distinct fruiting perianth, fruiting perianth deltoid ……………………………………………………………………………... *N. guianensis*

12’. Filaments free; indistinct fruiting perianth, fruiting pseudo-tepals acuminate ……………………………………………………………………………… *N. inaequalis*

11’. Leaves equilateral, usually acute-acuminate to obtuse or attenuate base

13. Leaves oblong; secondary veins narrowly straight to the margin .... *N. ternstroemiiflora*

13’. Leaves oblong-lanceolate, elliptic, obovate; secondary veins curved-arched 2-20 mm from the margin ………………………………………………………………. 13

14. Leaves elliptic …………………..……………………..…….……… *N. straminea*

14’. Leaves oblong, oblong-lanceolate or obovate

15’. Most of the leaves with perforations

16. Primary veins brown-reddish beneath; leaf with revolute margin ………..…*N. francisci*

16’. Primary veins yellow-greenish beneath; leaf with entire margin

17. Pistillate inflorescence with ovate bracts; pistillate flower with distinct perianth, connate, parted 4-6 at the apex; fruiting perianth oblate ..…………………….…....... *N. sp2*

17’. Pistillate inflorescence with deltoid bracts; pistillate flower with indistinct perianth, fruiting pseudo-tepals sublulate

18. Pistillate flower with tomentose to velutinous bracts; tomentose to velutinous free pseudo-tepals ……………………………………..………………………….. *N. sp3*

18’. Pistillate flower with glabrous to puberulent bracts; glabrous to puberulent free pseudo-tepals …………………………………………………...…..….. *N. krukovii*

15’. Leaves without perforations

19. Leaves chartaceous

20. Leaves obovate; attenuate base ……………………..…………………..… *N. pauciflora*

20’. Leaves lanceolate or oblong; acute to acuminate or obtuse

21. Stipules larger than 1,5 cm long; pistillate flowers with lanceolate bracts, larger than 2 cm …………………………………………...……………………….. *N. chiguila*

21’. Stipules smaller than 1,4 cm long; pistillate flowers with ovate to deltoid bracts, smaller than 1 cm

22. Leaves narrowly oblong; fruiting perianth oblate .... *N. oblongifolia*

22’. Leaves often lanceolate

23. Leaves often with caudate apex; staminate inflorescence 10-15 mm in diam. ……………………………………………………………………... *N. capirensis*

23’. Leaves with acute-acuminate apex; staminate inflorescence 3-9 mm in diam.

24. Leaves with veins brown-reddish beneath ……………….………………...*N. pseudonaga*

24’. Leaves with veins yellow-greenish or orange-yellowish beneath

25. Leaves with veins yellow-greenish beneath; fruiting pseudo-tepals subulate *N. krukovii*

25’ Leaves with veins orange-yellowish beneath; fruiting pseudo-tepals acuminate . *N. sp4*

19’. Leaves coriaceus

26. Staminate flower with verrucose bracts; pistillate flowers with glabrous bracts .*N. naga*

26’. Staminate flower with smooth bracts; pistillate flowers with pubescent bracts

27. Leaves oblong

28. Leaves with entire margin; cuspidate at the apex …………….………….... *N. concinna*

28’. Leaves with revolute margin; acute-acuminate at the apex ……….…... *N. herrerensis*

27’. Leaves lanceolate to oblong-lanceolate

29. Leaves caudate apex; fruiting perianth subulate …..……….….……….. *N. jamariensis*

29’. Leaves acute-acuminate at the apex; fruiting perianth deltoid, ovate or ovate to subulate

30. Leaves with acute or acute-attenuate base

31. Leaves with veins brown-reddish beneath; fruiting perianth ovate; …... *N. macrophylla*

31. Leaves with veins brown-reddish or yellow-greenish beneath; fruiting perianth ovate to subulate …………………………………………………………..……….... *N. glabra*

30’. Leaves with obtuse base

32. Leaves with veins brown-reddish beneath …………………………...….. *N. caloneura*

32’. Leaves with veins yellow-greenish beneath ………………………..…… *N. acreana*

1. *Naucleopsis acreana* (Mildbr.) Al. Santos & Romaniuc, *comb. nov.*

Basionym: *Ogcodeia acreana* Mildbr. (1932: 421-422). Lectotype (designated by Berg 1972):—BRAZIL. Acre: Rio Acre, Seringal Auristella, June 1911, (♂), *Ule 9320*, B!, isolectotype G [photo!], K!, L!, NY [photo!], RB!, U!.

Fig. 09 A-C.

Tree to treelet (2-)3-6 m tall; latex white. Leafy twigs with long internodes distinctly different in length, 4-5 mm thick, brown-grayish, glabrous to pubescent, slighty ridged; lenticels inconspicuous. Leaves lanceolate, 13-25 cm long., 4.5-8.5 cm broad, coriaceous, without perforations, both faces glabrous; smooth beneath; obtuse at the base, equilateral; acute-acuminate at the apex; margin entire; primary veins yellow-greenish beneath; secondary veins 13-19 pairs, plane beneath, curved-arched to the margin; petioles 1.0-1.5 cm long.; stipules 0.8-1.1 cm long., entire margin, caducous. Staminate inflorescences 3-7 together, 5-10 mm diam.; peduncle 2- 4 mm long., puberulous to pubescent; involucre with ovate to cucullate, puberulous to pubescent smooth bracts, in 3-4 series; perianth 1-1.2 mm high; tepals 3-5, free; stamens 3-4; filaments free. Pistilate inflorescences solitary to 2 together, 10-12 mm diam.; sessile; involucre with ovate, brownish pubescent, smooth bracts, in 4-6 series; distinct perianth, 1.5 mm high, connate, 4-6 parted at the apex, glabrous; stigma filiform; free pseudo-tepals peripheral, deltoid. Infructescences globoid, 3-5 cm diam., distinct fruiting perianth; fruiting perianth ca. 0.6 cm high, deltoid.

Representative specimens:—BRAZIL. Acre: Plácido de Castro, Rio Abunã, 10º17’42”S 67º08’01”W, 21 March 2010, (♂), *H. Medeiros 787* (RB). Amazonas: Boca do Acre, Rio Purus, 20 September 1966, (♂), *G. T. Prance et al. 2441* (K). PERU. Loreto: Maynas, Iquitos, Rio Momón, 22 June 1983, (♀), *M. Rimach Y. 6707* (US), Reserva del Pacaya Cocha Yarina, 29 June 1987, (♀), *C. Grández 1077* (K), Research Center Jenaro Herrera, 04º55’S 73°45’W, no date, (♀), *R. Spichiger & P. A. Loizeau 4501* (US).

Distribution and habitat:—Restricted to northwestern of Brazil (Acre and Amazonas), Bolivia and Peru, in Terra Firme forest of the Amazonian region, mostly in lowland moist area.

Vernacular Name:—renaco (Peru)

Etymology:—The epithet is a tribute to type locality, Acre (Brazil).

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis acreana* is considered Endangered, EN B1a,b(iii), because of the small extent of occurrence restricted to northwestern of Brazil (Acre and Amazonas), Bolivia and Peru (ca. 1.891 km2).

FIGURE 5. Distribution maps of *Naucleopsis acreana.*

Notes:—*Naucleopsis acreana* has been considered as synonymous of *Naucleopsis glabra* by Berg (1972, 2001). Both species are very similar vegetatively. However, the perianths of pistillate flowers are completely different. In reprodutive state, *N. acreana* is clearly distinct. In this species is possible to look clearly the single flowers and the free pseudo-tepals on receptacle. This is because its tepals are basally connate and its free pseudo-tepals are deltoid. The organization of these features on receptacle also facilitates the recognition of the species, wherein the free pseudo-tepals are concentrated in periphery. In contrast, in *N. glabra* these features are sparse on receptacle. Furthermore the tertiary veins beneath in *N. glabra* are more apparent that in *N. acreana.*

Berg (1972, 2001) considers these differences as phenotypic plasticity of group. However, these were considered independent species by Mildbraed (1932) that described *Ogcodeia acreana* and in the same work described *O. glabra*.

For these reasons, we proposed the reestablishment of *Naucelopsis acreana*.

2. *Naucleopsis caloneura* (Huber) Ducke (1922:38).

Basionym: *Olmedia caloneura* Huber (1909: 336). *Ogcodeia caloneura* (Huber) J.F. Macbr. (1931: 17). Type:—BRAZIL. Pará: Rio Cuminámirim, 16 Dec 1906, (♂), *A. Ducke s.n.* (holotype MG!, isotype BM!, F!, G [photo!])

Fig. 15 H-L

Tree (3-)8-20 m tall; latex white to cream. Leafy twigs with long internodes distinctly different in length, 3-5 mm thick, brownish to brown-grayish, glabrous to pubescent, ridged to peeling, lenticels conspicuous. Leaves lanceolate, 11-30 cm long., 5.5-8.5 cm broad, coriaceous, without perforations, both faces glabrous, smooth beneath; obtuse at the base, equilateral; acute to acuminate at the apex; margin entire; primary veins brown-reddish beneath; secondary veins 13-15 pairs, plane beneath, curved-arched to the margin; petioles 1.0-1.5 cm long.; stipules 0.9-1.4 cm long., entire margin, caducous. Staminate inflorescences 3-4 together, 3-6 mm in diam.; peduncle sessile to 3 mm long., puberulous to pubescent; involucre with ovate, puberulous to pubescent, smooth bracts, in 3-4 series; perianth 1-1.5 mm high; tepals 3-7, free; stamens 2-4; filaments, free. Pistilate inflorescences solitary, ca. 10 mm diam.; sessile; involucre with ovate to deltoid, brownish, pubescent, smooth bracts, in 4-5 series; distinct perianth 1.5-3 mm high, connate, 5-8 parted at the apex, puberulent; stigma filiform; free pseudo-tepals peripheral, deltoid. Infructescences globoid, 1.5-4 cm diam.; distinct fruiting perianth, fruiting perianth ca.0.8 cm high, deltoid.

Representative specimens:—BRAZIL. Acre: Rio Branco. Seringal Corredeira, 08 January 1984, (♀), *H. C. Lima et al. 2092* (SP). Amazonas: Manaus, Distrito Agropecuário as Suframa, BR 174, no date, (♀), *A. J. C. Ferreira e Equipe s.n.* (INPA). Parintins, 11 January 1936, (♂), *A. Ducke s.n.* (IAN 50550), (♂), *A. Ducke s.n.* (RB 35441). Pará: Águas Boas, Rio Pixuna, 10 April 1924, (♀), *J. G. Kuhlmann 1955* (SP). Altamira, Belo Monte, Rio Xingu, October – December 2007, (♀), *R. P. Salomão 1181* (SPF), near Embrapa station, at km 23 on Road Altamira-Itaituba, 29 October 1977, (♂), *C. C. Berg et al. BG 754* (MG), Belém-Brasília road, km 179, 13 May 1960, (♀), *E. Oliveira 753* (IAN). Santarém, km 72 Road to Cachoeira do Palhão, Rio Curuá Uma, 02 December 1966, (♂), *P. Cavalcante & M. Silva 1520* (IAN). Tucurui, Rio Tocantins, 02 October 1984, (♂), *J. F. Ramos & E. F. lima 1579* (INPA), 24 October 1984, (♀), *J. F. Ramos 1634* (INPA), 45 km from Tucuruí, SSW on new BR 422, 04º03’S 49º47’W, 3 November 1981, (♂), *D.C. Daly et al. 1179* (INPA, MG), approx. 70 km from Tucuruí, 65 km SSW on old BR422, then 5 km NW on logging Road, 04°11’S 49º44’W, 18-20 November 1981, (♂), *D. C. Daly et al. 1411* (INPA).

Distribution and habitat:—North of Brazil (Acre, Amazonas, Maranhão, Mato Grosso and Pará) and Bolivia (Santa Cruz), in Terra Firme forest of the Amazonian region, mostly in lowland moist area.

Vernacular Name:—janitá**,** muiratinga, muiratinga-branca, (Brazil, Amazonas region).

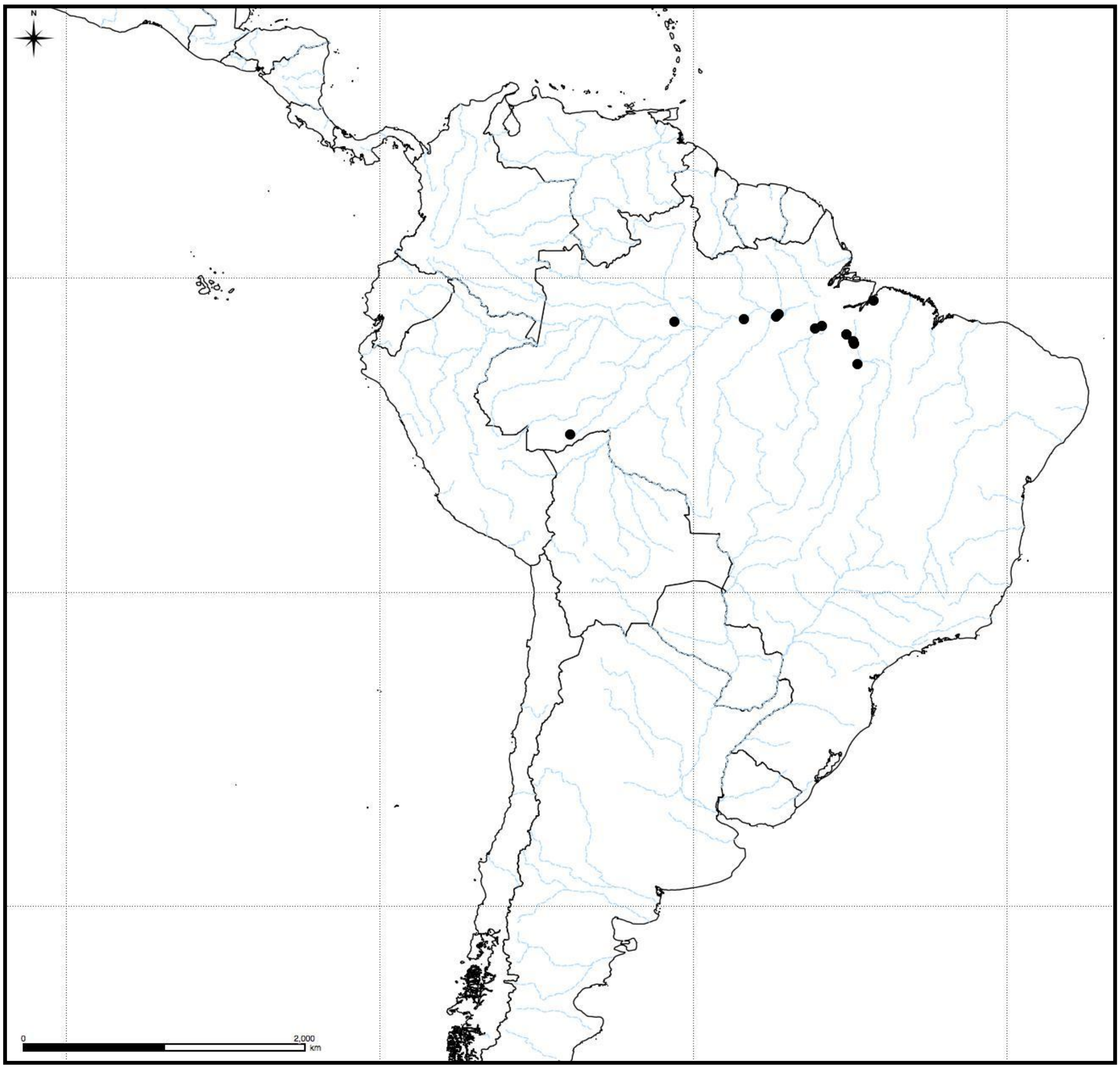

FIGURE 6. Distribution maps of *Naucleopsis caloneura.*

Etymology:—Probably the epithet has relation to term "*caloneurus*", which means beautifully nerved, according to Stearn (2004).

IUCN conservation status:—*Naucleopsis caloneura* is considered Vulnerable, VU B1a,b(iii), because of the small extent of occurrence in the amazon region (ca. 5.126 Km^2).

Notes:— Ducke (1922) recombines this species in *N. caloneura* and in (1939) proposes *N. insculptula*. However, these species are very similar mainly by leaves lanceolate. Probably the lack of knowledge about the pistillate inflorescences of *N. caloneura*, provoked a great problem in the identifications followed. Berg argued that *Naucleopsis caloneura* varies considerably in the indument of the leaves, in the size of the leaves, and the characters of the pistillate inflorescences and infructescences. In reality, Berg (1972) assumed the form of the pistillate inflorescences of *N. insculptula* as being of *N. caloneura.* Then, Berg (1972) synonymized *N. insculptula* in *N. caloneura* and considers a large phenotypic plasticity for the species. These species are completely different, *N. caloneura* can be easily recognized by leaves with surface smooth and fruiting periant deltoid. Differently, *N. insculptula* can be recognized by leaves with surface scabrous and fruiting perianth ovate.

3. *Naucleopsis capirensis* C.C. Berg (1996: 325).

Type:—PANAMA. Panamá: W of Interamerican Hwy., near Capira, ca. 60 km W of Panama City, on road to Cerro Campana, ca. 800 m, 21 March 1985, (♂), *McPherson 6913*, (holotype MO [photo!], Isotype BG!, BM!, CR *n.v.*, INB *n.v.*, MEXU *n.v.*, PMA [photo!].

Fig. 15 M-Q

Tree (5-)10-15(-35) m tall; latex white to cream. Leafy twigs with long internodes distinctly different in length, 2-3 mm thick, brown-grayish, sparsely puberulous, ridged to slightly peeling; lenticels inconspicuous. Leaves lanceolate to oblong, (5-)8-15 cm long., (l.7-)3-5.5 cm broad, chartaceous, without perforations; both faces glabrous, smooth beneath; acuminate to obtuse at the base, equilateral; caudate at the apex; margin entire; primary veins yellow-greenish, secondary veins 10-16 pairs; plane beneath, curved- arched to the margin; petioles 0.2-0.9(1.5) cm long.; stipules 0.4-1 cm long., caducous. Staminate inflorescences 1-3 together, 10-15 mm in diam.; peduncle 3-8 mm long., puberulous; involucre with ovate, puberulous, smooth bracts, in 4-5 series, perianth ca. 1.8-2 mm high; tepals 2-7, free; stamens 3-5; filaments free. Pistillate inflorescences solitary, ca. 15 mm diam., sessile or 2-6 mm long; involucre with narrowly ovate, minutely puberulou, smooth bracts, in 6-8 series; indistinct perianth, free pseudo-tepals aculeate, minutely puberulous; stigmas filiform. Infructescences globoid to discoid, (3-)4-8(-10) cm diam.; indistinct fruiting perianth; fruiting pseudo-tepals to 1 cm high, subulate to acuminate.

Representative specimens:—COSTA RICA. Guanacaste: Tilarán, Zona Proctectora Tenorio Tierras, Rio San Lorenzo, 10º36’30”N 85º00’00”W, 24 March 1991, (♂), *C. Alvarado 113* (BG), Cordillera de Tilarán, 1-2 km W of Lago de Cóte, 13 km N of Tilarán, slope of Volcán Tenorio, 10º35’00”N 84º56’00”W, 24 August 1993, *W. Haber & W. Zuchowski 11612* (BG!). ECUADOR. Carchi: Tulcan, Reserva Etnica Awá, Parroquia El Chical, centro Gualpi, Rio Canumbí, 01º02’N 78º15’W, 19-28 February 1993, (♀), *A. Grijalva et al.* 600 (NY). Tulcan Canton, Parroquia Tobar Donoso, Reserva Indígena Awá, 01º00’N 78º24’W, 19-28 June 1992, (♂), *G. Tipaz et al. 1309 (*BG), (♀), *G. Tipaz et al. 1362 (*BG). Esmeraldas: San Lorenzo Canton, Reserva Indígena Awá, Rio Mira, 01º02’N 78º26’W, 16-26 March 1991, (♂), *D. Rubio et al. 1268* (BG).

Distribution and habitat:—From Costa Rica (Alajuela, Guanacaste and Heredia), Panama (Darién, Panamá) to Colombia (Antioquia, Cordoba) and Ecuador, in moist evergreen forest, at an elevation up to ca. 1800 m above sea level.

Vernacular Name:—penni yu teig (Ecuador)

Etymology:—The epithet is a tribute to type locality, Capira in Panama.

FIGURE 7. Distribution maps of *Naucleopsis capirensis.*

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis capirensis* is considered Endangered, EN B1a,b(iii), because of the small extent of occurrence from Costa Rica to the Pacific Costal region of Colombia and of Ecuador (ca. 3.832 km^2).

Notes:—This species is related to *Naucleopsis naga* by presence of indistinct perianth, however, *N. capirensis* has the shorter perianth of the staminate flowers. Also, this species can be distinguished by leaves with to 15 cm long. In contrast, *N. naga* presents leaves larger than 20 cm long. This species also can be recognized by stipules with revolute to crisped margin. *N. capirensis* often reach to 15 m tall. However, some specimens are larger and can reach to 35 m tall, with infructescences of up to 10 cm in diameter.

4. *Naucleopsis chiguila* Benoist (1933: 78).

Type:—ECUADOR. Santo Domingo de los Colorados: no date, (♀), *R. Benoist 3035* (holotype P!; isotype P!).

Fig. 29 A-C

Tree 12-28 m tall; latex cream. Leafy twigs with long internodes distinctly different in length, 2-4 mm thick, brownish, glabrous to puberulous, ridged to slightly peeling; lenticels conspicuous. Leaves lanceolate to oblong, 11-16(-23) cm long., 4.5-5.5 cm broad, chartaceous, without perforations both faces glabrous, smooth beneath; acute to acuminate or obtuse at the base, equilateral; acute-acuminate at the apex; entire margin; primary veins brown-reddish, secondary veins 15-18 pairs; plane beneath, curved- arched to the margin; petioles 0.5-1.0 cm long.; stipules 1.5-2.3 cm long., entire margin, caducous. Staminate inflorescences solitary, 5-9 mm diam.; peduncle 2-6 mm long.; puberulent; involucre with ovate, puberulous bracts, smooth, in 4-5 series; perianth, 1.2-1.4 mm high; tepals 4-6, free, stamens 4-6; filaments free. Pistillate inflorescences solitary, 15-20 mm diam., sessile; involucre with lanceolate, puberulent bracts, to 3 cm long, in 7-8 series; indistinct perianth, fruiting pseudo-tepals subulate, minutely puberulous, 1.5-2.5 mm long; stigmas filiform. Infructescences globoid, 3-4 cm diam.; indistinct fruiting perianth, fruiting pseudo-tepals to 0.6 cm high, subulate.

Representative specimens:—ECUADOR. Esmeraldas, Eloy Alfaro, Parroquia Luis Vargas Torres, Playa de Oro, Rio Santiago, 00º43'N 79º45'W, 1-2 November 1993, (♀), *M. Tirado et al. 247* (NY). Pichincha, Canton Pedro Vicente Maldonado, Reserva Florestal Rio Pitzara, 0°18'N 79º12'W, November 1997, (♂), *T. D. Pennington et al.* 16103 (BG). Quito-Puerto Quito Road, 10 km N of main Road, km 113, Reserva Florestal ENDESA, Rio Silancha, 0°05'N 79°02'W, 19 May 1987, (♂), *P. Acevedo et al. 1721* (BG).

Distribution and habitat:—Ecuador (Esmeraldas, Santo Domingo de los Colorados, Pichincha), in moist evergreen forest, at an elevation up to ca. 700 m above sea level.

Vernacular Name:—chiguila (Ecuador).

Etymology:—The epithet is a tribute to vernacular name (chiguila).

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis chiguila* is considered Endangered, EN B1a,b(iii), because of the small extent of occurrence only in lowlands of Ecuador (ca. 973 km^2).

Notes:—This species is easily recognized because of the large bracts. Berg (2001) complements its description incluiding the staminate inflorescences. In vegetative state, *N. chiguila* is similar to *N. pseudonaga* by leaves consistency chartaceous, lanceolate or lanceolate to oblong and brown-reddish color of the primary veins. However, in reprodutive state *Naucleopsis chiguila* is clearly different of other species of group by its characteristics of the pistillate inflorescences with bracts lanceolate, very elongated (up to 3 cm long.).

FIGURE 8. Distribution maps of *Naucleopsis chiguila.*

5. *Naucleopsis concinna* (Standl.) C.C. Berg (1969: 465).

Basionym: *Perebea concinna* Standl. (1937: 179-180). Type:—BRAZIL. Amazonas: Humaitá, Livramento, Rio Livramento, (♂), *B. A. Krukoff 6687*, 12 Outober - 6 November 1934 (holotype F [photo!]; isotype BM!, BR [photo!], K!, LE [photo!], MICH [photo!], MO [photo!], NY [photo!], U!).

Fig. 29 D-G

Tree (5-)7-18 m tall; latex white to yellow. Leafy twigs with long internodes distinctly different in length, 3-4 mm thick, brown-grayish, glabrous to pubescent, ridged to slighty peeling; lenticels conspicuous. Leaves oblong, 16-24(-32) cm long., 3.5-7(-8.5) cm broad, coriaceous, without perforations, both faces glabrous; smooth beneath;acute to obtuse at the base, equilateral; cuspitade at the apex; margin entire; primary veins reddish, secondary veins 18-28 pairs, plane beneath, often straight to the margin; petioles (0.5-)1.2.5(-3.0) cm long.; stipules 0.5-1.4 cm long., entire margin, caducous. Staminate inflorescences 1-10 together, 3-8 mm diam.; peduncle sessile to 4 mm long., puberulous to pubescent; involucre with ovate, puberulous to pubescent, smooth bracts, in 3-6 series; perianth 2-2.2 mm high; tepals 3-5, free; stamens 2-3, filaments free. Pistilate inflorescences 1-3 together, up to 10 mm diam.; sessile; involucre with ovate, brownish, pubescent, smooth bracts, in 4-8 series; distinct perianth 3-4 mm high, connate, 4-6 parted at the apex, pubescent to velutinous; stigma filiform. Infructescences globoid, 4-5 cm diam.; distinct fruiting perianth; fruiting perianth to ca. 0.6 cm high, oblate.

Representative specimens:—BRAZIL. Acre: Cruzeiro do Sul, BR 364 km 44, 07º-08ºS 72º-73ºW, 18 October 1984, (♂), *C.A, Cid Ferreira et al. 5329* (INPA, RB). Amazonas: Boca do Acre, rio Inauiní, 08º33’10”S 67º33’58”W, 14 December 2009, (♀), *M.G. Bovini et al. 3134* (SP, RB). Tefé, subestação experimental do IAN, 05 January 1961, (♀), *W. Rodrigues 2060* (IAN). Pauini, Floresta Nacional do Purus, vila Céu do Mapiá,

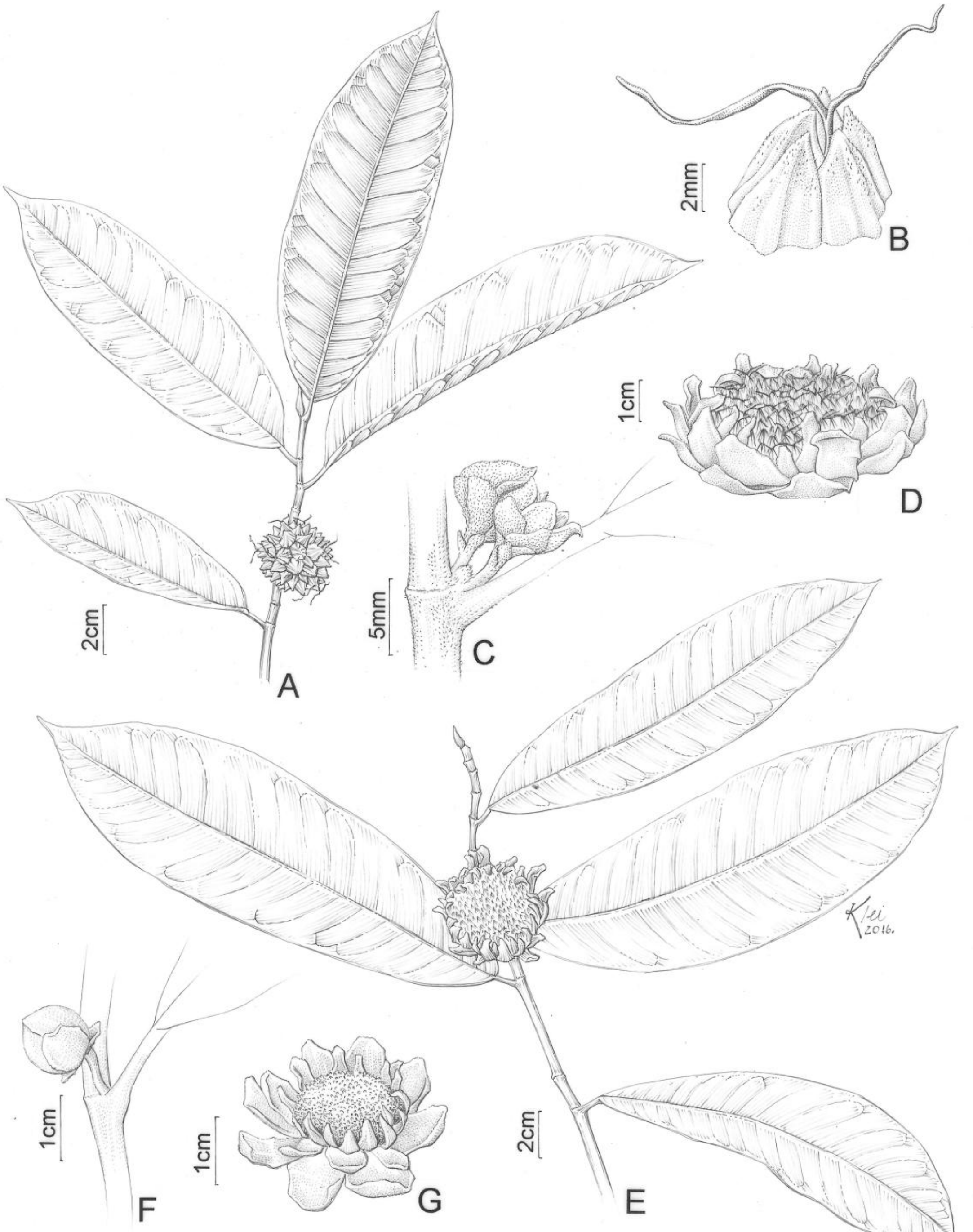

FIGURE 9. General morphology. *Naucleopsis acreana* **A.** Habit, *C. Grández 1*077 (K), **B.** Pistillate flower, *C. Grández 1*077 (K), **C.** Staminate inflorescence, *H. Medeiros 787* (RB), **D.** Pistillate inflorescence, *C. Grández 1*077 (K). *Naucleopsis meridionalis* **E.** Habit, **F.** Staminate inflorescence, *W. Palacios 9674* (BG), G. Pistillate inflorescence, *W. Palacios 9691* (BG).

08º17’30”S, 67º34’13”W, 15 July 2008, (♂), *A. Quinet 1198* (RB, SP). Rondônia: Ariquemes, BR 364, 15 km N de Ariquemes, 09º47’00”S 63º05’00”W, 13 March 1987, *M. Nee 34338* (SP). Porto Velho, 03 November 2008, (♀), *Equipe de resgate 1287* (RB). Santa Bárbara, Rodovia BR 364 km 120, 09º10’00”S 63º07’00”W, 25 May 1982, *L.O.A. Teixeira et al. 739* (MG). ECUADOR. Morona Santiago: Puerto Morona, Rio Morona, 02º52’00”S 77º41’00”W, 01 October 1975, *E.L. Little et al. 522* (US).

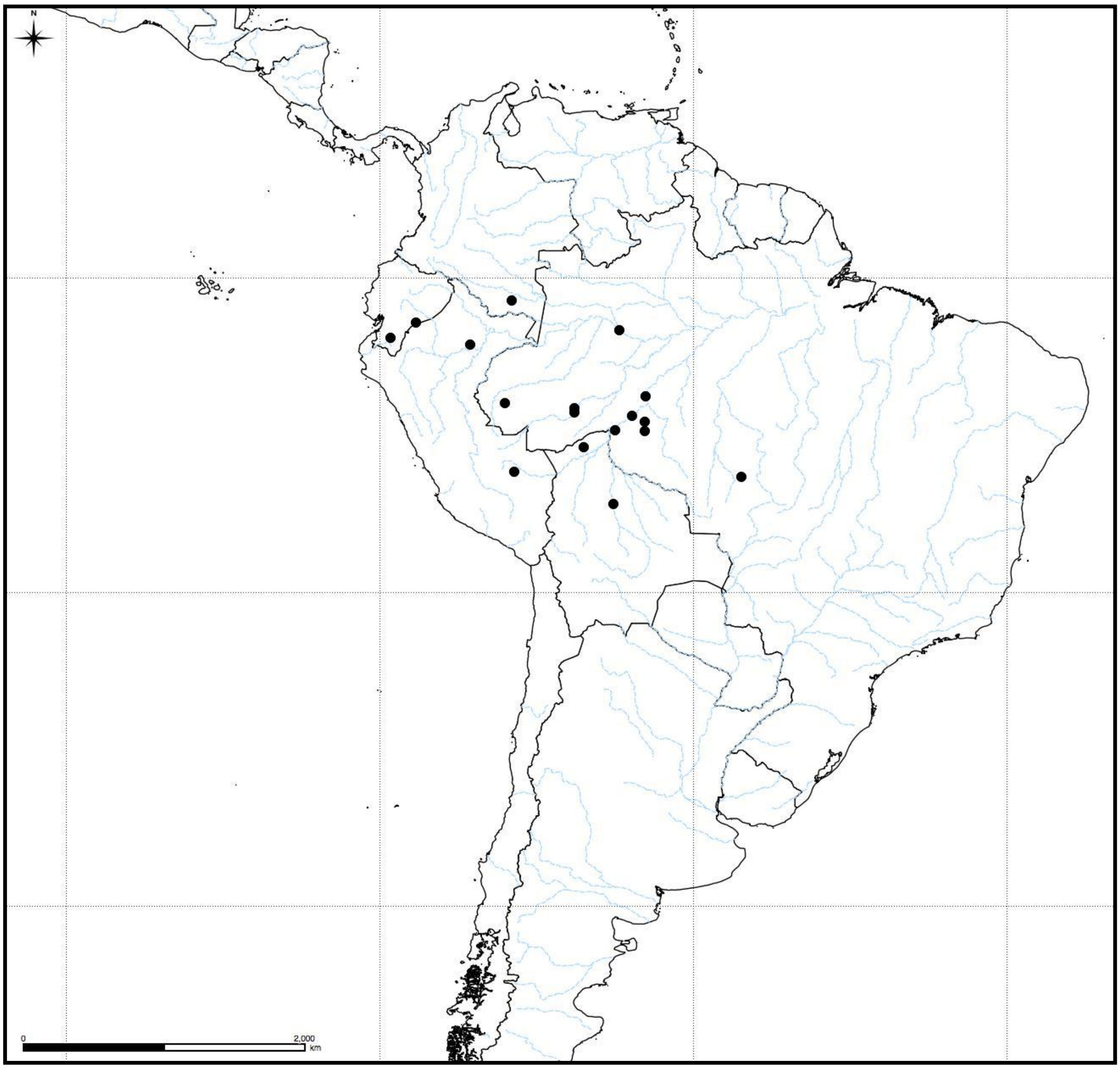

FIGURE 10. Distribution maps of *Naucleopsis concinna.*

Distribution and habitat:—North region of Brazil (Acre, Amazonas, Mato Grosso and Rondônia), Bolivia (Beni and Pando), Colombia (Amazonas and Vaupés), Ecuador (Morona-Santiago and Sucumbíos) and Peru (Loreto, Madre de Dios, Pasco and Ucayali), in Terra Firme forest of the Amazonian region, usually in lowland moist areas.

Vernacular Name:— pana, pama (Brazil).

Etymology:—The epithet probably suggests to the appearance of the leaf. It is often reddish and lustrous.

IUCN conservation status:—*Naucleopsis concinna* is considered Vulnerable, VU B1a,b(iii), because of the small extent of occurrence in the amazon region (ca. 6.073 Km^2).

Notes:—*Naucleopsis concinna* was described by Standley (1937) as *Perebea concinna*. Berg (1969) noted that this species shows similarly with the others *Naucleopsis* by ovary immersed in receptacle and transferred to *Naucleopsis*.

This species is particularly different from the others mainly by pistillate inflorescences and infructescences. In *N. concinna* were not found free pseudo-tepals. Furthermore, this species differs of the other *Naucleopsis* by velutinous, oblate perianth in pistillate flowers.

6. ***Naucleopsis francisci*** C.C.Berg & Homeier (2010: 197).

Type:—ECUADOR. Loja: Parque Nacional Podocarpus, Road Loja-Zamora, San Francisco, 2100 m, 4 May 1995, (fr), *B. Merino et al. 4504* (holotype LOJA [photo!], isotype BG!).

Fig. 29 H-I

Tree 18-25 m tall; latex yellowish. Leafy twigs with long internodes distinctly different in length, 4-5 mm thick, brown-grayish, glabrous to puberulous, ridged to peeling; lenticels conspicuous. Leaves lanceolate, 10-20 cm long., 3.5-7 cm broad, coriaceous, with perforations, both faces glabrous; smooth beneath; obtuse at the base, equilateral; acute-acuminate at the apex; margin revolute, primary veins brown-reddish, secondary veins 25-27 pairs; prominent beneath, curved-arched to the margin; petioles 0.6-1.5 cm long.; stipules 1-2 cm long., entire margin, caducous. Staminate inflorescences solitary, 5-10 mm diam.; peduncle 2-3 mm long.; puberulous; involucre with ovate, puberulent, smooth bracts, in 3-4 series; perianth 1-2 mm high; tepals 3-5, free; stamens 2-3, filaments free. Pistillate inflorescences solitary, 16-20 mm diam., peduncle 1-3 mm long; involucre with ovate brownish, glabrous to puberulous, smooth bracts, in 6-7 series; indistinct perianth, free pseudo-tepals 2-3 mm high, subulate, puberulent; stigmas filiform. Infructescences globoid, 4-5 cm diam.; indistinct fruiting perianth, fruiting pseudo-tepals to 0.5 cm high, subulate to aculeate.

Representative specimens:—ECUADOR. Zamora: Zamora-Chinchipe, region of the Cordillera del Cóndor, Parroquia San Carlos de Las Minas, Nambija, 04º04’20”S 78º46’54”W, 25 January 2005, (♀), *W. Quizhpe et al. 740* (BG), Estación Cientifica San Francisco, South of Loja-Zamora Road, 30 km east of Loja, 03º58’35”S 79º04’14”W, 12 November 2006, (♂), *D. Neill & Dendrology course 15334* (BG).

Distribution and habitat:**—**Endemic from the northeast of Ecuador (Zamora-Chinchipe), in montane forest region, at an elevation of about 1800 to 2150 m above sea level and Peru (Loreto).

Vernacular Name:**—**unknown.

Etymology:**—**The epithet probably is a tribute to type locality, San Francisco.

IUCN conservation status:—*Naucleopsis francisci* is known only tree collections in Zamora (Ecuador), made between 2005 and 2006 and Loreto (Peru), made in 1976. The extent of occurrence is 40 Km^2, and population size is unknown. For these reasons *N. francisci* is assessed as Data Deficient (DD) according to IUCN Red List criteria (IUCN 2015).

FIGURE 11. Distribution maps of *Naucleopsis francisci.*

Notes:—This species was established after review for the Flora Neotropica by Berg & Homeier (2010) from collections unnamed. *Naucleopsis francisci* is strongly characterized by large number of perforations present in the leaves. This species shows some similarities to *N. herrerensis* because leaves with both face glabrous, revolute margin and veins brown-reddish. However, *N. francisci* can be distinguished by the presence of perforations in leaves. *N. francisci* is rare and only found in Ecuador.

7. *Naucleopsis glabra* Spruce ex Pittier (1912: 440).

Ogcodeia glabra Spruce ex Mildbr. (1932: 418-419). Type:—BRAZIL. Amazonas: Panuré, Rio Uaupes, (♀), *Spruce 2793* (holotype B!, isotype P!, BM!, BR [photo!], K!, P!, LE [photo!]).

Duguetia glabra Britton (1889: 14). *Ogcodeia sandwithiana* Mildbr. (1932: 442). Type:—BOLIVIA. junction of the Rivers Beni and Madre de Dios, August 1886, (♀), *H. H. Rusby 1378* (holotype NY [photo!], isotype K!, MICH [photo!], NY [photo!]).

Ogcodeia pallescens Ducke (1939: 18-19). Type:—BRAZIL. Rondônia: Rio Ouro Preto, near affluence of Rio Pacas, no date, (♀), *J. G. Kuhlmann 485* (holotype RB!, isotype B!, K!, P!, U [photo!], US [photo!]).

Ogcodeia tamamuri J.F.Macbr. (1931: 64). Type:—PERU. Loreto: Timbuchi on Río Nanay, 26 June 1929, (♂), *Williams 992* (holotype F [photo!], isotype B!, US [photo!]).

Ogcodeia tessmannii Mildbr. (1927: 189). Type:—PERU. Loreto: Pongo de Manseriche, mouth of Río Santiago, 23 September 1924, (♂), *Tessmann 4109* (holotype B!, G [photo!], NY [photo!], S [photo!]).

Trees (6-)8-20 m tall; latex white to yellowish. Leafy twigs with long internodes distinctly different in length, 1-4,5 mm thick, glabrous or puberulous to pubescent, ridged; lenticels conspicuous. Leaves lanceolate, 7-30 cm long., 1.6-10 cm broad, coriaceous, without perforations, both faces glabrous; acute at the base, equilateral; acute-acuminate at the apex; margin entire; primary veins brown-reddish to yellow-greenish, secondary veins 12-23 pairs; plane beneath, curved, arched to the margin; petioles 5-20 mm long.; stipules 0.8-1.4 cm long., entire margin, caducous. Staminate inflorescences 3-8 together, 5-12 mm diam.; peduncle 1.5-7 mm long., glabrous to puberulous; involucre with deltoid to ovate, puberulent, smooth bracts, in 4-6 series; perianth 1-2.7 mm high; tepals 3-7, free; stamens 2-4. filaments free. Pistillate inflorescences solitary, 7-10 mm diam., sessile or 2-4 mm long.; involucre with ovate to deltoid, pubescent, smooth bracts, in 4-8 series; indistinct to distinct perianth, 2-5 mm high, free or basally connate, free pseudo-tepals, puberulent; stigmas filiform. Infructescences globoid, 2-4 cm diam.; indistinct to distinct fruiting perianth; fruiting pseudo-tepals to 0,4 cm high., ovate to subulate.

Representative specimens:—BRAZIL. Acre: Plácido de Castro, Rio Abunã, 10º17’42”S 67º08’04”W, 21 March 2010, (♀), *H. Medeiros 788* (RB). Rio Branco: Road to Quixadá, km 11, 18 October 1980, (♀), *C. A. Cid & A. Rosa 2945* (MG), 19 October 1980, (♀), *C. A. Cid. & B. W. Nelson 2964* (MG). Santa Rosa: Rio Purus, 09º07’49”S 70º10’37”W, 23 March 1999 (♀), *D. C. Daly et al. 9994* (RB). Tarauacá, Reserva Indígena Praia do carapanã, Basin of Alto Juruá, 08º26’56”S 71º20’56”W, 21 November 1995, *M. Siveira et al. 1060* (INPA). Amazonas: Jutaí: Rio Solimões 02º43’S 66º45’W, 24 October 1986, (♀), *C.A. Cid et al. 8282* (INPA, MG), Rio Capitarí, 28 August 1950, (♂), *R. L. Fróes 26421* (IAN), Rio Jamari, 11 September 1906, (♀), *A. Ducke s.n.* (RB 18300). Mato Grosso: Aripuanã, 19 September 1976, (♀), *M. Gomes & S. Miranda 325* (INPA). Pará: BR 230, Transamazonica, 10 km NE of Itaituba, 26 November 1977, (♀), *G. T. Prance et* *al. P 25796* (RB). Rondônia: Costa Marques, 16 km NW of Costa Marques, BR 429, 12º20'SP 64º18'W, 30 March 1987, *M. Nee 34575* (SP). Porto Velho, 12 August 1987, (♀), *F. Dionizia et al. 119* (INPA), Sub-base proj. RADAM, 14 September 1975, (♀), *M. R. Cordeiro 782* (IAN). COLOMBIA. Santander: approx. 15 km W of Berrío, 13 May 1949, (♀), *R. Scolnik et al. 19S005* (US). ECUADOR. Pastaza: Mazaramu, 01º27'S 76º54'W, 27 April 1990, (♀), *H. T. Beck et al. 1046* (NY).

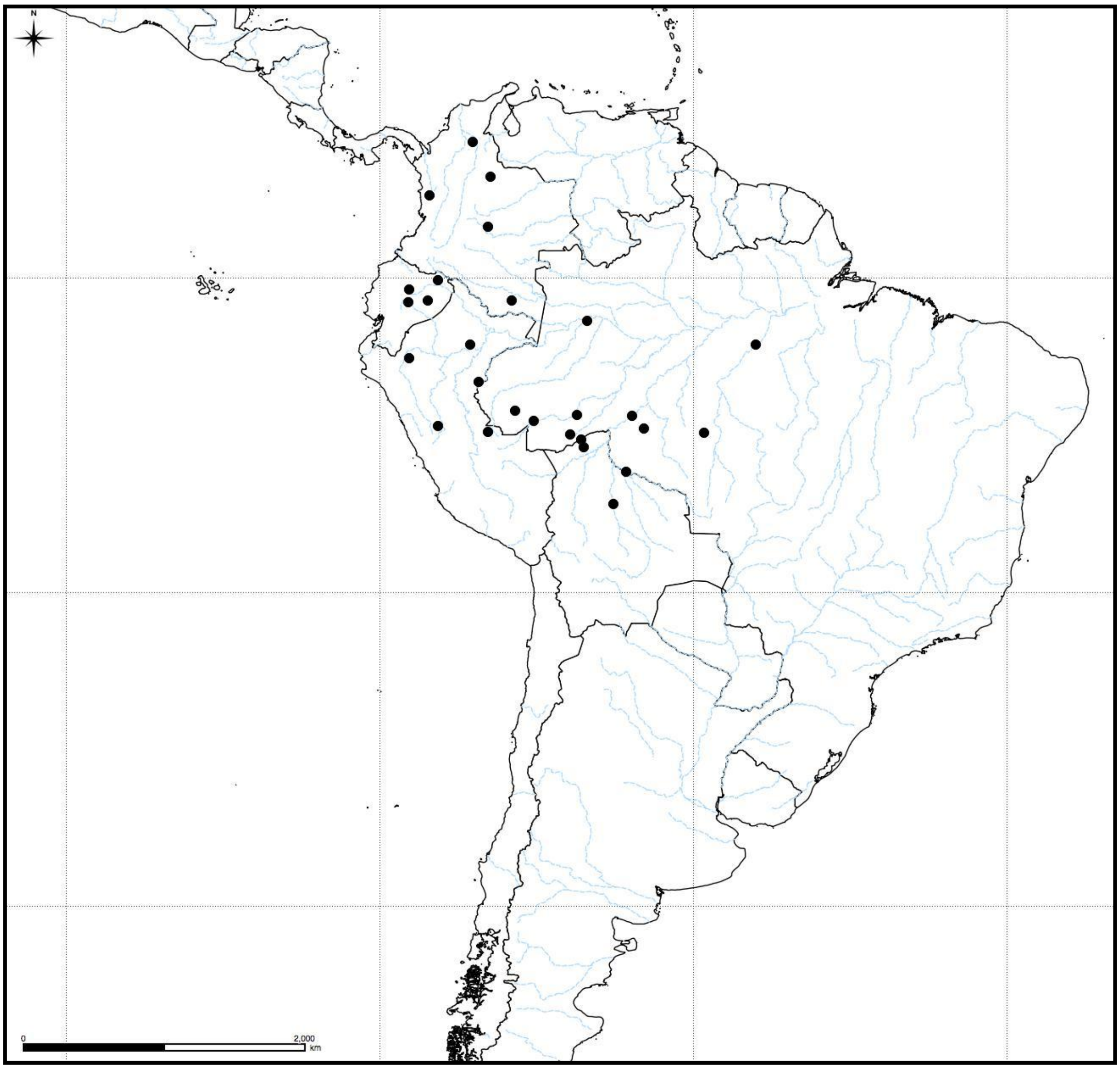

FIGURE 12. Distribution maps of *Naucleopsis glabra.*

Distribution and habitat:—Amazon region of Brazil (Pará and Rondônia), from Colombia to Bolivia (Beni and pando), and also Suriname; in Terra Firme forest, at low elevations.

Vernacular Name:—muiratinga, erva-de-veado, jaca-brava (Brazil), chimicua (Peru).

Etymology:—The epithet suggests to the glabrous indument leaf.

IUCN conservation status:—*Naucleopsis glabra* is considered Vulnerable, VU B1a,b(iii), because of the small extent of occurrence in the amazon region (from Colombia to Bolivia) and disjunctly in Suriname and northern Colombia (ca. 7.970 Km^2).

Notes:—This species has a historical marked by taxonomy controversy. The indistinct perianth, deltoid of the pistillate inflorescences is different of distinct perianth, ovate of the pistillate inflorescences of *N. macrophylla.* For this reason, Mildbraed (1932) transferred *N. glabra* to *Ogcodeia glabra.* However, theses two standards are common to others *Naucleopsis.* Furthermore, this species is similar to *N. acreana* due glabrous indument, but the pistillate inflorescences are completely different. In *N. glabra* the free pseudo-tepals are sparse on receptacle and in *N. acreana* the free pseudo-tepals are concentrated only in periphery.

8. *Naucleopsis guianensis* (Mildbr.) C.C.Berg (1969: 465).

Basiônimo: *Ogcodeia guianensis* Mildbr. (1932: 422-423). Type:—GUYANA: Cuyuni River, below the Akaio Falls, (♀), *Sandwith 698* (holotype B!; isotype K!, NY [photo!]).

Trees up to (4-)10-20 m tall; latex white to yellow. Leafy twigs with long internodes distinctly different in length, 1-3 mm thick, brownish, sparsely puberulous to pubescent, ridged; lenticels conspicuous. Leaves lanceolate to oblong, 6-17 cm long., 1.5-5.5 cm broad, coriaceous, without perforations, both faces glabrous, smooth beneath, one side obtuse and other attenuate at the base, distinctly inequilateral; acute-acuminate apex; margin entire; primary veins brown-reddish beneath, secondary veins 11-19 pairs, prominent beneath, curved to arched the margin; petioles 3-10 mm long.; stipules 0.7-1.7 cm long., entire margin, caducous. Staminate inflorescences 1-3 together, 0.6-0.8 mm diam.; peduncle 5-11 mm long., puberulous; involucre with ovate, puberulent, smooth bracts, in 3-4 series; perianth 1.5-2.0 mm high; tepals 2-7, free; stamens 2-4; filaments basally connate. Pistillate inflorescences solitary or 2 together, 10-15 mm diam., sessile to peduncle 2-4 mm long.; involucre with ovate to deltoid puberulous, smooth bracts, in ca 5 series; indistinct to distinct perianth 1-3 mm high, connate, 4-6 parted at the apex, puberulent; stigma filiform; free pseudo-tepals peripheral, acuminate. Infructescences globoid, 1.5-4 cm diam.; indistinct to distinct fruiting perianth; fruiting perianth ca. 0.3 cm high, deltoid.

Representative specimens:—BRAZIL. Amapá: Rio Araguari, 28 September 1961, (♀), *J. M. Pires et al. 51293* (RB). GUIANA. Mabura region, Kurupukari main, km 27, 29 November 1993, (♀), *Ek et al. 1027* (NY). GUYANE FRANÇAISE. Camp Pararé, Station de lÁrataye, 18 August 1983, (♂), *A. Vieillescazes 487* (SP). Fleuve Approuague: Riv. Arataye, Sauts Parare, 12 September 1983, (♀), (fr.), *S. Barrier 4300* (US). Saül: 03º37'N 53º12'W, 10 September 1982, (♂), *S. Mori et al. 14901* (MG).

Distribution and habitat:—In the three Guianas and Brazil (Amapá); in terra firme forest, at low elevations about 130-400 m above sea level.

Vernacular Name:**—**unknown.

Etymology:—The epithet is a tribute to type locality, the Guyana.

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis guianensis* is considered Endangered, EN B1a,b(iii), because of the small extent of occurrence only in the three Guianas and Brazil (ca. 2.200 km^2).

FIGURE 13. Distribution maps of *Naucleopsis guianensis.*

Notes:—This species was established by Mildbraed (1932) as *Ogcodeia guianensis* and only in the reorganization of group done by Berg (1969) the species was recombined in *Naucleopsis guianensis.* This species is related to *N. inaequalis* by distinctly inequilateral base. However these species clearly differ by morphological characters of the pistillate inflorescences. In addition, *N. guianensis* is restricted to Amapá and in the region of the Guyanas.

9. *Naucleopsis herrerensis* C.C.Berg (1996: 237-238).

Type:—PERU. Loreto: prov. Requena, Jenaro Herrera, arboretum, August - September 1976, (♂), *Bernardi 16201* (holotype G [photo!], isotype BG!)

Fig 29 J.

Tree 15-25 m tall; latex yellowish. Leafy twigs with long internodes distinctly different in length, 2-3.5 mm thick, brown-grayish, glabrous to puberulous, ridged to peeling; lenticels conspicuous. Leaves oblong, 6-24 cm long., 1.5-6 cm broad, coriaceous, without perforations, both faces glabrous, smooth beneath; obtuse at the base, equilateral; acute-acuminate at the apex; margin revolute, primary veins brown-reddish, secondary veins 12-25 pairs; prominent beneath, curved-arched to the margin; petioles 0.6-1.5 cm long.; stipules 1-2 cm long., entire margin, caducous. Staminate inflorescences solitary to 3-6 together, 8-10 mm diam.; peduncle 2-3 mm long.; puberulous; involucre with ovate, puberulent, smooth bracts, in 4-5 series; perianth 1.5-2 mm high; tepals 4-5 free or connate basally; stamens 3-4, filaments free. Pistillate inflorescences solitary, 15-20 mm diam., sessile; involucre with ovate brownish, glabrous to puberulous, smooth bracts, in 6-7 series; indistinct perianth, free pseudo-tepals 4-6 mm high, subulate, puberulent; stigmas filiform. Infructescences globoid, 4-6 cm diam.; indistinct fruiting perianth, fruiting pseudo-tepals to 0.6 cm high, subulate.

Representative specimens:—ECUADOR. Napo: Aguarico, Reserva Etnica Huaorani, 0º59’S 76º12’W, 11 January 1995, (fr.), *M. Aulestia et al. 2991* (BG). Cantón Archidona, Rio Huataraco, 00º43’S 77º32’W, *C. Cerón & M. Factos 7485* (BG), Parque Nacional Yasuní, 00º57’S 76º13’W, 9-19 January 1988, (♀), *D. Neill et al. 8335* (BG). PERU. Loreto: Maynas, Las Amazonas, Rio Sucusari, 03º20’S 72º55’W, 07 November 1989, (♂), *R. Vásquez & N. Jaramillo 13092* (BG).

FIGURE 14. Distribution maps of *Naucleopsis herrerensis.*

Distribution and habitat:—Colombia (Caquetá and Putumayo), Ecuador (Napo, Pastaza and Sucumbíos) and Peru (Amazonas and Loreto), in moist evergreen forest, mostly in lowland moist area.

Vernacular Name:—oincoca (Ecuador).

Etymology:—Probably the epithet is a tribute to type locality, Requena, Jenaro Herrera.

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis herrerensis* is considered Endangered, EN B1a,b(iii), because of the small extent of occurrence from Colombia to Peru (Loreto) (ca. 3.287 km^2).

Notes:—Berg (2001) complements its description incluinding new specimens examined. *Naucleopsis herrerensis* is related to *N. francisci* by margin revolute and primary veins brown-reddish, but distinguished by leaves without perforations. The leaves oblong of this species shows similarities with *N. ulei* subsp. *amara*. However, these species are completely different. *N. ulei* subsp. *amara* belongs to a group of species with short internodes with stipules persistent in the internodes. In contrast, *N. herrerensis* presents long internodes distinctly different in length and stipules terminals.

10. ***Naucleopsis humilis*** C.C.Berg (1996: 238).

Type:—ECUADOR. Pastaza: Rio Curaray, near Laguna Garzayacu, 250m, 20 August 1985, (♀), *Neill et al.* 6663 (holotype QCNE [photo!], isotype BG!, MO [photo!], QAME *n.v.*).

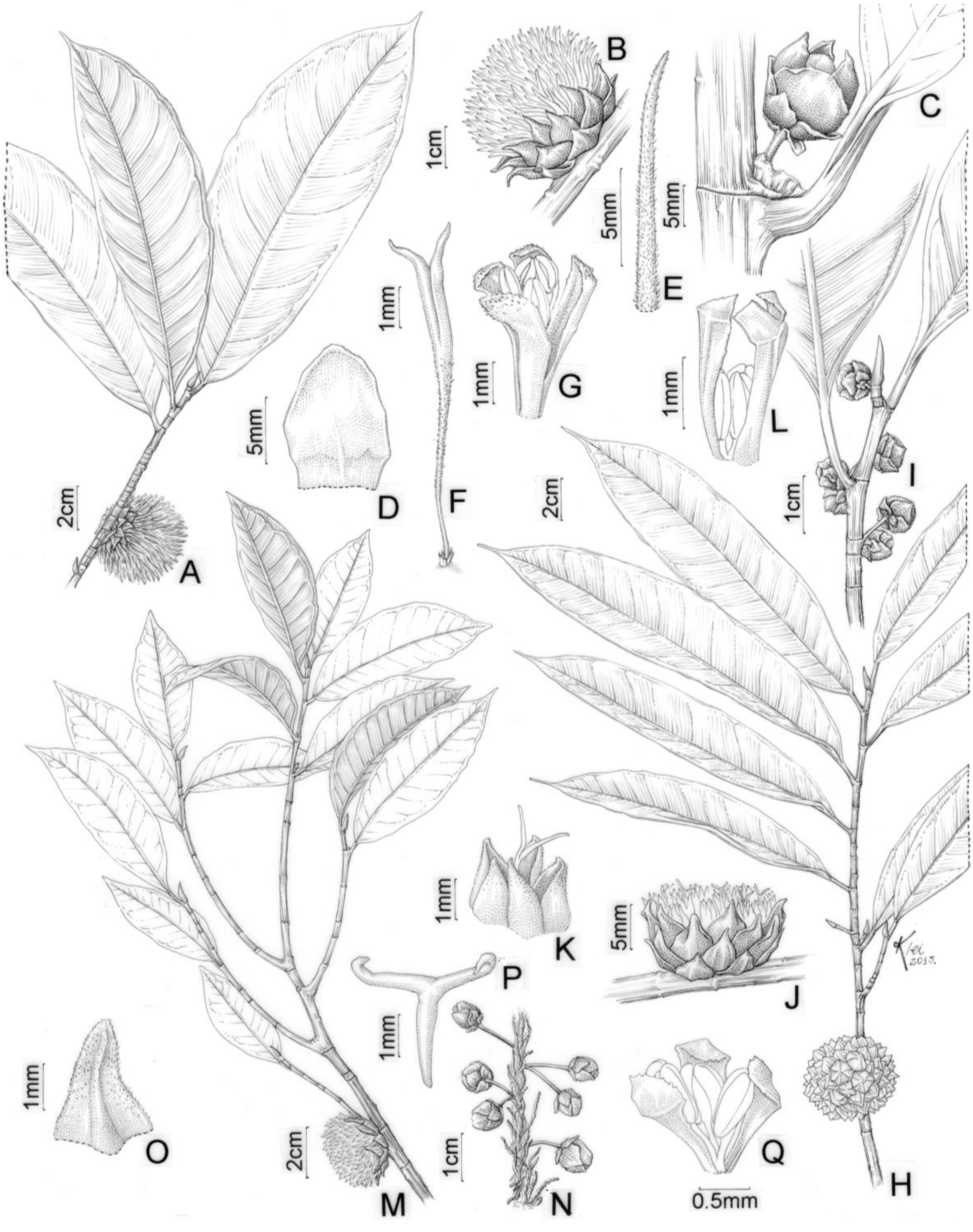

FIGURE 15. General morphology. *Naucleopsis ulei* subsp. *amara* **A.** Habit, *M.R. Santos, 98* (MG). **B.** Pistillate inflorescence, *A. Ducke s.n.* (RB 35438). **C.** Staminate inflorescence, *P. Cavalcnte 348* (MG). **D.** Ovate bracts, *A. Ducke s.n.* (RB 35438). **E.** Free pseudo-tepals, *A. Ducke s.n.* (RB 35438). **F.** Stigma *A. Ducke s.n.* (RB 35438). **G.** *Naucleopsis caloneura* **H.** Habit, *C. Dick 131* (INPA). **I.** Staminate inflorescence, *J. Lima et al. 135* (INPA), **J.** Pistillate inflorescence, *P. Kukle 172* (SP). **K.** Pistillate flower, *P. Kukle 172* (SP). **L.** Staminate flower, *J. Lima et al. 135* (INPA). *Naucleopsis capirensis* **M.** Habit, *G. Herrera 2018* (BG). **N.** Staminate inflorescence, *W. Haber & W. Zuchowski 11845* (BG), **O.** Deltoid bracts, *G. Herrera 2018* (BG). **P.** Pistillate flower, free pseudo-tepals, subulate-acuminate. **Q.** Staminate flower, *W. Haber & W. Zuchowski 11845* (BG).

Treelet to tree, 3-6 m tall; latex not seen. Leafy twigs with conspicuous short internodes, 3-5 mm thick, brown-grayish, glabrous to pubescent, ridged to slightly peeling; lenticels conspicuous. Leaves distinctly obovate, (9.5-)20-45 cm long., (2-)5-10 cm broad, coriaceous, without perforations; both faces glabrous; smooth beneath; attenuate at the base; caudate to acuminate at the apex; margin entire; primary veins yellow-greenish, less often brown-reddish, secondary veins 15-28 pairs; prominent beneath; curved- arched to the margin; petioles 1-2.6 cm long.; stipules 1-2 cm long., persistent in the internodes. Staminate inflorescences solitary, 4-7 mm diam.; peduncle 2-3 mm long., puberulous; involucre with ovate, pubescent, smooth bracts, in 4-5 series; perianth 2.3 mm high; tepals 3-5, basally connate; stamens 1-2; filaments free. Pistillate inflorescences often 2-4 together, 8-10 mm diam., sessile; involucre with ovate, brownish, puberulent smooth bracts, in 5-6 series; indistinct perianth, free pseudo-tepals, 3-5 mm high, subulate, glabrous to puberulent; stigmas filiform. Infructescences globoid (3-)4-8(-l0) cm diam.; indistinct fruiting perianth; fruiting pseudo-tepals to 0.5-1 cm high, subulate.

Representative specimens:—BRAZIL. Amazonas: Manaus, Reserva florestal Ducke, 23 November 2012, (♀), *A. Santos et al. 163* (SP). ECUADOR. Pastaza: Lorocachi, 01º36’S 75º59’W, 31 May 1980, (♂), *J. Jaramillo et al. 31580* (US). PERU. Loreto: Maynas, 03º28’S 72º50’W, (♀), *R. Vásquez et al. 12138* (BG), Rio Amazonas below Iquitos, 25 May 1991, (♀), *A. Gentry & R. Ortiz 74198* (BG), Indiana, 03º30S 72º58’W, (♀), *C. Grández et al. 4913* (BG), San Rafael, Rio Marañon, 03º46’S 73º03’W, 03 September 1989, (♀), *D.C. Daly et al. 6160* (NY).

Distribution and habitat:—Brazilian, Colombian, Peruvian and Ecuadorian Amazon, in varzea forest, rare terra firme forest, ca. up to 200 above sea level.

Vernacular Name:—unknown.

Etymology:—The epithet problaby refers to the low-growing of the plant.

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis humilis* is considered Endangered, EN B1a,b(iii), because of the small extent of occurrence only in the Amazon region (Brazil, Colombia, Ecuador and Peru) (ca. 3.301 km^2).

Notes:—*Naucleopsis humilis* is morphologically similar with *N. krukovii* due to the leaves with veins yellow-greenish beneath when dried and also shows similarities to *N.ulei* due to leafy twigs with conspicuous short internodes, but is distinguished of both especially by obovate leaf and acute-attenuate base.

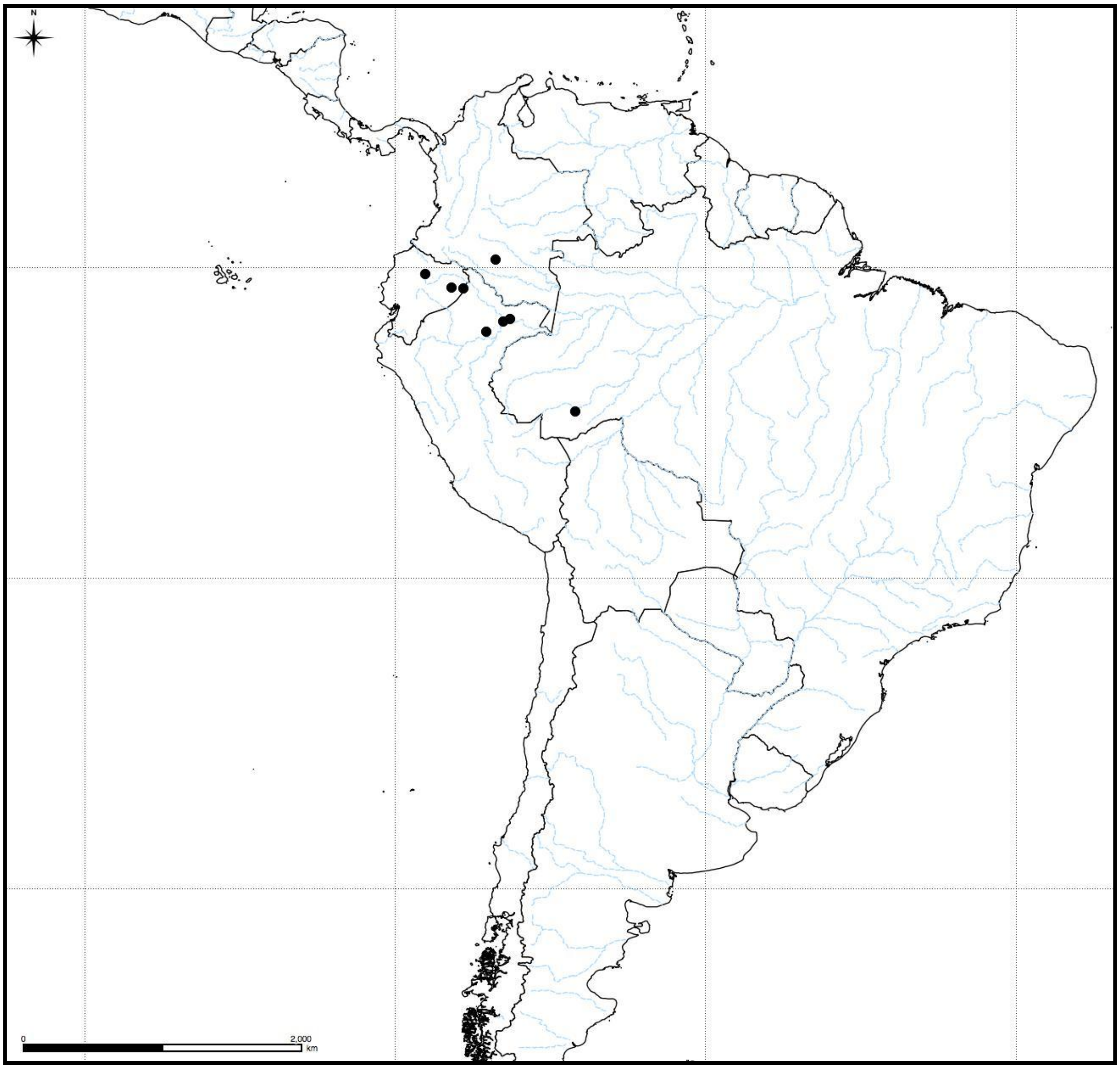

FIGURE 16. Distribution maps of *Naucleopsis humilis.*

11. ***Naucleopsis imitans*** (Ducke) C.C.Berg (1969: 465).

Basiônimo: *Ogcodeia imitans* Ducke (1939: 18). Lectotype (designated by Berg 1972):—PERU. Loreto: mouth of Río Pébas, (♀), *A. Ducke s.n.* (HJBR 19492), RB!, isotype B!, K!, U [photo!], US [photo!].

Fig. 22 A-D.

Treelet to tree, (3-)5-15 m tall; latex white to yellowish. Leafy twigs with long internodes distinctly different in length, 4-11 mm thick, brownish, pubescent, ridged to slightly peeling; lenticels inconspicuous. Leaves oblong-lanceolate, often wrinkled, 24-56 cm long., 7-11 cm broad, coriaceous, without perforations, both faces glabrous; acute to obtuse at the base, equilateral; acuminate at the apex, margin entire; primary veins yellow-greenish, secondary veins 18-26 pairs; strongly prominent beneath, curved-arched to the margin; petioles 13-35 mm long., upper portion smooth, thickened at the base; stipules 1.5-3.5 cm long., entire margin, caducous. Staminate inflorescences 3-8 together, 4-5 mm diam.; peduncle 4-8 mm long, puberulous; involucre with deltoid to ovate, densely pubescent, smooth bracts; in 7-8 series; perianth 2.3 mm high; tepals 3-7, free; stamens 3-4, filaments free. Pistillate inflorescences solitary 15-20 mm diam.; sessile to peduncle to 8 mm long.; involucre with deltoid to ovate, brownish, pubescent, smooth bracts, in 5-10 series; indistinct to distinct perianth, 1.5-5 mm high, connate at the base or free, 5-8 parted; stigma filiform; free pseudo-tepals peripheral or among the flowers, acuminate to subulate. Infructescences 4-8 cm diam.; indistinct to distinct fruiting perianth; fruiting pseudo-tepals to 1 cm high, deltoid to subulate.

Representative specimens:—BRAZIL. Acre: Sena Madureira, Fazenda São Jorge I, BR 364, km 107, 09º25’54”S 68º37’26”W, 22 April 2010, (♂), *C.C. Berg et al* 486 (SP),

(♀), *H. Medeiros 486* (RB). Quixadá, 30 km below of Rio Branco, along Rio Acre, 10ºS 67º50’W, 19 October 1980, *B. Nelson 744* (MG, RB), 33 km from Rio Branco, Rio Branco-Porto Acre, 12 October 1980, (♀), *S.R. Lowrie et al. 499* (INPA). Amazonas: Boca do Acre, N bank of Rio Purus, 20 September 1966, (♂), *G.T. Prance et al. 2426* (INPA). Esperança, Rio Jamari, 03 February 1942, (♀), *A. Ducke 1456* (IAN, RB). Fonte Boa, Paraná do Mineruá, 02º42’S 65º59’W, 03 November 1986, (♀), *C.A. Cid et al. 8391* (INPA). PERU. Loreto: Maynas, Iquitos, Mishana, ca. 45 km Iquitos, up Rio Nanay, 03 December 1976, (♀), *C. Davidson 5236* (US). Recreo, 03º42’S 72º50’W, 17 October 1983, *R. Vásquez & N. Jaramillo 4477* (NY).

Vernacular Name:— muiratinga (Brazil, Amazonas region).

Etymology:—The epithet probably refers to similarity with *N. glabra.*

IUCN conservation status:—*Naucleopsis imitans* is considered Vulnerable, VU B1a,b(iii), because of the small extent of occurrence only in the amazon region (Brazil, Colombia, Ecuador and Peru) (ca. 5.499 Km^2).

Notes:— Ducke (1939) proposed *Ogcodeia imitans* based in the indistinct perianth of pistillate flowers of this species. However, Berg (1969) noted that this species can present indistinct to distinct perianth and transferred to *N. imitans*. Berg (1972, 2001) argued that *N. imitans* is an intermediate between *Naucleopsis* and *Ogcodeia.*

Often, *N. imitans* presents indistinct perianth and for this reason is similar to *N. glabra*, but can be easily recognized because of petiole with upper portion smooth, thickened at the base.

As well as in *Naucleopsis acreana* and *caloneura*, in *N. imitans* also is possible to look clearly the distinct perianth with single flowers and the free pseudo-tepals peripherical on receptacle. The organization of these features on receptacle with free pseudo-tepals concentrated in periphery facilitates the recognition of these species, because the most other species of *Naucleopsis* present the free pseudo-tepals sparse on receptacle.

Distribution and habitat:—Brazil, Colombia, Ecuador and Peru in tropical moist evergreen forest, in mostly lowland moist area, often in riparian forest, at an elevation about 50 to 450 m above sea level.

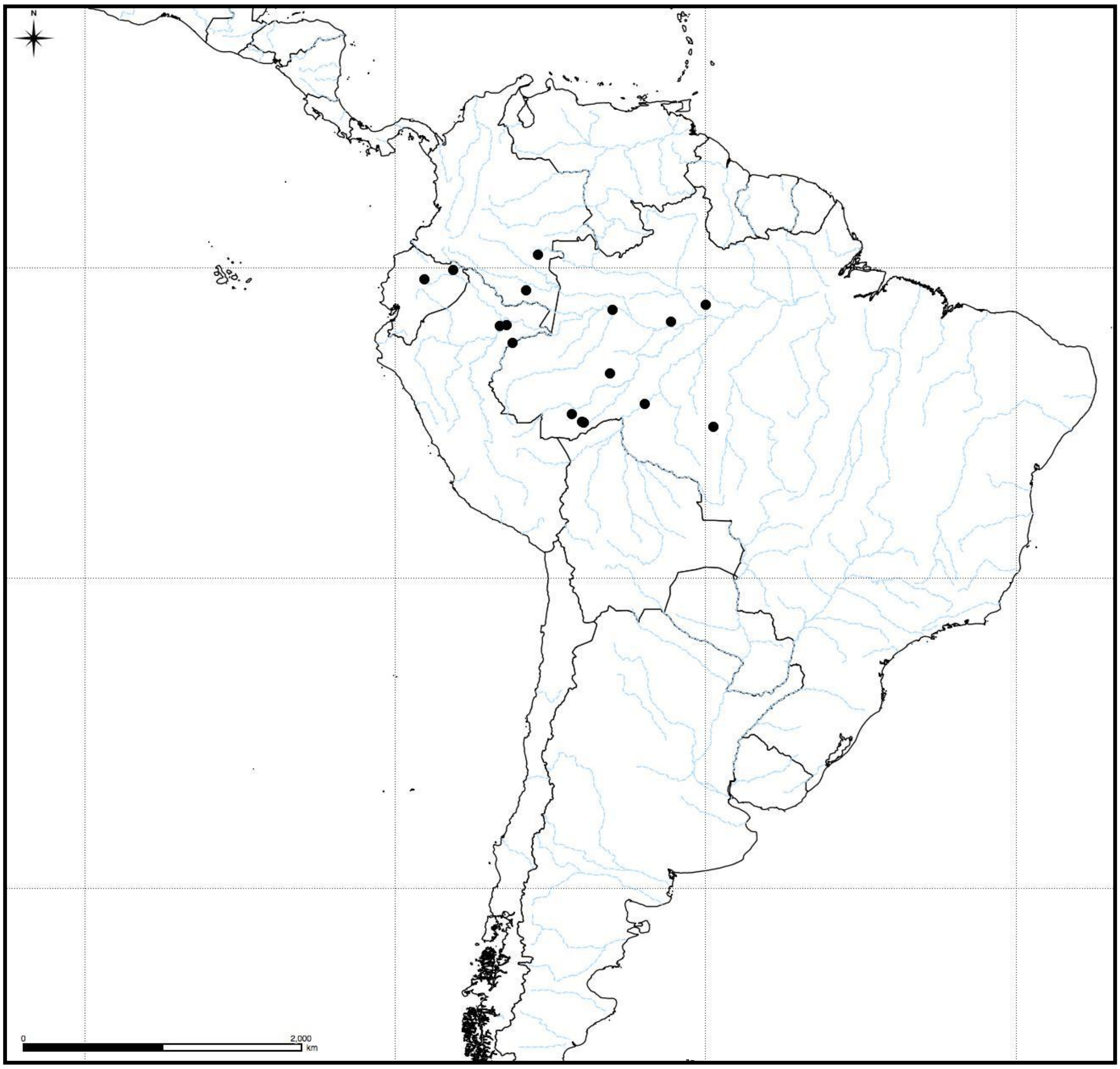

FIGURE 17. Distribution maps of *Naucleopsis imitans.*

12. *Naucleopsis inaequalis* (Ducke) C.C.Berg (1969: 465).

Basiônimo: *Ogcodeia inaequalis* Ducke (1939: 19). Lectotype (designated by Berg 1972):—BRAZIL. Amazonas: near Borba on rio Madeira, (♀) and (♂), *A. Ducke s.n.* (HJBR 23618), lectótipo RB!, isolectótipo B!, G [photo!], K!, P!, S [photo!], U!].

Fig. 22 E-J

Tree (4-)7-12(-15) m tall; latex not seen. Leafy twigs with long internodes distinctly different in length, 2-3 mm thick, brownish, glabrescente to puberulous or pubescent, slightly ridged; lenticels conspicuous. Leaves lanceolate to oblong, (8-)9-(19) cm long., 2.5-4.5(-5.5) cm broad, chartaceous, without perforations; both faces glabrous, smooth beneath; one side obtuse and other attenuate at the base, distinctly inequilateral; acute-acuminate at the apex; margin entire; primary veins brown-reddish, secondary veins 12-24 pairs, plane beneath, straight to arched to the margin; petioles 0.5-1 cm long.; stipules 0.4-1 cm long., entire margin, caducous. Staminate inflorescences 1-3 together, 06-12 mm diam.; peduncle 2-10 mm long., puberulous; involucre with ovate, puberulous, smooth bracts, in 3-4 series; perianth 1.5-2.5 mm high; tepals 2-5, free; stamens 2-4; filaments free. Pistillate inflorescences solitary or 2 together, 10-15 mm diam., sessile to 2 mm long.; involucre with ovate, puberulous, smooth bracts, in ca 4 series; indistinct to distinct perianth, 1.5-2 mm high, connate at the base, puberulent; stigma filiform; free pseudo-tepals peripheral, acuminate. Infructescences globoid, 1.5-2.5 cm diam.; indistinct fruiting perianth; fruiting perianth to 0.5 cm high, acuminate.

Representative specimens:—BRASIL. Acre: Acrelândia, rio Abunã, 10º02’53”S 66º48’59”W, 25 March 2011, (♀), *H. Medeiros et al. 824* (RB). Porto Acre, Reserva Florestal Humaitá, basin of Rio Purus, left of Rio Acre, 09º48’00”S 69º12’00”W, 02 November 1993, (♂), *M. Silveira et al. 700* (INPA). Senador Guiomar, Rio Iquiri, BR 364, Km 28, 10º04’59”S 67º32’42”W, 17 April 2010, (♀), *H. Medeiros et al. 388* (SP). Amazonas: Manaus, Porteira, 5 December 1973, (♂), *B.S. Pena 436* (IAN), Rio Madeira, 19 November 1968, (♀), *G.T. Prance 8644* (MG). Humaitá, 11 November 1977, (♂), *H. Ferreira 61* (RB). Rondônia: Road Presidente Médici-Alvorada, Rio Muqui, 18 November 1983, (♀), *M.G. Silva 6213* (SP), Rio Machado, February 1981, (♀), *M. Goulding 1415* (MG). BOLIVIA. Pando: South bank of Rio Abunã, 5 km above mouth, 14 November 1968, (♂), *G.T. Prance et al. 8411* (MG), W bank of Rio Madeira opposite Abunã, 19 November 1968, (♂), *G. T. Prance et al. 8646* (INPA).

FIGURE 18. Distribution maps of *Naucleopsis inaequalis.*

Distribution and habitat:—Amazon region (Brazil and Bolivia), in terra firme forest or varzea, in lowland moist area, at an elevation of up to about 150 m above sea level.

Vernacular Name:— muiratinga (Brazil, Amazonas region).

Etymology:—The epithet refers to the unequal base of the lamina leaf.

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis inaequalis* is considered Endangered, EN B1a,b(iii), because of the small extent of occurrence only in the Amazon region (ca. 2.395 km^2).

Notes:—*Naucleopsis inaequalis* is related to *N. guianensis* by distinctly inequilateral base, but can clearly differ by free pseudo-tepals sparse and fruiting indistinct perianth. In contrast, *N. guianensis* presents distinct periant deltoid and free pseudo-tepals peripherical. Also, *N. guianensis* only occurs in the region of the Guyanas, while *Naucleopsis inaequalis* occurs in Amazon region of Brazil and Bolivia.

13. *Naucleopsis insculptula* Ducke (1939: 16)

Type:—BRAZIL. Amazonas: near Serra do Dedal, W of Lado de Faro, no date, (♀), *A. Ducke s.n.* (HJBR 19493), (holotype RB!, isotype B!, INPA!, K!, [photo!]).

Fig. 22 K-N

Tree 7-20 m tall; latex cream. Leafy twigs with long internodes distinctly different in length, 4-6 mm thick, brownish, glabrescente to puberulous or pubescent to tomentose, ridged; lenticels conspicuous. Leaves lanceolate, 15-27 cm long., 4-7.5 cm broad, coriaceous, without perforations, glabrous above, scabrous beneath; acute to obtuse at the base, equilateral; acute-acuminate at the apex; margin entire; primary veins brown-reddish, secondary veins 14-18 pairs, plane beneath, straight to arched the margin; petioles 1-2 cm long.; stipules 0.7-1 cm long., entire margin, caducous. Staminate inflorescences 1-5 together, 5-10 mm diam.; peduncle 2-9 mm long., puberulous; involucre with ovate, puberulous smooth bracts; perianth 2-2.5 mm high; tepals 3-7, free; stamens 2-4; filaments free. Pistillate inflorescences solitary, 10-20 mm diam., sessile to 0.6 mm long.; involucre with ovate, puberulous, smooth bracts, in 4-5 series; distinct perianth 3-5 mm high, connate, 4-6 parted, puberulent; stigma filiform; free pseudo-tepals peripheral, acuminate. Infructescences glodoid, 2-5 cm diam.; distinct fruiting perianth, fruiting perianth to 1.5 cm high, ovate.

Representative specimens:—BRAZIL. Amazonas: Manaus, 14 January 1972, (♀), *O. P. Monteiro 147* (EAFM), Reserva Florestal Ducke, 11 December 1963, (♂), *W. Rodrigues & D. Coelho 5593* (RB), 02°53’S 59°58’W, 20 January 1965, (♂), *W. Rodrigues & Osmarino 6842* (RB), (♀), 22 March 1994, *J. E. L. S. Ribeiro et al. 1231* (MG, SP), 25 October 1995, (♂), *J. E. L. S. et al. 1741* (SP), Manaus-Itacoatiara Road., km 26, 6 December 2001, (♀), *C. V. Castilho 437* (INPA), Distrito Agropecuário da Suframa, BR 174, km 64, then 23 km east on ZF3, Fazenda Esteio, 02°25’S 59º52’W, 24 March 1987, (fr.), *E. Setz s.n.* (UEC 43755), 08 February 1991, (♀), *E. Setz s.n.* (UEC), 02º23’S 59º51’W, 28 January 1992, (♂), *M. Nee 42333* (INPA), Fazenda Porto Alegre, 02º22’S 59º57’W, 26 October 1984, (♂), *M. J. R. Pereira & Equipe s.n.* (INPA 174074), km 72, Fazenda Dimona, 02º19’S 60º05’W, 24 November 1989, (♂), *P. Kukle 93* (INPA, SP), 27 March 1992, *C. Dick 82* (SP), Reserva Biológica do INPA, Manaus-Caracaraí Road., km 60, 18 February 1977, (♀), *J. R. Nascimento & J. G. Oliveira 515* (INPA). Pará: Rio Tapajóz, 10 December 1919, (♀), *A. Ducke s.n.* (RB 13028). Pará: Igarapé kazuo, km 1221, 20 November 1977 (♀), *G.T. Prance et al. P 25594* (MG).

Distribution and habitat:—North of Brazil (Amazonas and Pará) often in Terra Firme forest of the Amazonian region, usually in lowland moist areas.

Vernacular Name:—muiratinga (Brazil)

Etymology:—The epithet probably suggests to the sunken markings veins of the leaf.

FIGURE 19. Distribution maps of *Naucleopsis insculptula.*

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis insculptula* is considered Endangered, EN B1a,b(iii), because of the small extent of occurrence only in the Brazilian Amazon region (ca. 1.425 km^2).

Notes:—This species was synonymized by Berg (1972) in *N. caloneura*, but these are completely different. In *N. insculptula* the leaves are glabrous above, scabrous beneath, the pistillate inflorescences are larger, and the perianth is connate. In contrast, *N. caloneura* has its leaves with both faces glabrous, the pistillate inflorescences are smaller, and the perianth is deltoid. For these reasons, we proposed the reestablishment of *Naucelopsis insculptula*.

14. *Naucleopsis jamariensis* C.C.Berg (1969: 465).

Type:—BRAZIL. Rondônia: Papagaios, Rio Jamary, (fr.), *J. G. Kuhlmann s.n.* (HJRB 13030) (holotype RB!).

Tree; latex not seen. Leafy twigs with long internodes distinctly different in length, 4-8 mm thick, brown-grayish, glabrous to pubescent, ridged; lenticels conspicuous. Leaves lanceolate, 17-32 cm long., 5-9 cm broad, coriaceous; without perforations, both faces glabrous, smooth beneath; acute at the base, equal; caudate at the apex; margin entire; primary veins brown-reddish, secondary veins 18-19 pairs; prominent beneath, curved-arched the margin; petioles, 6-10 mm long.; stipules 1-1.4 cm long., entire margin, caducous. Staminate inflorescences 2-5 together, 5-10 mm diam.; peduncle 5-8 mm long., puberulous; involucre with ovate, puberulous to pubescent, smooth bracts, in 4-5 series; perianth 1-1.2 mm high; tepals 4-5, free; stamens 3-5, filaments free. Pistillate inflorescences not seen. Infructescence globoid ca. 6 cm diam.; indistinct fruiting perianth, fruiting pseudo-tepals to 0.7 cm high., subulate.

Representative specimens:—BRAZIL. Acre: Colocação Apui, 29 November 1991, (♂), *Sothers et al. 66* (NY).

Distribution and habitat:—North region of Brazil (Acre and Rondônia) in Terra Firme forest of the Amazonian region, usually in lowland moist areas, in riparian forest, at an elevation of about 100 m above sea level.

FIGURE 20. Distribution maps of *Naucleopsis jamariensis.*

Vernacular Name:—unknown

Etymology:—The epithet is a tribute to type locality, the river Jamari.

IUCN conservation status:—*Naucleopsis jamariensis* is known only two collections in the state of Rondônia and Acre (Brazil), made between 1919 and 1999. Their extent of occurrence is ca. 957 km^2, however, the population size is unknown. For these reasons *N. jamariensis* is assessed as Data Deficient (DD) according to IUCN Red List criteria (IUCN 2015).

Notes:—*Naucleopsis jamariensis* resembles *N. caloneura* when in state vegetative, but distinguished when in state reproductive, by fruiting pseudo-tepals subulate. In contrast, *N. caloneura* presents fruiting perianth deltoid. This species is very rare. Berg (2001) complements its description including the staminate inflorescences and others specimens examined.

15. *Naucleopsis krukovii* (Standl.) C.C. Berg (1969: 465).

Basiônimo: *Pseudolmedia krukovii* Standl. (1937: 186). Type:—BRAZIL. Amazonas: São Paulo de Olivença, near Palmares, (♂), *B.A. Krukoff 8159* (holotype NY [photo!], isotype BM!, G [photo!], K!, LE [photo!], MO [photo!], P!, S [photo!], U [photo!], US [photo!].

Trees 7-25 m tall; latex white-yellowish to cream. Leafy twigs with long internodes distinctly different in length, 1.5-4.5 mm thick, brown-grayish to greenish, glabrous to sparsely puberulous, ridged to peeling; lenticels conspicuous. Leaves oblong to lanceolate, 4-22(-33) cm long., 6-10 cm broad, coriaceous, with or without perforations; both faces glabrous, smooth beneath; acute to obtuse at the base, equilateral; acuminate at the apex;

margin entire; primary veins yellow-greenish beneath; secondary veins 15-22 pairs, prominent beneath, curved- arched to the margin; petioles 0.5-1 cm long.; stipules 0.3-1.0 cm long., entire margin, caducous. Staminate inflorescences 2-8 together, 3-5 mm diam.; sessile to peduncle 3 mm long., puberulous; involucre with ovate to deltoid, puberulous, smooth bracts, in 7 series; perianth 2 -3 mm high, basally connate; stamens 1-3; filaments free. Pistillate inflorescences solitary or occasionally accompanied by staminate ones, 2-5 mm diam., sessile; involucre with deltoid to ovate, brownish, puberulous, smooth bracts, in 5-6 series; indistinct perianth, free pseudo-tepals, glabrous to puberulent, subulate; stigmas filiform. Infructescences globoid, 4-4.5 cm diam.; indistinct fruiting perianth; fruiting pseudo-tepals 3-7 mm long, subulate.

Representative specimens:—BRAZIL. Acre: Campinas, Highway Abunã to Rio Branco, km 242-246, 18 July, 1968, (♀), *E. Forero et al. 6343* (INPA). Cruzeiro do Sul, Rio Juruá and Rio Moa, 26 April 1971, (♂), *G.T. Prance et al. 12467* (MG). Senador Guiomar, Fazenda Catuaba, (♂), *A. Santos et al. 202* (SP). Amazonas: Highway Manaus to Porto Velho, 14 September 1972, (♀), *M.F. Silva & pessoal da botânica 757* (INPA). Tabatinga, 02 December 1945, (♀), *A. Ducke 1785* (SP). Telheiro, Rio Padauirí, near Rio Negro, 20 April 1952, (♂), *R.L. Fróes 28329* (IAN). Rondônia: Nova Mamoré, Rio Formoso, 10º19'S 64º53'35"W, 28 August 1996, (♀), *L. Carlos et al. 1370* (MG).

Distribution and habitat:—Bolivia, Brazil, Colombia, Ecuador and Peru, often in Terra Firme forest of the Amazonian region, at low elevations, 150 to 450

Vernacular Name:—unknown

Etymology:—The epithet honors B. A. Krukoff, a botanical collector

IUCN conservation status:—*Naucleopsis krukovii* is considered Vulnerable, VU B1a,b(iii), because of the small extent of occurrence only in the amazon region, Bolivia, Brazil, Colombia, Ecuador and Peru (ca. 7.680 Km^2).

Notes:—Morphologically, this species shows similarities with *N. humilis*, *N. sp2* and *N. sp3* due to the leaves greenish, veins yellow-greenish beneath when dried and lamina with perforations. In constrast, *N. humilis* can be distinguished by leaves without perforations and leaves obovate and short internodes.

N. krukovii, *N. sp2* and *N. sp3* are very similar vegetatively, however, they show great differences in pistillate inflorescences and infructescences. The fruiting perianth in *N. krukovii* is glabrous to puberulent, subulate, in *N. sp2* is puberulous to velutinous, oblate and in *N. sp3* tomentose, subululate.

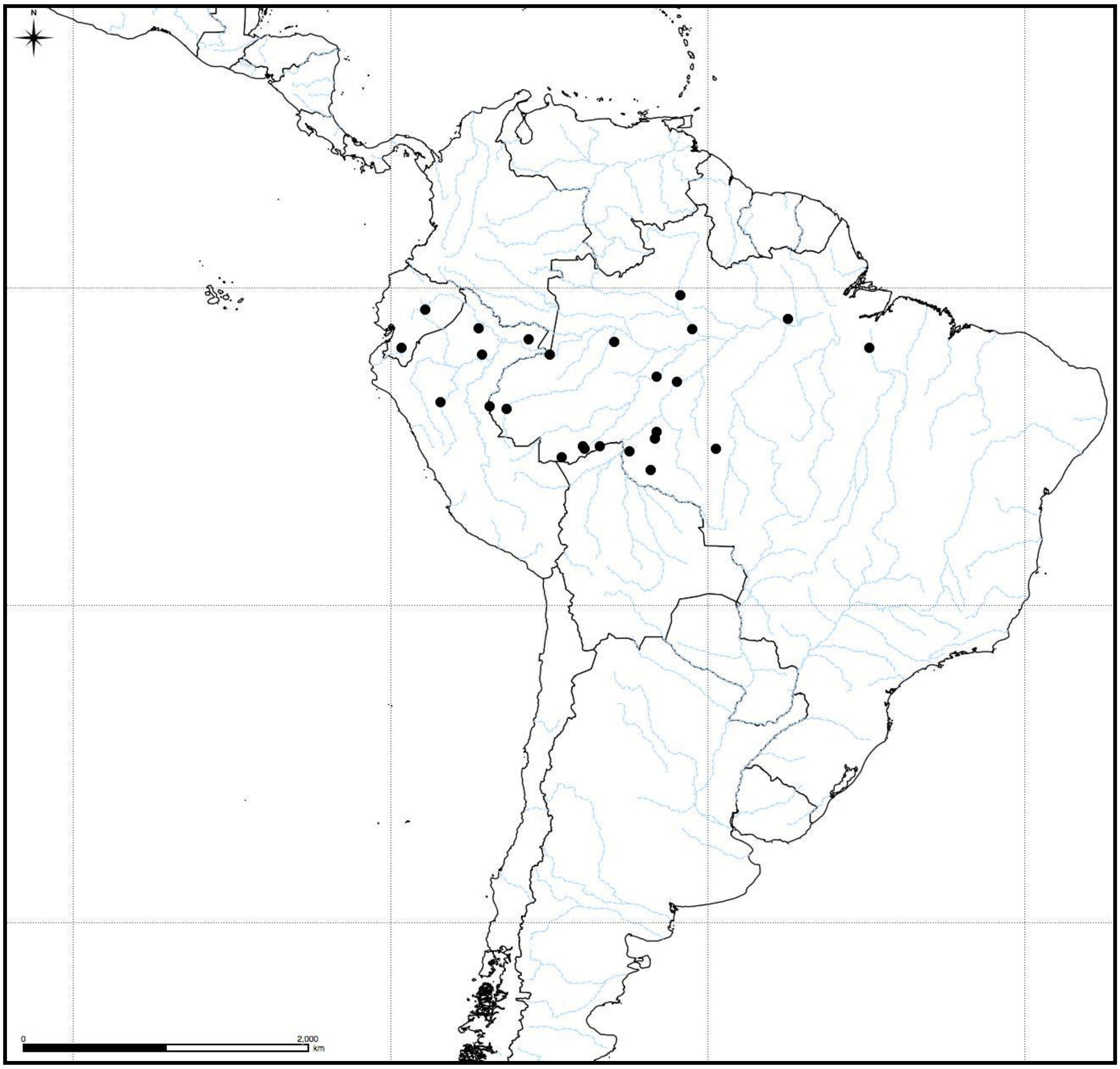

FIGURE 21. Distribution maps of *Naucleopsis krukovii.*

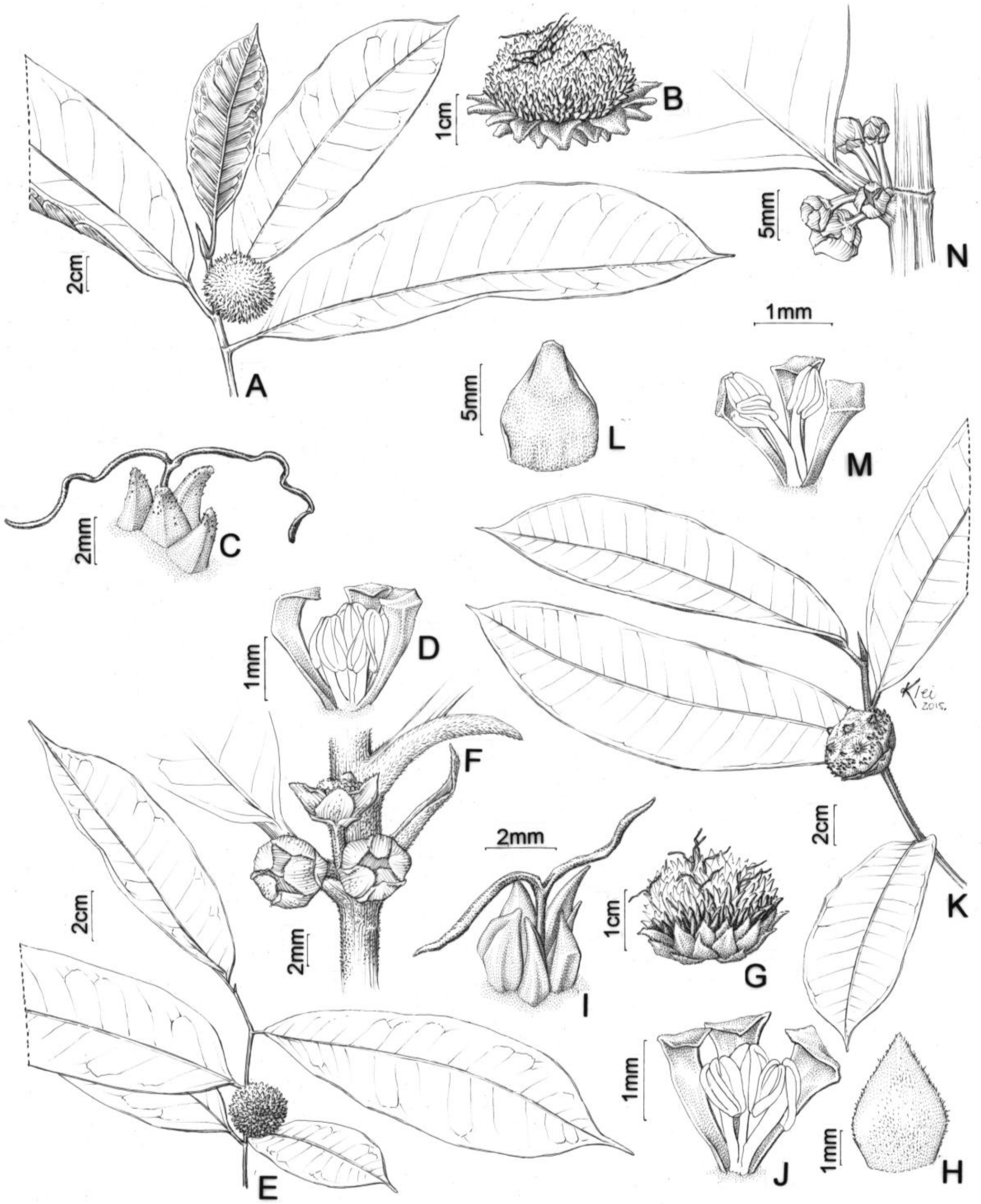

FIGURE 22. General morphology. *Naucleopsis imitans* **A.** Habit, *S.R. Lowrie et al. 499* (INPA). **B.** Pistilate inflorescence, *A. Ducke 1456* (RB). **C.** Pistillate flower, free pseudo-tepals, *A. Ducke 1456* (RB). **D.** Staminate flower, *G.T. Prance et al. 2426* (INPA). *Naucleopsis inaequalis* **E.** Habit, *H. Medeiros, 824* (SP). **F.** Staminate inflorescence, *B.S. Pena 436* (IAN). **G.** Pistillate inflorescence, distinct to indistinct perianth, *M.G. Silva 6213* (SP). **H.** Details ovate bracts of the pistillate inflorescence, *M.G. Silva 6213* (SP). **I.** Pistillate flower, free pseudo-tepals, *M.G. Silva 6213* (SP). **J.** Staminate flower, *B.S. Pena 436* (IAN). *Naucleopsis insculptula* **K.** Habit, *E. Setz s.n.* (UEC 43755). **L.** Details bracts of the pistillate inflorescence, *G.T. Prance et al. P 25594* (MG). **M.** Staminate flower, *W. Rodrigues & D. Coelho 5593* (RB). **N.** Staminate infloresce, *W. Rodrigues & D. Coelho 5593* (RB).

16. *Naucleopsis macrophylla* Miq. (1853: 120).

Type:—BRAZIL. Amazonas: rio Japurá, no date, *Martius s.n.* (holotype M [photo!], isotype U!).

Perebea macrophylla (Miq.) Renner (1907: 372). Type:—BRAZIL. Amazonas: rio Japurá, no date, *Martius s.n.* (holotype M [photo!], isotype U!).

Ogcodeia venosa Ducke ex Mildbr. (1932: 423). Type:—BRAZIL. Rondônia: Porto Velho, Rio Madeira, 07 November 1923, (♂), *A. Ducke s.n.* (HJBR 19491) (holotype B!).

Tree 5-12 m tall; latex white-yellowish to cream. Leafy twigs with long internodes distinctly different in length, 5-6 mm thick, brownish, puberulous to pubescent or velutinous, slightly ridged; lenticels conspicuous. Leaves lanceolate to oblong-lanceolate, 25-36 cm long., 7-12 cm broad, coriaceous, without perforations; glabrous above, pubescent to puberulent beneath, smooth beneath; acute-attenuate at the base, acute-acuminate at the apex; equilateral; margin entire; primary veins brown-reddish, secondary veins 16-18 pairs, strongly prominent beneath, curved-arched to the margin; petioles 1.5-3.0 cm long.; stipules (1.2-)1.5-2.0 com long., entire margin, caducous. Staminate inflorescences 2-8 together, 8-20 mm diam.; sessile to peduncle 10 mm long., pubescent to tomentoso-velutinous; involucre with ovate to deltoid, puberulous to pubescent, smooth bracts, in 3 series; perianth 1.5-3 mm high; tepals 2-5, free or basally connate; stamens 3-4, filaments free. Pistillate inflorescences solitary, 20-30 mm diam., sessile to peduncle 2-3 mm long.; involucre with ovate to deltoid, brownish, pubescent, smooth bracts, in ca 4 series; distinct perianth 4-6 mm high, connate, parted 4-6 at the apex, puberulent to velutinous, stigma filiform. Infructescences globoid, 3-8 cm diam.; distinct fruiting perianth, perianth fruiting 1-1.5 cm high; ovate.

Representative specimens:—BRASIL. Amazonas: Manaus, 17 September 1929, (♂), *A. Ducke s.n.*, 25 April 1932, (RB 141607), (RB 19491), *A. Ducke s.n.* (INPA 15594), 04 June 1932, (♂), *A. Ducke s.n.*, (RB 23985), Estrada do Tarumã, 25 April 1932, (♂), *A. Ducke s.n.* (INPA 14959), Rio Taruná, 27 September 1932, (♀), *A. Ducke s.n.* (SP 444901). Rondônia: Buritis, BR 421, km 162, 02 December 1996, (♀), *L.C.B. Lobato et al. 1333* (MG), Vila Caneco-Mineirão, Jacundá, 106 km de Porto Velho, 09º07’24”S 62º54’00”W, 26 October 1979, (♀), *G. Vieira et al. 289* (INPA, RB), Madeira, 07 November 1923, (♂), J. *Kuhlmann* 270 (INPA), Cujubim, 05 November 1997, (♂), *L.C.B. Lobato et al. 1952* (MG), represa Samuel, 09º00’00”S 63º15’00”W, 07 June 1986 (♂), *W. Thomas et al. 4950* (BG). Porto Velho. BOLIVIA. Pando: W bank of rio Madeira, opposite Penha Colorado, 20 November 1968, (♀), *G.T. Prance et al. 8704* (INPA).

Distribution and habitat:—Brazil and Bolivia; often in Terra Firme forest of the Amazonian region, usually in lowland moist areas, sometimes in riparian forest, at an elevation of about 50 to 150 m above sea level.

Vernacular Name:—quina (Brazil).

Etymology:—The epithet refers to the size of the leaves.

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis macrophylla* is considered Endangered, EN B1a,b(iii), because of the small extent of occurrence only in the amazon region (ca. 4.675 km^2).

Notes:—Nearly all the species of *Naucleopsis* are glabrous or puberulent in the abaxial face leaf, but *N. macrophylla* is in the group with leaves pubescent beneath. This species is related to *N. riparia.* However, *N. riparia* is distinguished by pistillate inflorescences with yellowish dense-velutionous bracts and perianth fruiting deltoid. In contrast, in *N. macrophylla* pistillate inflorescences with ovate to deltoid, pubescent bracts and perianth fruiting ovate.

FIGURE 23. Distribution maps of *Naucleopsis macrophylla.*

17. *Naucleopsis meridionalis* (C.C. Berg) Al. Santos & Romaniuc, *stat. nov.*

Naucleopsis naga subsp. *meridionalis* C.C. Berg (1996: 238).

Type:—COLOMBIA. Nariño: La Planada Reserve, near Ricaurte, 21 December 1987, (♀), A. H. Gentry 59669 (holotype PSO [photo!], isotype BG!, COL [photo!], MO [photo!], SI *n.v.*).

Fig 9 E-G.

Tree 10-25 m tall; latex yellowish to cream. Leafy twigs with long internodes distinctly different in length, 3-5 mm thick, brownish, glabrescente to puberulous-pubescent, ridged; lenticels conspicuous. Leaves lanceolate to elliptic, 16-22 cm long., 6-8 cm broad, coriaceous, without perforations; glabrous above, scabrous beneath; acute to obtuse at the base, equilateral; acute-acuminate apex; margin entire; primary veins brown-reddish, secondary veins 16-20 pairs, strongly prominent beneath, straight to curved-arched to the margin; petioles 0.7-1 cm long.; stipules 1.2-2 cm long., entire margin, caducous. Staminate inflorescences 1-2 together, 0.6-3.0 mm diam.; puberulous; peduncle 2-7 mm long.; involucre with ovate to deltoid, puberulent, smooth bracts, in 5-9 series; perianth 2-2.5 mm high; tepals 3-5, free; stamens 2-4, filaments free. Pistillate inflorescences solitary, 10-20 mm diam., sessile to peduncle 6 mm long.; involucre with ovate, puberulous smooth bracts, in ca 3-5 series; indistinct perianth, free pseudo-tepals, puberulent, acuminate to subulate; stigma filiform. Infructescences discoid, 5-8 cm diam.; indistinct fruiting perianth; fruiting perianth to 1 cm high, subululate.

Representative specimens:—ECUADOR. Carchi: Mira Canton, 00º51’N 78º13’W, 10 February 1992, (♂), *W. Palacios et al. 9674* (BG), 00º17’N 78º13’W, 10 February 1992, (♂), *W. Palacios et al. 9691* (BG). Cotopaxi: Cantón La maná, Reserva Ecológica lós Ilinizas, 00º44’18S 78º04’45”W, 12 June 2003, (♀), *P. Silverstone-Sopkin et al. 9048* (BG).

Distribution and habitat:—Andean region, from Colombia (Antioquia, Nariño, Risaralda) to Ecuador (Azuay, Bolívar, Carchi, Cotopaxi, Esmeraldas), at an elevation of about 600 to 2100 m above sea level.

FIGURE 24. Distribution maps of *Naucleopsis meridionalis.*

Vernacular Name:—unknown.

Etymology:—The epithet refers to distribution of the species in relation to *N. naga.*

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis meridionalis* is considered Endangered, EN B1a,b(iii), because of the small extent of occurrence only on the slopes of the Andes (Colombia to Ecuador) (ca. 2.540 km^2).

Notes:—This species was originally proposed as a subspecies of *Naucleopsis naga* by Berg & Franco (1996). These binomial are completely different: *N. meridionalis* can be easily distinguishable by leaves scabrous beneath and infructescences discoid, 5-8 cm diam. Differently, *N. naga* is distinguishable by leaves glabrous beneath and infructescences globoid, 4-6 cm diam.

For this reason, we proposed the species *Naucleopsis meridionalis* and synonymized of *N. naga* subsp. *meridionalis*.

18. *Naucleopsis naga* Pittier (1912: 83-85).

Ogcodeia naga (Pittier) Mildbr. (1932: 420). Type:—COSTA RICA. in pastures at La Colombiana, plains of Santa Clara, June 1899, (♀), *H. Pittier s.n.* (holotype US [photo!], isotype CR [photo!]).

Trees 6-15 m tall; latex white to yellow. Leafy twigs with long internodes distinctly different in length, 2-6 mm thick, greyish to brownish, puberulous, ridged; lenticels conspicuous. Leaves lanceolate, 20-40 cm long., 5-10 cm broad, coriaceous, without perforations, both faces glabrous, smooth beneath; acute to obtuse at the base, equilateral; acuminate to acute at the apex; margin entire; primary veins brown-reddish, secondary veins 22-30 pairs, prominent beneath, straight to curved-arched to the margin; petioles 7-22 mm long.; stipules 1-1.4 cm long., entire margin, caducous. Staminate inflorescences 3-

5 together, 5-10 mm diam.; peduncle 1.5-4 mm long.; involucre with deltoid to ovate verrucose bracts, in 4-6 series; perianth 2-2.5 mm high; tepals 3-5, free; stamens 2-4, filaments free. Pistillate inflorescences solitary, 7-15 mm diam., sessile; involucre with deltoid to ovate or lanceolate, glabrous, smooth bracts, in 3-5 series; indistinct perianth, free pseudo-tepals, puberulent, subulate; stigmas filiform. Infructescences globoid, 3-7 cm diam.; indistinct fruiting perianth; fruiting pseudo-tepals to 0.4 cm high, subulate.

Representative specimens:—COLOMBIA. Antioquia: Frontino, Vereda Venados, Parque Nacional Natural Las Orquídeas, 06º32'N 76º19'W, 04 February 1995, (♀), *J. Pipoly et al. 18394* (BG, K, NY). COSTA RICA. Limon: Cantón de Limón, 09º47'18'N 83º45'W, 10 April 1989, (♂), *G. Herrera & A. Chacón 2674* (BG), Finca La Lola, Madre de Dios, April 1949, (♂), *L.P. Holdridge 2536* (US). PANAMA. Panamá: Cerro Azul, 13 November 1975, (♀), R.C. Ho & J. Madrid 45 (NY).

Distribution and habitat:—From the Atlantic Costal region of Honduras to Pacific Costal region of Colombia, often moist areas, at an elevation of about to 2000 m above sea level.

Vernacular Name:—naga (Costa Rica), veneno teiug (Ecuador).

Etymology:—The epithet is a tribute to vernacular name (naga).

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis naga* is considered Endangered, EN B1a,b(iii), because of the small extent of occurrence from Atlantic Costal region of Honduras to Pacific Costal region of Colombia (ca. 4.366 km^2).

FIGURE 25. Distribution maps of *Naucleopsis naga.*

Notes:—In general, the species of *Naucleopsis* presents the staminate inflorescences morphologically very similar, but in this sense that *Naucleopsis naga* differs of other species of group. The verrucose bracts of staminate inflorescences are unique in *Naucleopsis.* The pistillate inflorescence shows resemblances with *N. jamariensis*, but distinguished by leaves secondary veins 22-30 pairs. In constrast, *N. jamariensis* presents leaves secondary veins 18-19 pairs.

19. *Naucleopsis oblongifolia* (Kuhlm.) Carauta (1994: 262).

Basionym: *Ogcodeia oblongifolia* Kuhlm. (1940: 77). Lectotype (designated by Berg 1972):—BRAZIL. Rio de Janeiro: Horto Florestal, no date, (♂), *Pessoal do Horto Florestal s.n.*, lectotype RB!, isolectotype G [photo!], U!.

Brosimum mello-barretoi Standl. (1940: 70). *Naucleopsis mello-barretoi* (Standl.) C.C. Berg (1969: 465). Type:—BRAZIL. Minas Gerais: Tombos, Fazenda Cachoeira, 16 July 1935, (♀), *Mello-Barreto 1658* (holotype F [photo!], isotype P!).

Trees 10-30 m tall; latex white to cream. Leafy twigs with long internodes distinctly different in length, 0.5-2.5 mm thick, brownish, glabrous or sparsely puberulous, ridged; lenticels conspicuous. Leaves narrowly oblong, (5-)13-20 cm long., 1.5-4.5(5) cm broad, chartaceous, without perforations, both faces glabrous, smooth beneath; acute to attenuate to obtuse at the base, equilateral; acute-acuminate at the apex; margin entire; primary veins brown-reddish, secondary veins 14-20 pairs, prominent beneath, often curved-arched to the margin; petioles 5-15 mm long.; stipules 0.4-1.4 cm long., entire margin, caducous. Staminate inflorescences 2-5 together, 4-8 mm diam.; peduncle 1-4 mm long., sparsely puberulous; involucre with deltoid to ovate, sparsely puberulous, smooth bracts, in ca 3-5 series; perianth 1-2 mm high, tepals 3-5, connate, 5-7 parted at the apex; stamens 1-4, filaments free. Pistillate inflorescences solitary, 4-8 mm diam., sessile to 1.5 mm long.; involucre with ovate to deltoid, puberulent, smooth bracts, in 4-5 series; distinct perianth 6-9 mm high, connate, parted 4-6 at the apex, stigmas filiform; free pseudo-tepals peripherical. Infructescences globoid, 1.5-2.0 cm diam.; distinct fruiting perianth; fruiting perianth 0.6-1 high, oblate.

Representative specimens:—BRAZIL. Bahia: Água Preta, 03 February 1937, (fr.), *G. Bondar 2179* (SP). Amargosa, Serra do Timbó, 13º10’00”S 39º09’W, 12 May 2007, (♀), *J.L. Paixão et al. 1250* (SP). Itabuna, 29 October 1970, (♂), *T.S. Santos 1226* (RB). Espírito Santo: Linhares, Reserva Natural da Companhia Vale do Rio Doce, 19°14’53”S 39º57’25”W, 23 January 2008, (♀), *J.A. Lombardi et al. 7109* (SPF). Sooretama, Reserva Biológica de Sooterama, Barra Seca, ca. 10 km of the BR 101, 19º05’09”S 39º56’54”W, 17 January 2011, *P. Fiaschi et al. 3460* (SP). Minas Gerais: Caratinga, Estação Biológica de Caratinga, 17 February 2002, (fr.), *J.V. Gomes 10* (SPF). Rio de Janeiro: Rio das Ostras, Reserva Biológica União, 09 June 1997, (fr.), *P.P. Oliveira 264* (SPF).

Distribution and habitat:—Amazon region (Brazil, Colombia, Ecuador and Peru) and in the Atlantic Forest (eastern of Brazil), in Terra Firme forest of the Amazonian region and in dense ombrophilous forest of the Atlantic forest, in lowland moist areas, often in riparian forest, at an elevation of about 15 to 500 m above sea level.

Vernacular Name:—amora-do-leite, bainha-de-espada, tramoia (Brazil).

Etymology:—The epithet refers to the oblong form of the lamina leaf.

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis oblongifolia* is considered Vulnerable, VU B1a,b(iii), because of the small extent of occurrence only in the amazon region (Brazil, Colombia, Ecuador and Peru) and in the atlantic forest (ca. 12.764 Km^2).

Notes:—*Naucleopsis oblongifolia* is more commonly found in Atlantic Forest, in Costal region of Brazil, but also occurs in the amazon region. *N. oblongifolia* is completely different of others of genus, because its oblate, connate fruiting perianth. In vegetative state is similar to *N. pauciflora,* but differs by its oblong leaf.

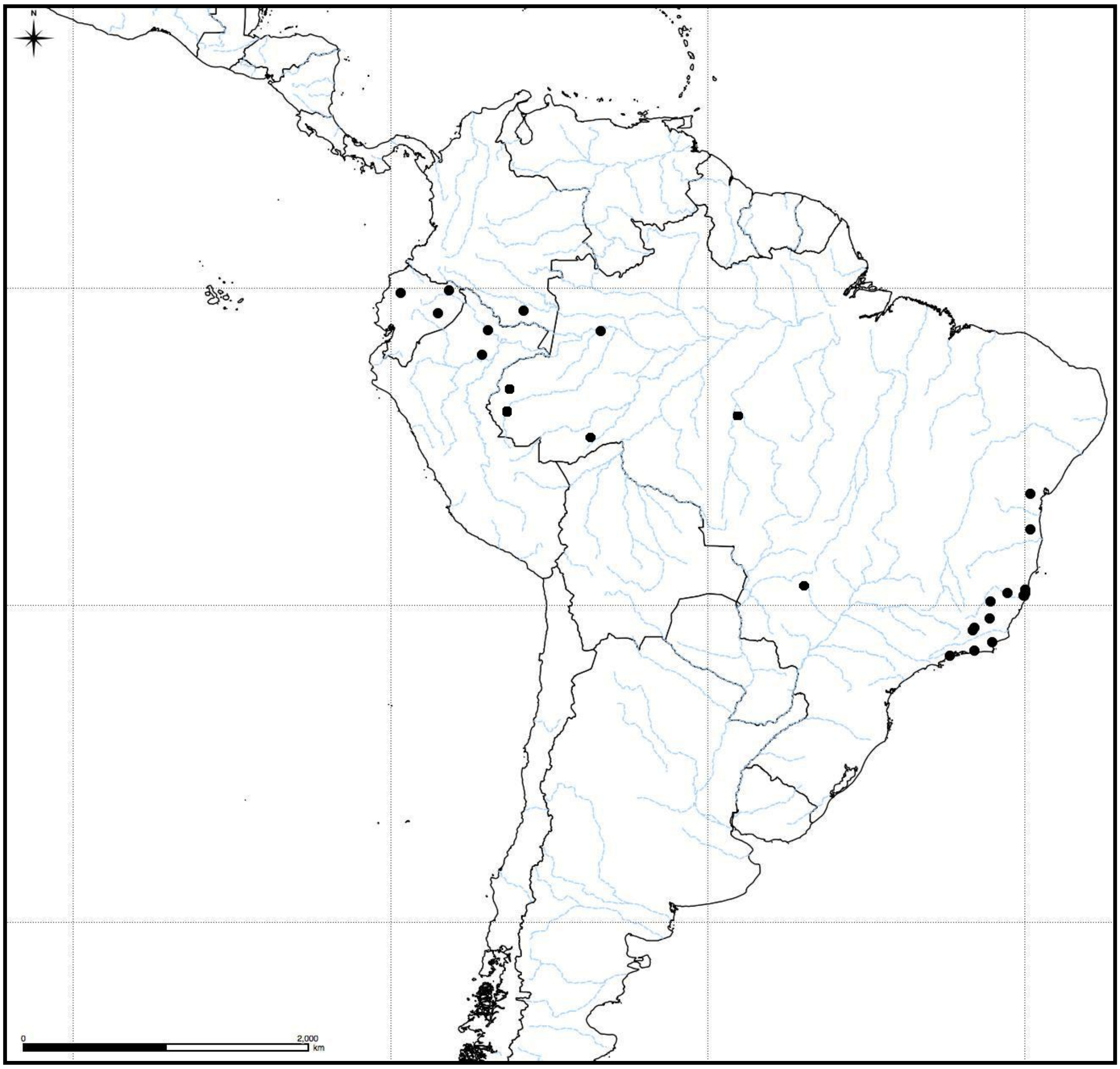

FIGURE 26. Distribution maps of *Naucleopsis oblongifolia.*

20. *Naucleopsis pauciflora* Ducke (1939: 16).

Lectotype (designated by Berg 1972):—BRAZIL. Amazonas: near Parintins, no date, (♀), *A. Ducke s.n.*, lectotype RB!, isolectotype G [photo!], K!, P!, U!, US [photo!].

Tree (4-)6-16 m tall; latex white to yellow. Leafy twigs with long internodes distinctly different in length, 2-3 mm thick, brownish, glabrous to puberulous, ridged to peeling;

lenticels conspicuous. Leaves obovate, 10-16 cm long., 2-4 cm broad, chartaceous to coriaceous, without perforations, both faces glabrous; attenuate at the base, equilateral; acute-acuminate at the apex; margin entire; primary veins brown-reddish, secondary veins 11-14 pairs, prominent beneath, straight to curved-arched to the margin; petioles 0.5-1.0 cm long.; stipules 0.4-0.9 cm long., entire margin, caducous. Staminate inflorescences 1-4 together, 2-7 mm diam.; sessile; involucre with ovate, pubescent, smooth bracts, in ca 3 series; perianth 1-1.2 mm high; tepals 3-5, free; stamens 4, filaments free. Pistilate inflorescences 1-2 together, 9-10 mm diam.; sessile; involucre with ovate to cucullate, pubescent, smooth bracts, in 4-8 series; indistinct perianth to distinct perianth, 3-4 mm high; free pseudo-tepals, puberulent; stigmas filiform. Infructescences globoid, 1.5-1.8 cm diam.; indistinct fruiting perianth, fruiting pseudo-tepals to 1.5-3 mm high, subulate.

Representative specimens:—BRAZIL. Amazonas: Manaus, ca. 90 km NNE of Manaus, Distrito Agropecuário da Suframa, 02º24'26"S 59º45,50"W, 13 November 1989, (fr.), *M.T. Campos & B. Boom 21* (SP), 05 November 1991, (♂), *A.A. Oliveira et al. 207* (SPF), Reserva Florestal Ducke, Manaus-Itacoatiara Road, km 26, 07 November 1973, (♀), *C.C.Berg et al. P17624* (MG), 02º53'S 59º58'W, 11 October 1994, (fr.), *A. Vicentini et al. 727* (SP). Manaus-Porto Velho Road, BR 319, km 510, 6 km N of Rio Puruzinho, 17 October 1974, (♀), (fr.), *G.T. Prance et al. 23002* (MG, US), Rio Cuieiras, October 1993, (♂), *S.G. Egler et al. 1495* (SP, SPF), *S.G. Egler et al. s.n.* (SP 330807). Novo Airão, Aldeia Maré, Área Indígena Waimiri Atroari, Rio Camanaú, 01º45'S 61º15'W, 31 August 1989, (♀), (fr.), *R. Miller et al. 605*. Pará: Altamira, Juruá, 27 November 1986, (fr.), *S.A.M. Souza et al. 545* (MG), Basin of Rio Xingu, 03°22'20"S 50º47'50"W, 23 November 1980, (♂), *G.T. Prance et al. P26406* (UEC), Rio Trombetas, 16 November 1985, (♀), *L.S. Coelho et al. 90* (INPA). PERU. Loreto: Boqueron Padre Abad, 26 March 1962, (fr.), *J.S. Vigo 5830* (US).

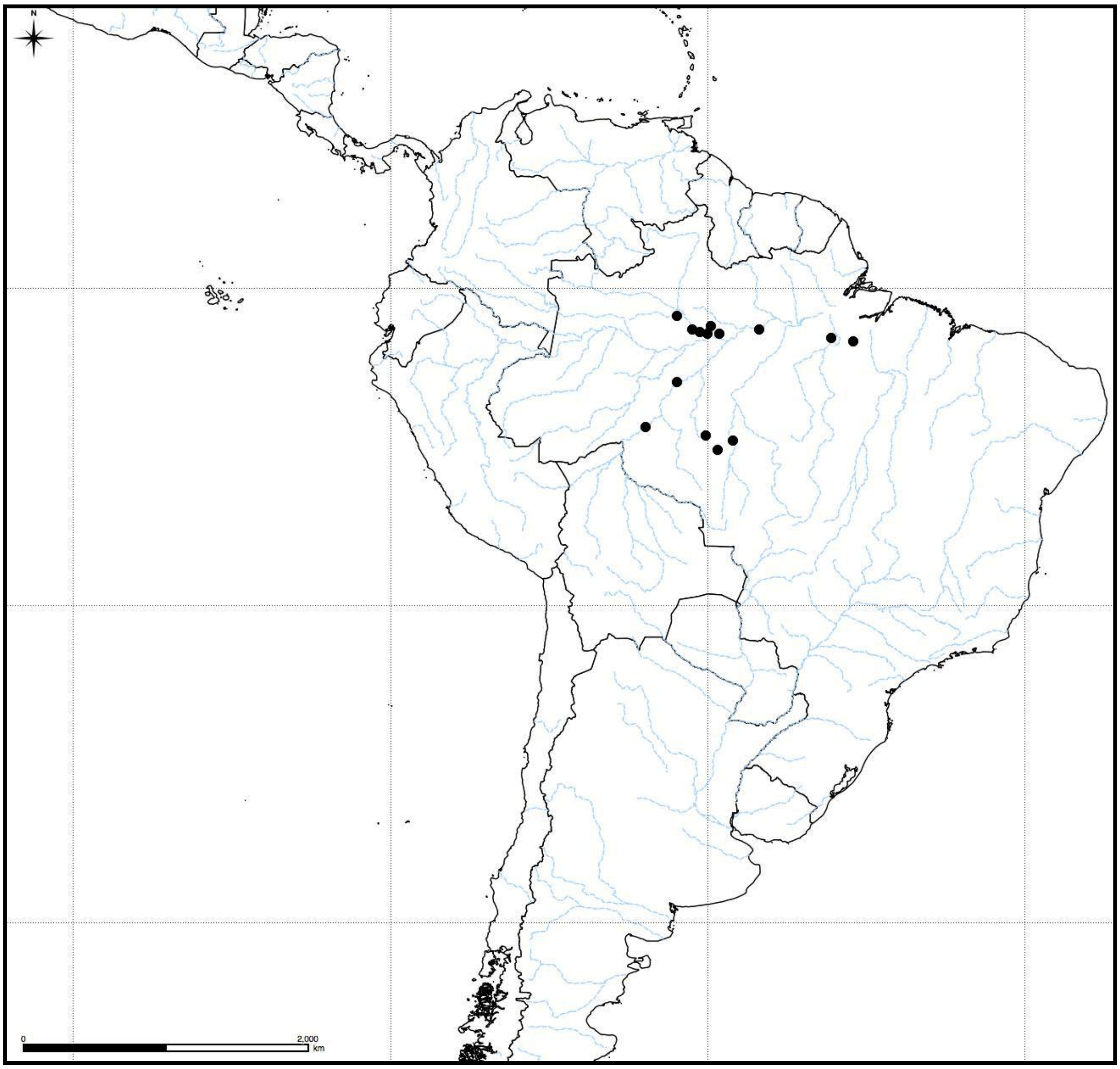

FIGURE 27. Distribution maps of *Naucleopsis pauciflora.*

Distribution and habitat:**—**Brazilian Amazon region (Brazil and Peru), in Terra Firme forest, in lowland moist areas, at an elevation of about 50 to 500 m above sea level.

Vernacular Name:**—**chinicua Amarillo (Peru)

Etymology:**—**The epithet refers to number of the flowers in pistillate inflorescences.

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis pauciflora* is considered Vulnerable, VU B1a,b(iii), because of the small extent of occurrence only in the Brazilian Amazon region (ca. 6.582 Km^2).

Notes:—*Naucleopsis pauciflora* is easily recognized because of the leaves obovate. *Naucleopsis pauciflora* was considered as synonymous of *Naucleopsis ternstroemiiflora* by Berg (1972), but *N. ternstroemiiflora* is completely different because of the fruiting perianth ovate, connate and leaves oblong. In contrast, *N. pauciflora* can be recognized by leaves obovate and fruiting perianth subulate. For these reasons, we proposed the reestablishment of *Naucelopsis pauciflora*.

21. *Naucleopsis pseudonaga* (Mildbr.) C.C. Berg (1969: 465)

Basionym: *Ogcodeia pseudonaga* Mildbr. (1932: 419). Lectotype (designated by Berg 1972):—BRAZIL. Acre: Seringal São Francisco, Rio Acre, no date, (♂), *Ule 9321*, lectotype B!, isolectotype G [photo!], K!, L [photo!], RB!, U!, US[photo!].

Fig. 4 F.

Trees 8-12 m tall; latex white to yellowish. Leafy twigs with long internodes distinctly different in length, 1-3 mm thick, brownish, glabrous or sparsely puberulous; ridged; lenticels conspicuous. Leaves lanceolate, 9-20 cm long., 2.4-5 cm broad, chartaceous, without perforations both faces glabrous; acute to acuminate at the base, equilateral; acute-acuminate at the apex; margin entire; primary veins brown-reddish beneath, secondary veins 15-19 pairs; prominent beneath, mostly curved, arched 1-2(-3) mm from the margin; petioles 5-9 mm long.; stipules 0.4-1.0 cm long., entire margin, caducous. Staminate inflorescences 3-5 together, 7-9 mm diam.; peduncle 3-12 mm long., involucre with ovate, sparsely puberulent, smooth bracts, in 3-4 series; perianth 1-2 mm high; tepals 3-6, free; stamens 1-4, filaments free. Pistillate inflorescences solitary, 20-25 mm diam., sessile; involucre with deltoid to ovate to lanceolate, puberulent smooth bracts, in 6-7 series; indistinct to distinct perianth, 1-1.5 mm high, free pseudo-tepals, puberulent; stigmas filiform. Infructescences globoid, 2-4 cm diam.; indistinct to distinct fruiting perianth; fruiting pseudo-tepals to 0.5 cm high., subulate to acuminate.

Representative specimens:—BRAZIL. Acre: Santa Rosa, Rio Purus, Seringal Santa Helena, 09º07’49”S 70º10’37”W, 23 March 1999, (♀), (fr.), *D.C. Daly et al. 9996* (BG). Tarauacá, Basin of Alto Juruá, Rio Tarauacá, 08º35’12”S 71º30’57”W, 18 November 1995, (♂), *M. Silveira et al. 987* (BG), Seringal Joaci, 08º16’44”S 71º05’16”W, 23 September 1994, (♂), *D.C. Daly et al. 8329* (INPA). PERU. Dantas: Unidad Modelo de Manejo y Producción Florestal, 09º40’S 75º02’W, 01-15 September 1990, (♂), *Tello 201* (NY).

Distribution and habitat:**—**Bolivia**,** Brazil, Colombia and Peru, in Terra Firme forest or Varzea of the Amazonian region, in moist areas, at an elevation of about 100 to 2500 m above sea level.

Vernacular Name:**—**pama-amarela (Brazil).

Etymology:**—**The epithet refers to morphological similarity with *Naucleopsis naga*.

IUCN conservation status:**—**According to the IUCN Red list categories (IUCN 2015), *Naucleopsis pseudonaga* is considered Vulnerable, VU B1a,b(iii), because of the small extent of occurrence only in the Amazon region (Bolivia, Brazil, Colombia and Peru) (ca. 5.652 Km^2).

Notes:**—***Naucleopsis pseudonaga* presents the indistinct to distinct perianth with free pseudo-tepals acuminate to subulate. It shows similarity with *N. pauciflora* and *N.*

naga. However, *N. pseudonaga* can be distinguished by leaves lanceolate and it can be distinguished of *N. naga* by absence verrucose bracts in the staminate inflorescences. In contrast, *N. pauciflora* differs by its obovate leaves.

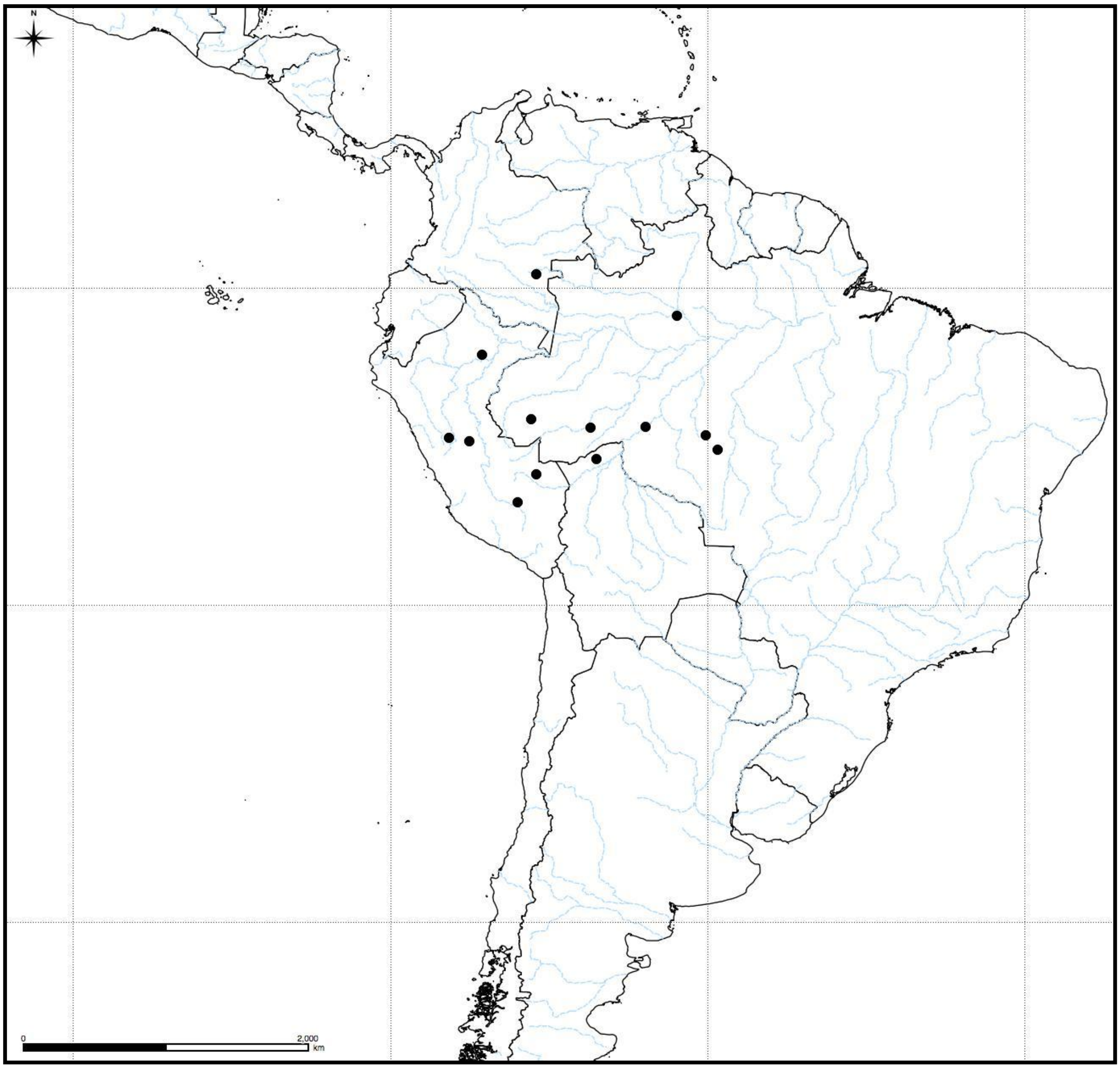

FIGURE 28. Distribution maps of *Naucleopsis pseudonaga.*

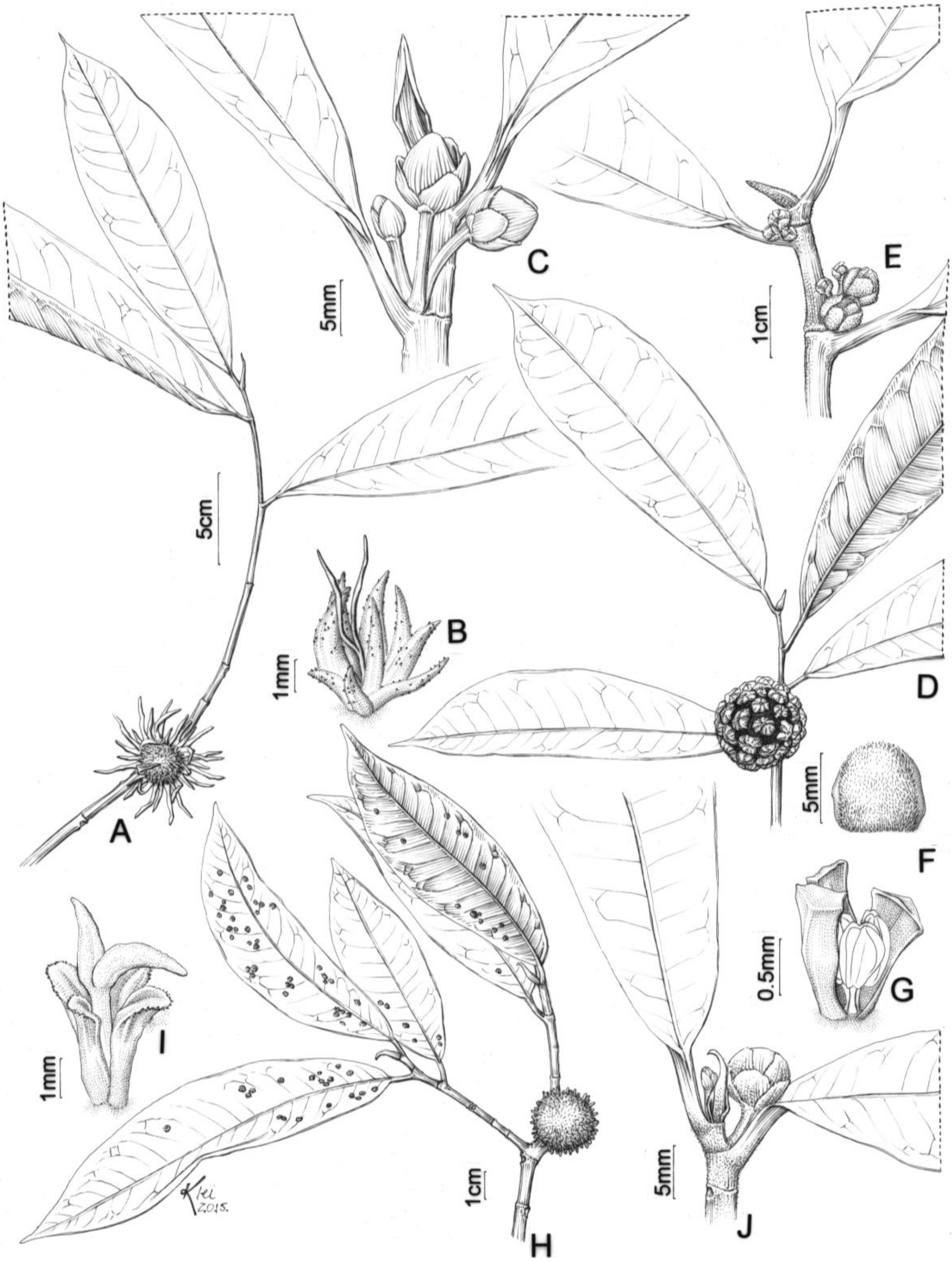

FIGURE 29. General morphology. *Naucleopsis chiguila* - **A.** Habit, *M. Tirado et al. 247* (NY). **B.** Pistillate flower, free pseudo-tepals, *M. Tirado et al. 247* (NY). **C.** Staminate inflorescence, *P. Acevedo et al. 1721* (BG). *Naucleopsis concinna* **D.** Habit, *G.T. Prance et al. 8777* (INPA). **E.** Staminate inflorescence, *M.F. Silva & pessoal da Botânica 632* (INPA). **F.** Details bracts of the pistillate inflorescence, *G.T. Prance et al. 8421* (INPA). **G.** Staminate flower, *G. Pereira-Silva et al. 16357* (UEC). *Naucleopsis francisci* **H.** Habit, *N. Cumbicus & J. Peña 841* (BG), **I.** Pistillate flowers, free pseudo-tepals, *N. Cumbicus & J. Peña 841* (BG). *Naucleopsis herrerensis*, **J.** Staminate inflorescence, *Bernardi 16201* (BG).

22. *Naucleopsis riparia* C.C.Berg (1969: 464).

Type: BRAZIL. Amazonas: Esperança, mouth of Rio Javary, (♀), *A. Ducke 1786* (holotype RB!; isotype K!, NY, US).

Tree (7-)18-22 m tall; latex white to yellowish. Leafy twigs with long internodes distinctly different in length, 3-5 mm thick, brownish, glabrous to pubescent, ridged; lenticels conspicuous. Leaves lanceolate, (15-)20-29 cm long., 7-12 cm broad, coriaceous, without perforations, glabrous above, pubescent beneath; obtuse- at the base, equilateral; acute-acuminate to obtuse in the apex; margin entire; primary veins brown-reddish, secondary veins 18-22 pairs, prominent beneath, often straight to curved-arched to the margin; petioles 1.0-1.5 cm long.; stipules 1-2 cm long., entire margin, caducous. Staminate inflorescences 2-4 together, 10-14 mm diam.; sessile; involucre with ovate, pubescent, smooth, bracts, in ca 3 series; perianth 1.5-2 mm high; tepals 3-5, free; stamens 3-4, filaments free. Pistilate inflorescences 1-4 together, 9-10 mm diam.; sessile; involucre with ovate to cucullate, yellowish dense-velutinous bracts, in 4-8 series; distinct perianth, 3-4 mm high, connate, 4-8 parted in apex, tomentose to velutinous; stigma filiform. Infructescences globoid, 3-4 cm diam.; distinct fruiting perianth; fruiting perianth to 0.6 cm high; fruit oblate-deltoid.

Representative specimens:—BRAZIL. Acre, Marechal Thaumaturgo, rio Juruá, 08º58’16’S 72º42’52”W, 08 December 2000, (♀), *D.C. Daly et al. 10512* (BG), Santa Lucia, Rodovia Transamazônica, km 40, E de Cruzeiro do Sul, 07º08’00”S 72º33’00”W, 14 Oct 1987, (♀), *J. Pruski et al. 3476* (BG, INPA, K, NY), 08º15’00”S 72º44’00”W, 05 Nov 1991, (♀), *C.A. Cid Ferreira et al. 10601* (INPA), Feijó, rio Juruparí, 26 October 2009, (♂), *H. Medeiros et al. 204* (RB, SP). Amazonas, alto rio Solimões, rio Jutaí, 08

November 1975, (♀), *L. Coelho et al. 401* (INPA), 17 November 1975 (♀), *N. A. Rosa & L. Coelho 570* (IAN).

Distribution and habitat:—Brazilian and Peruvian Amazon region, in Terra Firme forest, in lowland moist areas, often in riparian forest, at an elevation of about 25 to 400 m above sea level.

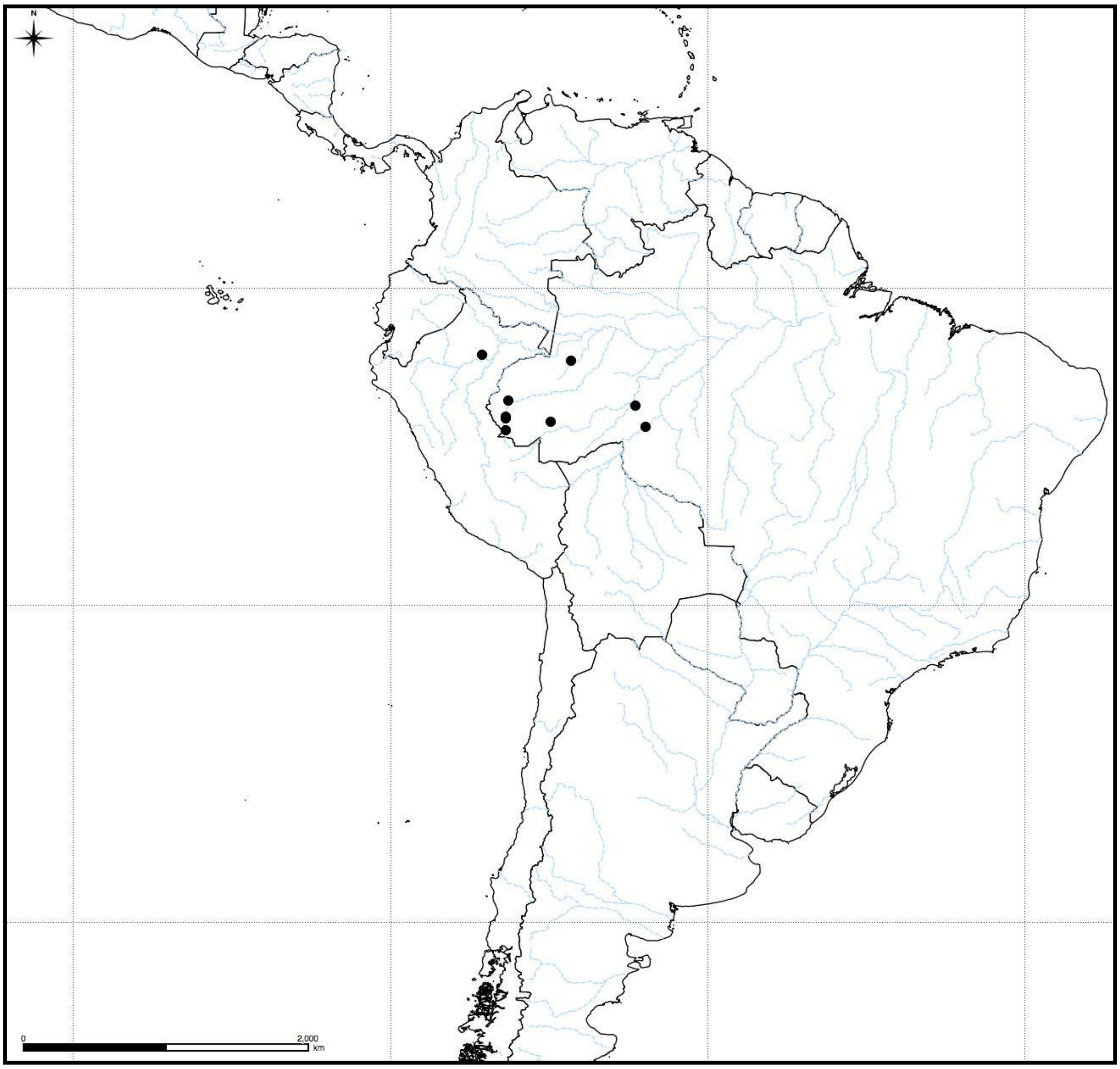

Figure 30. Distribution maps of *Naucleopsis riparia.*

Vernacular Name:—pama, muiratinga falsa (Brazil).

Etymology:—The epithet probably refers to habitat, in riparian forest.

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis riparia* is considered Endangered, EN B1a,b(iii), because of the small extent of occurrence in the Brazilian and Peruvian Amazon region (ca. 2.946 km^2).

Notes:—This species is recognized by leaves pubescent beneath and perianth tomentose to velutinous. *N. riparia* is included in the group with leaves pubescent beneath. *N. riparia* shows more similarities with *N. macrophylla*. However, *N. macrophylla* can be differentiated by perianth fruiting ovate, in constrast, in *N. riparia* it is oblate-deltoid.

23. *Naucleopsis stipularis* Ducke (1932: 580).

Palmolmedia stipularis (Ducke) Ducke (1939: 20). Lectotype (designated by Berg 1972):—BRAZIL. Pará: near the lower cataracts of Rio Tapajóz, no date, (♂), *A. Ducke s.n.*, lectotype RB!, isolectotype B!, K!, S [photo!], US [photo!].

Treelets 3-8(-12) m tall; latex withe. Leafy twigs absent; lenticels inconspicuous. Leaves lanceolate to oblong-lanceolate, (57-)60-80 cm long., 14-23 cm broad, coriaceous, without perforations, both faces glabrous; attenuate at the base, equilateral; acute-acuminate at the apex; margin entire; primary veins brown-reddish, secondary veins 19-23 pairs, strongly prominent beneath, curved-arched to the margin; petioles 1.5-2.0 cm long.; stipules 1.5-3.0 cm long., entire margin, persistent in internodes. Staminate inflorescences solitary, 10-15 mm diam., peduncle (1-)2-4 cm, sparsely puberulous; involucre with ovate to deltoid, puberulous, smooth bracts, in 5-6 series; perianth 4-7 mm high; tepals 3-5, free; stamens 2-4, filaments free. Pistillate inflorescences solitary, 3-5 cm in diam.; sessile to 2 mm long., involucre with ovate to deltoid, puberulous, smooth bracts, in 5-6 series; distinct perianth

2-3 mm high, connate, parted 4-7 at the apex, puberulent to puberulous; stigma linguiform. Infructescences globoid, 4-5 cm diam.; distinct fruiting perianth, fruiting perianth 2-4 mm long., oblate.

Representative specimens:—BRAZIL. Amazonas: Anixim, 8 September 1983, (♂), *J. L .Zarucchi 2990* (INPA, RB). Manaus, Reserva Florestal Ducke, 02º53'S 59º58W, 01 February 1996, (♀), *J. E. L. S. Ribeiro et al. 1800* (INPA), 24 April 1996, (♀), *C. A. Sothers & P. A. C. L. Assunção 850* (INPA), 22 September 2012, (♂), *A. Santos et al. 154* (SP), Rio Madeira, 04 December 1949, (♂), *N. T. Silva 425* (IAN). Maués, igarapé Albino, 09 September 1983, (♀), *L. Lima 549* (INPA). Nova Olinda, Rio Marimarí, 02 July 1983, (♂), C. A. Cid 3999 (RB, MG). Pará: Altamira, Rio Iriri, 12 January 1985, (♂), *C. S. Rosário & M. R. Santos 721* (MG). Rondônia: Ariquemes, 10º35'S 63º35"W, 20 May 1982, *L. O. A. Teixeira et al. 622* (NY). Porto Velho, Road Porto Velho-Cuiabá, BR 364, km 186, 10 February 1983, (♀), C. A. A. Freitas et al. 69 (INPA).

Distribution and habitat:—Northwest of Brazil, in primary Terra Firme forest of the Amazonian region, in lowland moist areas, at an elevation of about 25 to 600 at an elevation of about 25 to 400 m above sea level.

Vernacular Name:—not known.

Etymology:—Probably the epithet refers to presents of the stipules persistent along branches.

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis stipularis* is considered Vulnerable, VU B1a,b(iii), because of the small extent of occurrence only in the Brazilian Amazonian (ca. 5.245 Km^2).

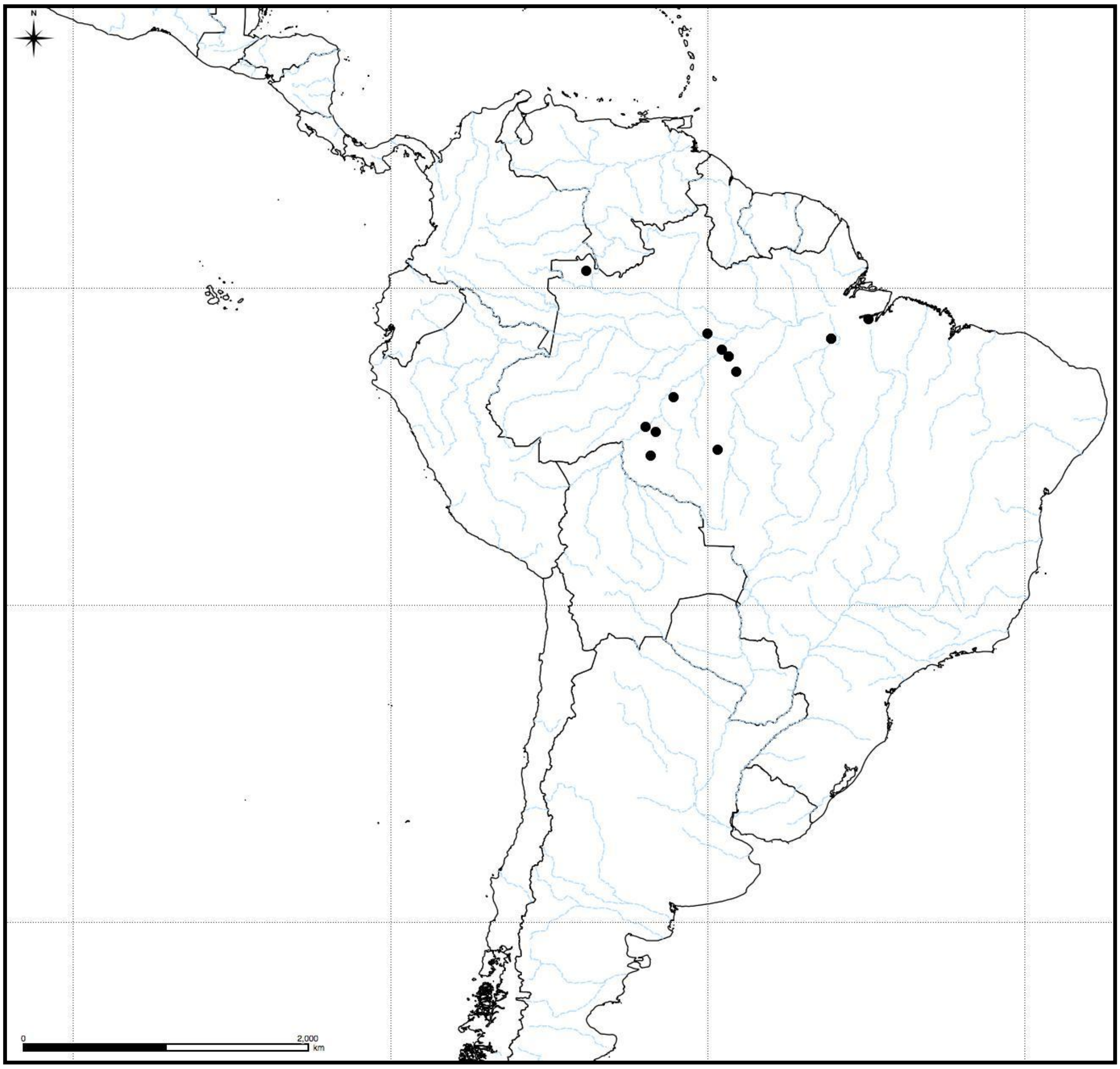

Figure 31. Distribution maps of *Naucleopsis stipularis.*

Notes:—*Naucleopsis stipularis* is clearly different from the others of genus. A treelets with 3 to 8, rare 12 m tall, without branches and with its leaves concentrated at the apex of the trunk. Also, the size of its leaves to 80 cm long., staminate inflorescences, with peduncle to 4 cm long and pistillate flowers with stigma linguiform are unique in genus. For theses reasons, Ducke (1939) proposed the genus *Palmolmedia*. Berg (1972, 2001) synonymized *Palmolmedia* in *Naucleopsis*. Our molecular analyses (chapter 1) do not support the position of *Palmolmedia* as an independent genus.

24. *Naucleopsis straminea* C.C.Berg (1996 : 240).

Type:—COLOMBIA. Chocó: 31 km E of Quibdó, ca. 14 km E of Tutunendo, 300-450 m, 14 Jun 1982, Gentry *et al*. *36924,* (♀) (holotype COL [photo!], isotype BG!, JAUM [photo!], MO [photo!].

Tree 8-15 m tall; latex not seen. Leafy twigs with long internodes distinctly different in length, 2-3 mm thick, greyish, glabrescent to puberulous; slightly ridged; lenticels conspicuous. Leaves elliptic, 7.5-13 cm long., 3-5.5 cm broad, chartaceous, without perforations, both faces glabrous; acute at the base, equilateral; acute-caudate at the apex; margin entire; primary veins yellow-greenish, secondary veins 8-13 pairs, plane beneath, curved-arched to the margin; petioles 0.4-0.8 cm long.; stipules 0.5-1.3 cm long., entire margin, caducous. Staminate inflorescences not seen. Pistillate inflorescences solitary, 8-10 mm diam., sessile to peduncle 2 mm long., involucre with ovate, glabrous to puberulous, smooth bracts, in ca 5 series; indistinct perianth, free pseudo-tepals, subulate, minutely puberulous; stigma filiform. Infructescences globoid, 2,5-4 cm diam.; indistinct fruiting perianth, fruiting pseudo-tepals to 1 cm high, subulate.

Representative specimens:—COLOMBIA. Choco: 31 km e of Quibdo, ca. 14 km E of Tutunendo, 14 June 1982, (♀), *A. Gentry & J. Brand M. 36924* (BG).

Distribution and habitat:—Northern Pacific Coastal (Colombia, Antioquia, Choco), (Panama, Darién), (Costa Rica, Heredia) at an elevation of about 450 m above sea level.

FIGURE 32. Distribution maps of *Naucleopsis straminea.*

Vernacular Name:**—**unknown.

Etymology:**—**The epithet suggests to the appearance of the stramineus leaf.

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis straminea* is considered Endangered, EN B1a,b(iii), because of the small extent of occurrence from Pacific Costal (Colombia, Panama and Costa Rica) (ca. 2.234 km^2).

Notes:—*Naucleopsis straminea* is related to *N. krukovii* by leaves with primary veins yellow-greenish and pistillate inflorescence indistinct with free pseudo-tepals, subulate. However, it can be easily distinguishable by its small, elliptical leaves. Also, in constrast, *N. straminea* does not present lamina with perforations, such as, *N. krukovii.*

25. ***Naucleopsis ternstroemiiflora*** (Mildbr.) C.C.Berg (1969: 465).

Ogcodeia ternstroemiiflora Mildbr. (1927: 188). Type:—PERU. Loreto: Yarina-Cocha on rio Ucayali, 18 August 1925, (♂), *Tessmann 5467* (holotype B!; isotype G [photo!], NY [photo!], S *n.v*).

Tree (6-)7-15 m tall; latex white to yellow. Leafy twigs with long internodes distinctly different in length, 3-4 mm thick, brown-grayish, glabrous to pubescent, ridged; lenticels conspicuous. Leaves oblong, (11-)15-29 cm long., 3.5-7.5 cm broad, coriaceous, without perforations; both faces glabrous; acute to obtuse at the base, equilateral; acuminate to caudate at the apex; margin entire; primary veins brown-reddish, secondary veins 22-25 pairs, plane beneath, often straight to the margin; petioles 0.8-1.2 cm long.; stipules 1-1.2 cm long., entire margin, caducous. Staminate inflorescences 3-4 together, 5-10 mm diam.; peduncle sessile to 4 mm long., puberulous to pubescent; involucre with ovate, puberulous to pubescent smooth bracts, in 3 series; perianth 1-1.2 mm high; tepals 3-5, free; stamens 3-4; filaments free. Pistilate inflorescences 1-3 together, 9-10 mm diam.; sessile; involucre with ovate to cucullate, puberulous, smooth bracts, in 4-6 series; distinct perianth 3-4 mm high, ovate, connate, 4-6 parted in apex, pubescent to velutinous; stigma filiform. Infructescences globoid, 2-3 cm diam.; distinct fruiting perianth, fruiting perianth to 0.5 cm high., ovate.

Representative specimens:—BRAZIL. Acre: Capixaba, bacia rio Acre, 30 km W de Capixaba, 10º29’35”S 69º49’45”W, 30 September 2003, (♂), *P. Acevedo-Rodríguez et al. 13577* (RB). Senador Guiomar, Fazenda Catuaba, 18 February 2014, (♂), *A. Santos et al. 199* (SP). Rodovia Rio Branco-Porto Acre, 12 October 1980, (♀), *C.A. Cid & B.W. Nelson 2872* (MG, RB), km 33, 09º00’00”S 67º50’00”W, (♀), *B. Nelson 689* (RB). Mato Grosso: Alta Floresta, 17,5 km N de Alta Paraíso, 22,5 km W of Rio Apiacá, 09º57’00”S 57º06’00”W, 30 September 1985, (♂), *W. Tomas et al. 4119* (BG, K, SP). Pará, BR 163, km 1004, Cuiabá-Santarém, 14 November 1977, (♀), *G.T. Prance et al. P 25386* (MG, RB, UEC). Marabá, 13 November 1991, (♀), *R.S. Monteiro 306* (MG). Porto Deserto, Rio Itacaiunas, 20 July 1970, (♂), *J.M. Pires 13110* (IAN). Pará, Tucurui, margem direita do rio Tocantins, 14 December 1979, (♀), *Silva, M.F.F. et al. 360* (MG), foz do rio Pitinga, 20 September 1985, (♀)*, J. Ramos & E.F. Lima 1510* (INPA).

Distribution and habitat:—Amazonian Brazilian, in Terra Firme forest, in lowland moist areas, rare varze, at an elevation of about 25 to 400 m above sea level.

Vernacular Name:—pama (Brazil).

Etymology:—unknown.

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis ternstroemiiflora* is considered Vulnerable, VU B1a,b(iii), because of the small extent of occurrence only in the Amazonian Brazilian (ca. 6.338 Km^2).

Notes:—As well as *Naucleopsis caloneura* and *N. ternstroemiiflora* based on a staminate material. Differently of the pistillate inflorescences, the staminate inflorescences shown few modifications morphological. Mildbraed (1927) proposed *Ogcodeia ternstroemiiflora* and it was transferred to *Naucleopsis* by Berg (1969). *N. ternstroemiiflora* showns similarities to *N. pauciflora* and *N. caloneura*. Over the course of his studies and researches Berg (1969, 1972) assumed the form of the pistillate inflorescence of *N. pauciflora* as being of *N. ternstroemiiflora*. *N. pauciflora* is synonymized in *N. ternstroemiiflora* and the form of the pistillate inflorescence of *N. ternstroemiiflora* is confused with *N. caloneura*. *Naucleopsis ternstroemiiflora* can be recognized by leaves oblong and fruiting perianth ovate, connate. In contrast, *Naucleopsis pauciflora* can be recognized by leaves obovate and fruiting perianth subulate and *N. caloneura* by leaves lanceolate and fruiting perianth deltoid.

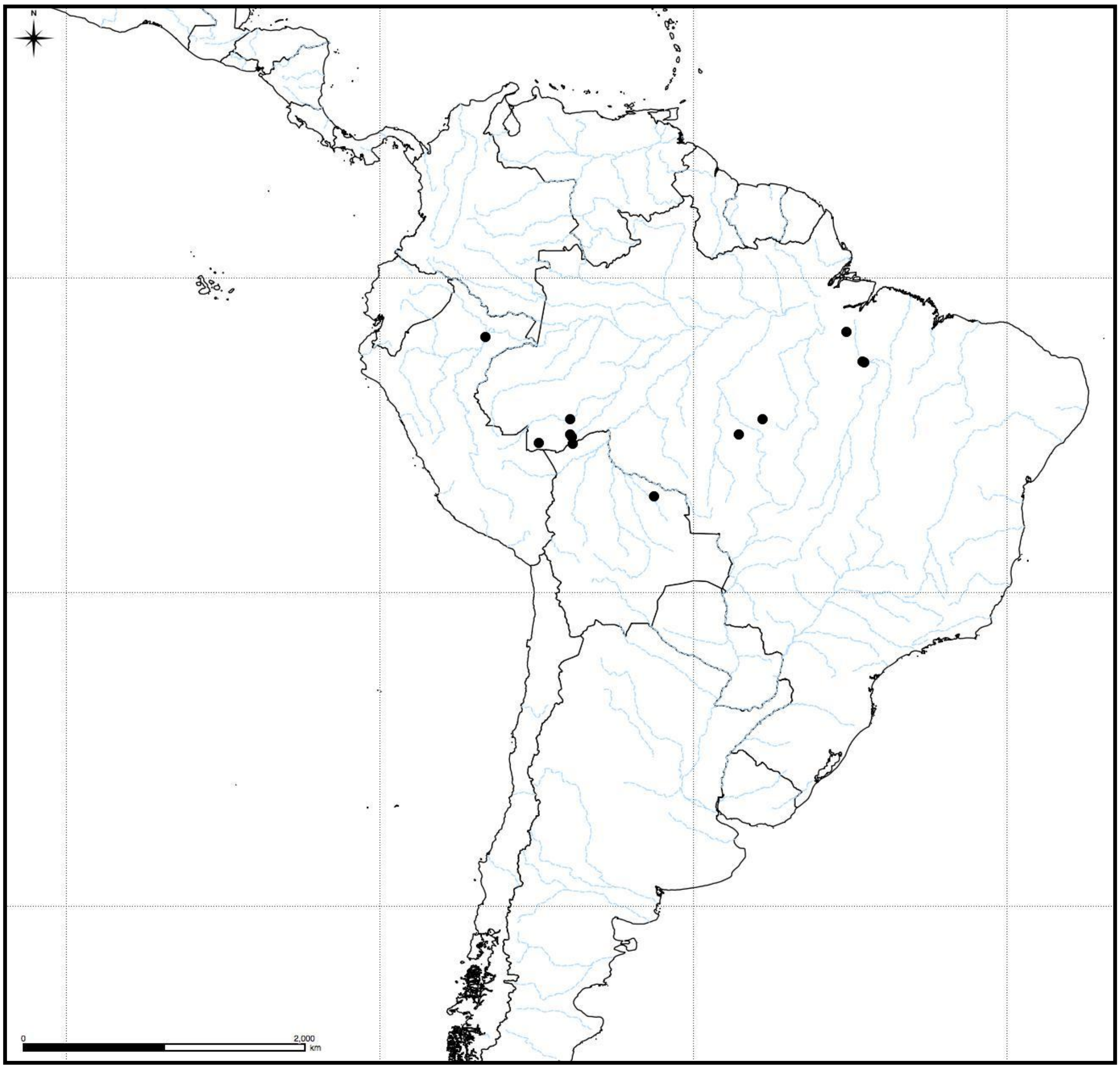

FIGURE 33. Distribution maps of *Naucleopsis ternstroemiiflora*.

26. *Naucleopsis ulei* (Warb.) Ducke (1922: 38).

Basionym: *Acanthosphaera ulei* Warb. (1909: 336). Lectotype (designated by Berg 1972):—PERU. Loreto: Iquitos, July 1904, (♂), *E. Ule 6257*, lectotype B! isolectotype G [photo!], MG!.

Trees (5-)15-20 m tall; latex white to yellowish. Leafy twigs with conspicuous short internodes, (5-)7-12 mm thick, greyish to brownish, puberulous, ridged to peeling; lenticels conspicuous. Leaves lanceolate to oblong, 20-56 cm long., 7-18 cm broad, coriaceous, both faces glabrous, without perforations; smooth beneath;cordate to truncate, rare acute to obtuse at the base, equilateral; attenuante or acute-acuminate at the apex; margin entire; primary veins brown-reddish, secondary veins 22-25(-36) pairs, prominent beneath, often curved-arched to the margin; petioles 0.8-2.2 cm long.; stipules (1-)2-3.5 cm long., persistent in internodes. Staminate inflorescences globoid to cupuliform, up to 8 together, 2-5 mm diam.; peduncle 2-12 mm long.; involucre with deltoid to ovate, cucullate or lanceolate, sparsely puberulous smooth bracts, in 6-10 series; perianth 2-4 mm high, stamens 1-2, filaments free. Pistillate inflorescences solitary or occasionally accompanied by staminate ones, 7-13 mm diam., peduncle sessile to 2 mm long. involucre with deltoid to ovate or cucullate, sparsely puberulous, smooth bracts, in 6-8 series; indistinct perianth, free pseudo-tepals subulate, puberulous; stigmas filiform. Infructescences globoid 5-7 cm diam.; indistinct fruiting perianth, fruiting pseudo-tepals 2.5-3 cm high, subulate.

Key to the subspecies of *Naucleopsis ulei*

1. Leaves conspicuously scabrous beneath …………………..……………. subsp. *puberula*

1’. Leaves smooth beneath

2. Leaves with base acute to obtuse …………………...…...……………… subsp. *amara*

2’. Leaves with base cordate to truncate

3. Leaves with attenuante apex; staminate inflorescences peduncled ….... subsp. *subandina*

3’. Leaves with acute-acuminate apex; staminate inflorescences sessile …..….. subsp. *ulei*

26.1. *Naucleopsis ulei* subsp. *ulei*

Leaves oblong to oblong-lanceolate, 30-52 cm long., 10-17 broad., base cordate to truncate; stipules 1.5(-2) cm long, mostly persistent. Staminate inflorescence sessile, often several along branches. Pistillate inflorescences 1-10 together along branches; ovate to deltoid bracts.

Representative specimens:—BRASIL. Acre: Cruzeiro do Sul, Sub-base Projeto RADAM/BRAZIL, Serra do Divisor, 05 March 1976, (♀), *J. Ramos & G. Mota 311* (INPA). Marechal Thauma, Rio Juruá, Reserva Extrativista do Alto Juruá, Fazenda Paraguay, 09º11’S 72º41’W, 04 April 1993, (♀), *D.C. Daly et al. 7772* (INPA). Amazonas: Boca do Acre, Rio Purus and Acre, 20 September 1966, (♂), *G.T. Prance et al. 2428* (SPF), Rio Inauini, 08º21’44”S 67º52’47”W, (♀), *M.G. Bovini et al. 2986* (SP), Rio Solimões, Igarapé Belém, 10 December 1948, (♀), *R.L. Fróes 23702* (IAN). São Paulo de Olivença, 17 October 1942, (♀) and (♂), *A. Ducke 1045* (IAN). Rondônia: Alvorada-Costa Marques Road, km 90, 28 June 1983, (♂), (♀), *M.G. Silva 6476* (INPA, RB). Porto Velho, Rio Madeira, 09 June 1936, (♂), *A. Ducke s.n.* (RB 18290). PERU. Loreto: Nauta, Rio

Marañon, 04º29’S 73º35’W, 09 November 1982, (♀), *R. Vásquez & N. Jaramillo 3422* (NY), betwen Yurimaguas and Balsapuerto, 26-31 August 1929, (♀), *E.P. Killip & A.C. Smith 2844* (NY), Iquitos, 21 September 1906, (♀), *A. Ducke s.n.* (RB 35440).

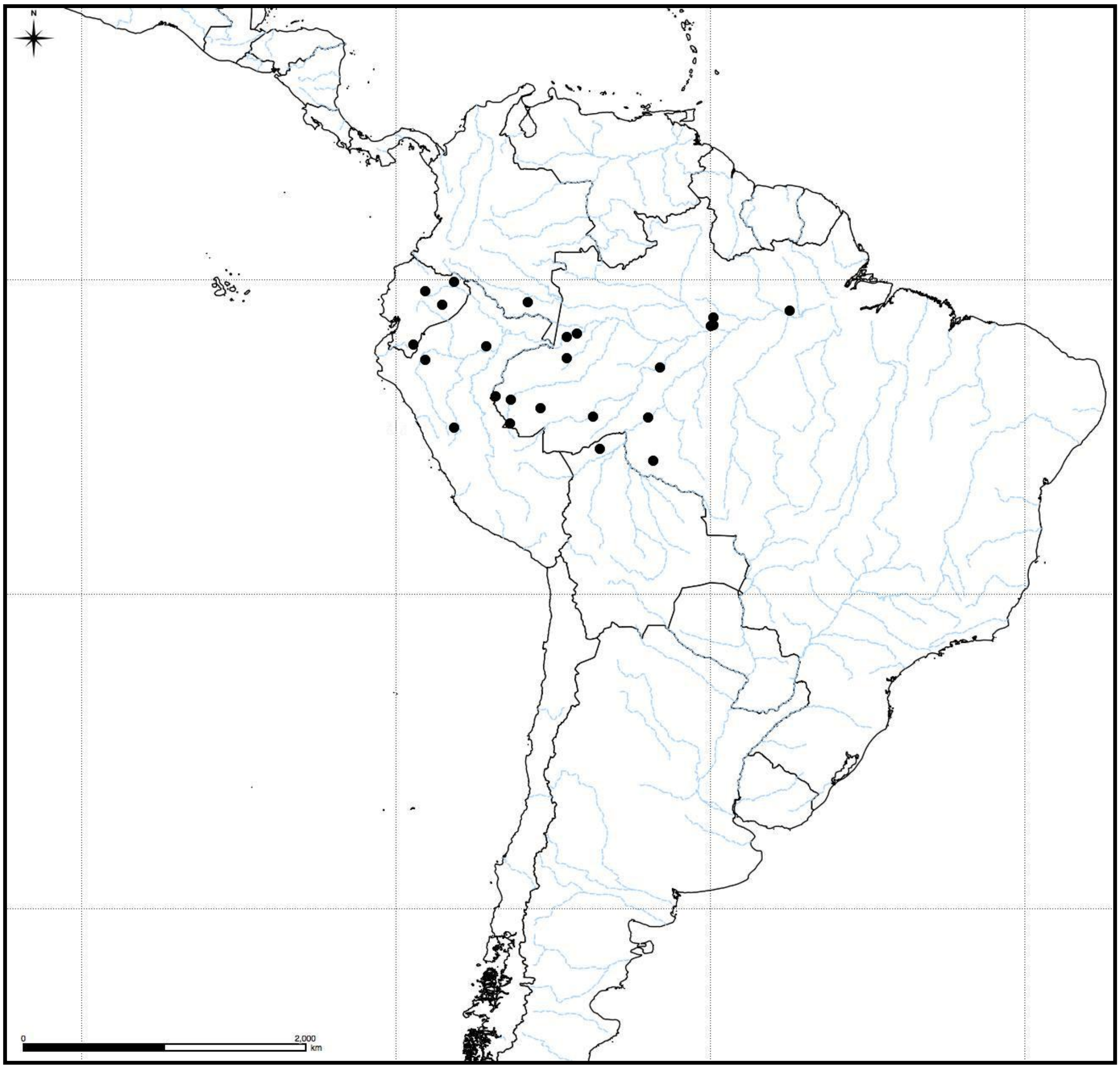

FIGURE 34. Distribution *Naucleopsis ulei* subsp. *ulei*

Distribution and habitat:—Amazon region (Brazil, Colombia and Peru), in Terra Firme forest or rare varzea of the Amazonian region, in lowland moist area, at an elevation of about 50 to 450 m above sea level.

Vernacular Name:—cabeça-de-arara (Brazil).

Etymology:—The epithet honors E. H. G. Ule, a botanical collector.

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis ulei* subsp. *ulei* is considered Vulnerable, VU B1a,b(iii), because of the small extent of occurrence only in the Amazonian region (Bolivia, Brazil, Colombia, Ecuador and Peru) (ca. 9.979 Km^2).

Notes:—The subspecies of *Naucleopsis ulei* in general are easily recognized because of internodes often distinctly different in length. In addition to those species only *N. humilis* present this feature more evident. However, *Naucleopsis ulei* can be distinguished by leaves oblong to oblong-lanceolate. In contrast, *N. humilis* is strongly characterized by obovate leaves.

26.2. ***Naucleopsis ulei* subsp. *amara*** (Ducke) C.C. Berg (Berg 2001: 283).

Basionym: *Naucleopsis amara* Ducke (1925: 6). *Ogcodeia amara* (Ducke) Ducke (1930: 102). *Acanthosphaera amara* (Ducke) Ducke (1939: 21). Lectotype (designated by Berg 1972):—BRAZIL. Pará: near catarracts of Mangabal, Rio Tapajóz, 14 December 1919, (♀), *A. Ducke s.n.*, lectotype RB!, isolectotype BM!, G [photo!], P!, U [photo!], US [photo!].

Fig. A-G.

Leaves oblong-lanceolate, 14-30 cm long., 3-7 broad., base acute to obtuse; stipules 0.9 1.5(-2) cm long, mostly caducous. Staminate inflorescences sessile. Pistillate inflorescences 1-4 together along branches; cucullate bracts.

Representative specimens:—Brazil. Amazonas: Distrito Agropecuário, 90 km NNE of the Manaus, 02º24’26”S-02º25’31”S, 59º43’40”-59º45’50”W, 11 January 1992, (fr.), *A.A. Oliveira et al. 305* (INPA, SPF), Manaus, Reserva Florestal Ducke, Manaus-Itacoatiara Road, km 21, 07 November 1963, (♂), *E. Oliveira 2881* (IAN); km 26, 02º53’S 59º58’W, 23 January 1998, *J.E.L.S. Ribeiro & P.A.C.L. Assunção 1964* (INPA), Rio Javari, 16 October 1976, (♀), *G.T. Prance et al. 23841* (INPA, MG), Rio Negro and Rio Jauaperi, 24 February 1977, *M.R. Santos 98* (MG). Parintins, 11 January 1936, *A. Ducke s.n.* (RB 35438). São Paulo de Olivença, 06 December 1937, *A. Ducke s.n*. (RB 35439). Pará, Belém, Horto do Museu Goeldi, 11 February 1958, *P. Cavalcante 348* (MG), 12 December 1962, *P. Cavalcante 987* (IAN). PERU. Loreto: Yanomono, 03º22’S, 72º50’W, *A. Gentry et al. 36547* (NY). Yurimaguas, 22 September-09 November 1929, *E.P. Killip & A.C. Smith 28179* (US).

Distribution and habitat:**—**Amazon region (Brazil, Colombia and Peru), in terra firme forest or rare varzea of the Amazonian region, in lowland moist area, at an elevation of about 50 to 450 m above sea level.

Vernacular Name:—muiratinga (Brazil).

Etymology:**—**The epithet probably suggests to the term “*amarus*” (bitter, fruit or latex).

IUCN conservation status:**—**According to the IUCN Red list categories (IUCN 2015), *Naucleopsis ulei* subsp. *amara* is considered Endangered, EN B1a,b(iii), because of the small extent of occurrence only Amazon Basin (ca. 1.987 km^2).

Notes:**—***Naucleopsis ulei* subsp. *amara* is an example of how the group is complex and morphological diversified. Ducke (1925, 1930, 1939) transferred to three different genera. All the subspecies of *Naucleopsis ulei* showns shorts internodes (smaller that 10 cm long.); stipules persistent in the internodes. In addition, *N.ulei* subsp. *amara* can be distinguished from all other subspecies by the size leaf and pistillate inflorescences with cucullate bracts.

FIGURE 35. Distribution *Naucleopsis ulei* subsp. *amara*

26.3. *Naucleopsis ulei* subsp. *puberula* C.C. Berg (Berg 1996: 240).

Type:—PANAMA. Panamá: Cordillera de San Blas, ca. 20 km NE of Chepo, 12 December 1973, (♀), C.C. Berg & Nee 313 (holotype MO [photo!], isotype AAU *n.v.*, BG!).

Leaves oblong to oblong-lanceolate, 26-36 cm long., 7-19 broad., conspicuously scabrous beneath; base acute to obtuse; stipules 2-2.5 cm long, often persistent. Staminate inflorecences sessile. Pistillate inflorescences 1-4 together axilary and along branches; deltoid to lanceolate bracts.

Representative specimens:—COSTA RICA. Limon: Reserva Indígena Talamanca, 09º29'40"N 82º59'40"W, 27 June 1989, (♀), *A. Chacón 8* (BG). ECUADOR. Esmeraldas: Awá Indigenous Territory, Community of Mataje, 01°15'N 78º40'W, 29 October 1994, (♀), *A. Ortiz et al. 17* (US), Reserva Cotacachi-Cayapas, 0º39'N 78º59'W, 06 May 1998, (♀), *X. Cornejo & C. Bonifaz 6247* (BG). PANAMA. Panamá: Colón, Santa Rita Ridge Road, between Transisthmian Highway and Agua Clara, 11 December 1973, (♂), *C.C. Berg & R.L. Dressler 307* (RB, US).

Distribution and habitat:—From Costa Rica to Ecuador, in lowland moist area, at altitudes up to 50 to 450 meters above sea level.

Vernacular Name:—veneno (Ecuador)

Etymology:—The epithet probably suggests to the scabrous indument of the leaf beneath.

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis ulei* subsp. *puberula* is considered Endangered, EN B1a,b(iii), because of the small extent of occurrence from Costa Rica to western Ecuador (ca. 4.033 km^2).

Notes:—*Naucleopsis ulei* subsp. *puberula* shows similarities with *Naucleopsis ulei* subsp. *ulei* due to leaves with base cordate to truncate that both subspecies present, but distinguished by leaves conspicuously scabrous beneath.

FIGURE 36. Distribution *Naucleopsis ulei* subsp. *puberula*

26.4. *Naucleopsis ulei* subsp. *subandina* C.C. Berg (Berg 2001: 283).

Type:—PERU. Madre de Dios, ca. 5 km from Puerto Maldonado, near Rio Tambopata, 24 January 1976, (♀), (fr.), *Gentry et al. 16275*, (holotype MO [photo!], Isotype F, NY *n.v.*).

Leaves obovate-lanceolate, 30-52 cm long., 10-15 broad., glabrous beneath; attenuante apex; base acute to obtuse; stipules 1-1.5 cm long, often persistent. Staminate inflorescences with peduncle up to 10 mm long. Pistillate inflorescences 1-2 together along branches; ovate to deltoid bracts.

Representative specimens:—COSTA RICA. Puntaneras: Osa, Distrito Sierpe, Reserva Florestal Golfo Dulce, Estación Biológica Los Charcos de Osa, 08º40’18”N 83º30’17”W, 04 January 2008, (♀), *R. Aguilar 10741* (BG, NY), (♂), *R. Aguilar 10744* (BG). BRAZIL. Acre: Mancio Lima, Rio Moa, Serra do Divisor, betwen Pedernal and Fazenda Boa Vista, 07º25’S 73º38’W, 12 October 1989, (♀), *C.A. Cid Ferreira et al, 10018* (INPA). PERU. Pasco: Oxapampa, Palcazu, Parque Nacional Yanachaga-Chemellén, Estación Biológica Paujil, 10º11’S 75º09’W, (♀), *R. Vásquez et al. 30711* (BG).

FIGURE 37. Distribution *Naucleopsis ulei* subsp. *subandina*

Distribution and habitat:**—**Costa Rica and subandean region Peru to the Acre (Brazil), in lowland moist areas, at an elevation of about 50 to 400 m above sea level.

Vernacular Name:—unknown

Etymology:**—**Probably the epithet is relation to subandean region.

IUCN conservation status:**—**According to the IUCN Red list categories (IUCN 2015), *Naucleopsis ulei* subsp. *subandina* is considered Endangered, EN B1a,b(iii), because of the small extent of occurrence in Costa Rica and subandean Peru to the state of Acre (Brazil) (ca. 2.758 km^2).

Notes:**—***Naucleopsis ulei* subsp. *subandina* is clearly different of the others subspecies of group. The leaves with attenuante apex are very evident and when in state reproductive by staminate inflorescences peduncled, with peduncle with ca. 1 cm. However, shows similarities with *Naucleopsis ulei* subsp. *ulei* by similarities of the pistillate inflorescences.

27. *Naucleopsis velutina* C.C.Berg (1996: 241).

Type: PERU. Loreto: Província Maynas, Iquitos, Allpahuayo, Estación Experimental de IIAP, 23 August 1990, (♂), *R. Vásquez et al*. *14263* (holotype MO [photo!]).

Tree to 25 m tall; latex not seen. Leafy twigs with long internodes distinctly different in length, 3-6 mm, brownish, glabrous, strongly peeling; lenticels inconspicuous. Leaves oblong to lanceolate, 22-40 cm long., 8-14 cm broad, coriaceous, without perforations; glabrous above, pubescent beneath, smooth beneath; obtuse-rounded at the base, equilateral; acute-acuminate to obtuse at the apex; margin entire, primary veins brown-reddish, secondary veins 18-26 pairs, strongly prominent beneath, curved-arched to the margin; petioles 0.6-1 cm long.; stipules 0.5-1.0 cm long., entire margin, caducous. Staminate inflorescences 2-5 together, 0.8-1.3 cm diam.; peduncle 3-5 mm long.; involucre with ovate, pubescent to velutinous, smooth bracts, in ca 7 series; perianth 2.5-3 mm high; tepals 4-6, free to basally connate; stamens not seen. Pistillate inflorescences not seen. Infructescences globoid, 4-8 cm in diam.; indistinct fruiting perianth; fruiting pseudo-tepals 8-1.5 mm high, tomentose-velutinous, subulate.

FIGURE 38. Distribution maps of *Naucleopsis velutina.*

Representative specimens:—PERU. Maynas: Quebrada Yanomono, above mouth of Rio Napo on Rio Amazonas, 05 November 1979, (♀), *A. Gentry et al. 27466* (BG).

Distribution and habitat:—This species is only known from Amazonian Peru, in terra firme forest.

Vernacular Name:—unknown

Etymology:—The epithet refers to the velutinous indumenta of free pseudo-perianth.

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis velutina* is considered Near Threatened (NT), because of the low number of locations (1) and cannot be calculated their extent of occurrence.

Notes:—This species is very rare. It is easily recognized because of the pubescent to tomentose indument on abaxial surfaces. *Naucleopsis velutina* is similar to *N. sp3*, however, the pistillate inflorescences are larger in *Naucleopsis velutina* and the pubescent indument differt.

28. *Naucleopsis sp1* Al. Santos & Romaniuc, *sp nov.*

Type:—BRAZIL. Amazonas: Manaus, Estação Experimental de Silvicultura Tropical, 1997, (♀), *M. C. Lemos 174* (holotype INPA!).

Tree (6-)10-22 m tall; latex white to yellow. Leafy twigs with long internodes distinctly different in length, 4-5(-9) mm thick, brownish, puberulous to velutinous, ridged; lenticels conspicuous. Leaves narrowly oblong, 19-39 cm long., (5.5-)6.5-9.5 cm broad, coriaceous, without perforations; glabrous above, scabrous beneath; acute to obtuse at the base; acute-acuminate at the apex; margin mostly semi-revolute; primary veins bronwn-reddish, secondary veins 20-28 pairs, prominent beneath, often straight to the margin; petioles 1.5-3 cm long.; stipules 1-1.5 cm long., entire margin, caducous. Staminate inflorescences 4-10 together, 4-8 mm diam.; peduncle 3-6 mm long., puberulous to pubescent; involucre with ovate puberulent to pubescent bracts, in 3 series; perianth 1-2 mm high; tepals 3-5, free; stamens 3-4, connate at the base. Pistilate inflorescences 1-3 together, 9-10 mm diam.; sessile; involucre with ovate puberulous to pubescent, smooth bracts, in 4-6 series; perianth 2-4 mm high, connate, 4-6 parted at the apex, pubescent to velutinous; stigma filiform. Infructescences globoid, 1.8-3 cm diam.; distinct perianth, fruiting perianth 0.5-1.5 cm high, tubular.

Representative specimens:—BRAZIL. Amazonas: Manaus, ca. 90 km NNE Manaus, Distrito Agropecuário da Suframa, 02º24’26”-02º25’31”S, 59º43’40”-59º45’50”W, 10 November 1989, (♀), *P. Kukle 18* (K, SP, INPA), 21 November 1990, (♂), *M. A. Freitas et al. 455* (INPA), (♀), *A. A. Oliveira et al. 225* (INPA, SPF), BR174, Fazenda Dimona, 02º19’S” 60º05’W”, (♂), *P.A.C.L. Assunção s.n.* (INPA 174252), Rodovia Manaus-Caracaraí km 39, Reserva Experimental de Silvicultura Tropical, 14 November 1977, (♂), *J. Ribamar & J. Ramos 212* (INPA), Rodovia Itacoatiara-Manaus km 31, 09 November 1963, (♂), *E. Oliveira 2933* (IAN), Rodovia Manaus-Itacoatiara km 99, 19 September 1965, (♂), *W. Rodrigues & Loureiro 7132* (INPA). Pará: Oriximiná, Área de Mineração Rio Norte, Platô da serra Sacazinho, 40 km ao Sul da vila de mineração, 01º45’S 56º30’W, (♀), *C.A. Cid Ferreira 9506* (INPA, K, MG, RB, UFACPZ).

Distribution and habitat:—It is known only in Brazilian Amazon, in the states of Amazonas and Pará, in Terra Firme forest, at low elevation up to 125 m.

Etymology:—The epithet refers to the tubular format of the perianth of the pistillate flower and fruit.

Vernacular Name:**—**muiratinga (Brazil).

IUCN conservation status:—According to the IUCN Red list categories (IUCN 2015), *Naucleopsis sp1* considered Endangered, EN B1a,b(iii), because of the small extent of occurrence only in Brazilian Amazon, in the states of Amazonas and Pará (ca. 1.340 km^2).

FIGURE 39. Distribution maps of *Naucleopsis sp1*.

Notes:—The pistillate inflorescence of *Naucleopsis sp1* is clearly different any other of group. The fruiting perianth shaped velutinous tubes, 0.5-1.5 cm high. Also, the leaves are narrowly oblong and scabra beneath. This species has been identified as *N. caloneura* by leaf size and veins color. The great diversity polymorphic of the species of *Naucleopsis*, has led to several controversies taxonomic issues.

29. ***Naucleopsis sp2*** **Al. Santos & Romaniuc,** ***sp. nov.***

Type: —BRAZIL. Amazonas, Manaus, BR 174, km 159, Manaus-Caracaraí Road, 20 September 1974, (♀), *G.T. Prance et al. 22716* (holotype: INPA!).

Tree (06-)10-16 m tall; latex colorless. Leafy twigs with long internodes distinctly different in length, 3-4 mm thick, brownish, glabrous to puberulent to puberulous, peeling to ridged; lenticels conspicuous. Leaves lanceolate, 15-19 cm long., 4-5.5 cm broad, , with perforations, both faces glabrous; smooth beneath; acute to attenuate at the base, equilateral; acute-acuminate at the apex; margin entire; secondary veins 13-15 pairs, prominent beneath, curved-arched to the margin; petioles 0.6-1 cm long.; stipules 0.5-1.0 cm long., entire margin, caducous. Staminate inflorescences not seen. Pistillate inflorescences solitary, up to 2 cm diam.; sessile; involucre with ovate, puberulous to pubescent smooth bracts, in 4-5 series; distinct perianth, connate, parted 4-6 in apex, puberulent; stigma not seen. Infructescences globoid, 4-5 cm diam.; distinct fruiting perianth, fruiting perianth 2-3 mm high, oblate.

Representative specimens:—BRAZIL. Amazonas, Manaus, BR 174, km 159, Rodovia Manaus-Caracaraí, 20 September 1974, (♀), *G.T. Prance et al. 22713* (K). PERU. Cusco, Distrito Echarate, Kepashiato, 12º41’00”S, 73º15’45”W, 20 March 2007, (♀), *L. Valenzuela et al. 9295* (BG MO).

Distribution and habitat:—It is known only from Brazilian Amazon to Peru, in Terra Firme forest, at elevation up to 1200 m.

Etymology:—The epithet refers to morphological of fruiting perianth.

Vernacular Name:—unknown.

FIGURE 40. Distribution maps of *Naucleopsis sp2.*

IUCN conservation status:— *Naucleopsis sp2* is known from two collections in the state of Manaus (Brazil) and in the distrito Echarate (Peru), made between 1974 and

2007. The extent of occurrence of *N.sp2* is 4.527 Km^2, however, the population size is unknown. For these reasons *N. sp2* is assessed as Data Deficient (DD) according to IUCN Red List criteria (IUCN 2015).

Notes:—Morphologically, this species show similarities with *N. krukovii* due to the leaves greenish, veins yellow-greenish beneath when dried and lamina with perforations, but *N. sp2* is distinguished especially by structure of its pistillate flower and fruit. In *N. sp2* the perianth is oblate and the tepals are connate, differently than in *N. krukovii*, which presents the perianth with free pseudo-tepals. In addition to *N. krukovii*, the new species also resembles the *N. humilis* from which it can be distinguished by its leaves obovate with cuneate base.

30. *Naucleopsis sp3* Al.Santos & Romaniuc, *sp. nov.*

Type: ECUADOR. Morona Santiago, Puerto Morona Rio Morona, 02º52’00”S, 77º41’00”W, 30 September 1975, (♀), *E.L. Little et al. 501* (holotype: US!)

Tree (8-)10-20 m tall; latex white. Leafy twigs with long internodes distinctly different in length, 3-4 mm thick, greyish to brownish, glabrous, peeling; lenticels conspicuous. Leaves lanceolate, 12-21 cm long., 3-6.5 cm broad, coriaceous, with perforations, both faces glabrous, smooth beneath; acute to obtuse at the base, equilateral; acute to obtuse at the base; acute-acuminate apex; margin entire; secondary veins 10-13 pairs, prominent beneath, curved-arched to the margin; petioles 0.6-1 cm long.; stipules 0.5-0.6 cm long., entire margin, caducous. Staminate inflorescences not seen. Pistillate inflorescences solitary, 1-1.5 cm diam.; sessile; involucre with ovate to deltoid, tomentose to velutinous smooth bracts, in 4-5 series; indistinct perianth, free pseudo-tepals 0.4-0.6 cm high, subulate, tomentose to velutinous; stigma not seen. Infructescences globoid, 2-2.5 cm diam.; indistinct fruiting perianth, fruiting pseudo-tepals 2-3 mm high, subulate.

Representative specimens:—BRAZIL. Rondônia: Rio Jamari, cachoeira Santa Cruz, 28 June 1965, (♀), *J.M. Pires 9955* (IAN), *J.M. Pires 9956* (IAN).

Distribution and habitat:—Northwest of Brazil (Rondônia) and Ecuador, in Terra Firme forest, in lowland moist areas, at an elevation up to 120 m.

FIGURE 41. Distribution maps of *Naucleopsis sp3.*

Etymology:—The epithet refers to the tomentose indument.

Vernacular Name:—cauchillo (Ecuador)

IUCN conservation status:—*Naucleopsis sp3* is known from two collections in the Ecuador (Santiago) and in the state of Rondônia (Brazil), made between 1965 and 1975. Nevertheless, the extent of occurrence of *N.sp4* is 1.908 Km^2 and the population size is unknown. For these reasons *N. sp3* is assessed as Data Deficient (DD) according to IUCN Red List criteria (IUCN 2015).

Notes:—As with *N. sp2,* morphologically this new species also show similarities with *N. krukovii* due to the leaves with veins yellow-greenish beneath when dried and lamina with perforations, but *N. tomentosa* is distinguished mainly by tomentose indument of its free pseudo-tepals.

31. *Naucleopsis sp4* Al. Santos & Romaniuc, *sp. nov.*

Type:—BRAZIL. Acre: Mancio Lima, Alto Rio Moa, Serra do Divisor, behind Fazenda Boa Vista, 07º25'S 73º38'W, 15 October 1989, (♀), *C.A. Cid Ferreira et al. 10104* (holotype NY!, Isotype INPA!).

Fig. 42 A-H.

Tree 7-10 m tall; latex colorless. Leafy twigs with long internodes distinctly different in length, 2-4 mm thick, greyish to yellowish, glabrous, smooth to ridged; lenticels inconspicuous. Leaves lanceolate, 12-17 cm long., 3.5-4.5 cm broad, chartaceuos, without perforations, both faces glabrous, smooth beneath; acute to attenuate at the base, equilateral; acute-acuminate at the apex; margin entire; primary veins orange-yellowish beneath, secondary veins 12-13 pairs, plane beneath, curved to the margin; petioles 0.8-1.2

cm long., puberulent; stipules ca. 1.2 cm long., entire margin caducous. Staminate inflorescences not seen. Pistillate inflorescences solitary, 1-1.7 cm diam.; sessile; involucre with ovate to deltoid puberulent, smooth bracts, ca 4-5 series; distinct to indistinct perianth, free pseudo-tepals 0.3-0.4 cm high, stigma filiform. Infructescences globoid, 2.5-3.5 diam.; indistinct fruiting perianth, fruiting pseudo-tepals acuminate.

Representative specimens:—BRAZIL. Acre: Rio Branco, BR 364, km 44 Rio Branco-Porto Velho Road, 09 October 1980, (♀), *C.A. Cid & B.W. Nelson 2811* (RB). Pará: Marabá: 05º28'S 49º31'W, 27 November 1986, (♀), *J.B.S. Pereira et al. 01 (*MG).

Distribution and habitat:—The species is known only by two collections in the state of Acre (Brazil), in Terra Firme forest of the Amazonian region, mostly in lowland moist area.

Vernacular Name:—unknown

Etymology:—The epithet honors C. C. Berg, a botanical collector.

IUCN conservation status:—*Naucleopsis sp4* is known from only one collections in the state of Acre (Brazil), made between 1980 and 1989. Nevertheless, the population size is unknown. For these reasons *N. sp4* is assessed as Data Deficient (DD) according to IUCN Red List criteria (IUCN 2015).

Notes:—The species is endemic to the Brazilian Amazon and presumably very rare. *N. sp4* species has been identified incorrectly as *N. caloneura* for a long time. However, it can be clearly distinguished from all other species of *Naucleopsis* by fruiting free pseudo-tepals oblate in layers, oblong at the apex. In addition, the secondary veins are stained when dried. Differently, *N. caloneura* present the secondary veins brownish and similar to leaf color when dried. In *N. caloneura* the leaves are largest and broadest and the fruiting perianth is ovate-deltoid.

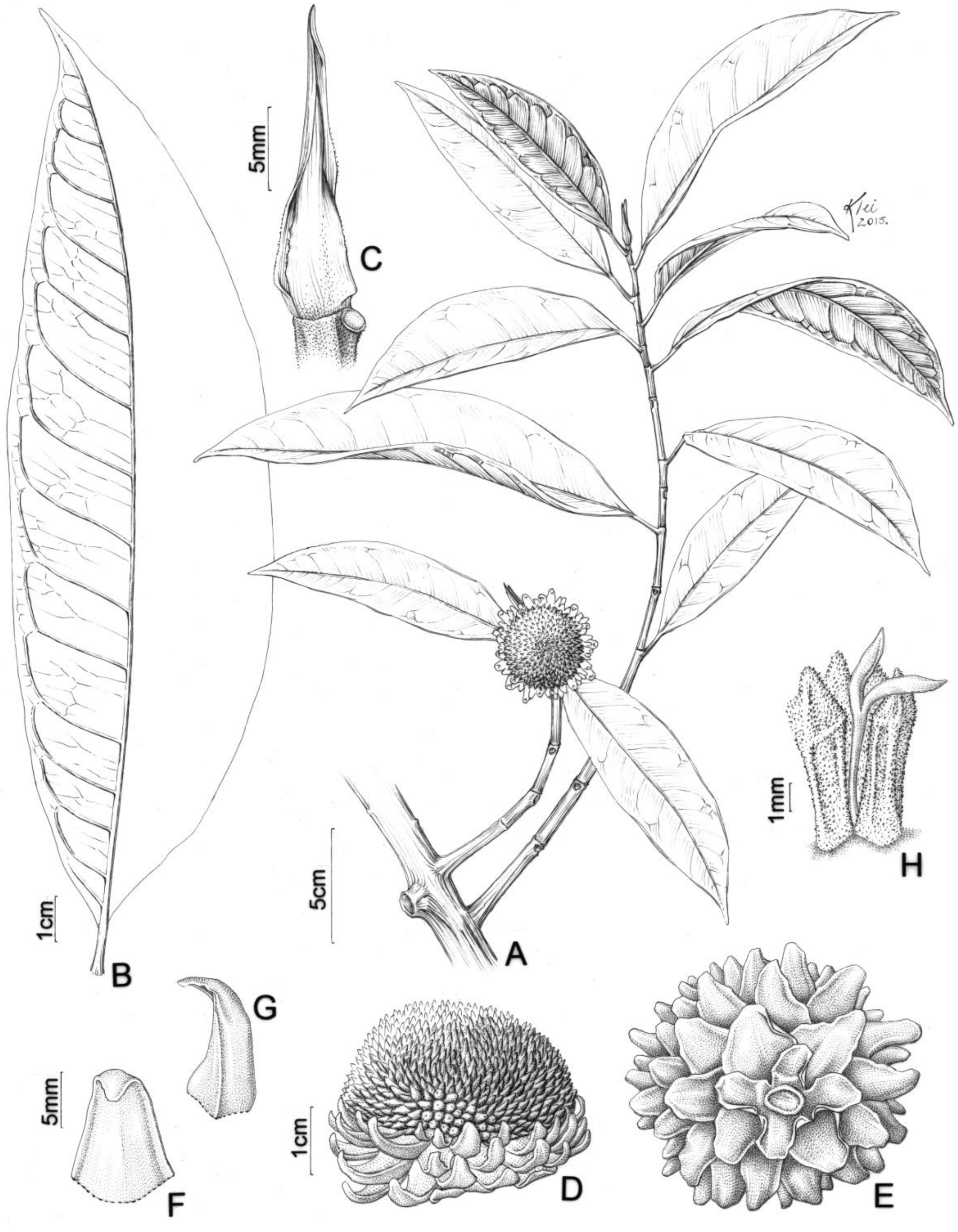

FIGURE 42. *Naucleopsis sp4* - **A.** Habit. **B.** Detail of the lower surface of the lamina. **C.** Details of stipules. **D.** Pistillate inflorescence. **E.** Details of involucre of imbricate bracts. **F-G.** Details of bracts of the pistillate inflorescence. **H.** Pistillate flower, *C.A. Cid Ferreira et al. 10104* (NY).

FIGURE 43. Distribution maps of *Naucleopsis sp4*

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Appendix I. Index to numbered collections examined.

The number in parentheses refer to the corresponding names in the text and in the Numerical list of species presented above (Appendix I).

Acevedo, P. et al. 1721 (4).

Acevedo-Rodríguez, P. et al. 13577 (25).

Aguilar, R. 10741 (26.4); 10744 (26.4).

Alvarado, C. 113 (3).

Assunção, P.A.C.L. s.n. (INPA 174252) (28).

Aulestia, M. et al. 2991 (9).

Barrier, S. 4300 (8).

Beck, H.T. et al. 1046 (7).

Berg, C.C. et al. 486 (11); BG 754 (2); P 17624 (20).

Berg C.C. & Dressler R.L. 307 (26.3).

Bondar, G. 2179 (19).

Bovini, M.G, et al. 2986 (26.1); 3134 (5).

Chacón, A. 8 (26.3).

Campos, M.T. & Boom, B. 21 (20).

Carlos L. et al. 1370 (15).

Castilho, C.V. 437 (13).

Cavalcante, P. 348 (26.2); 987 (26.2).

Cavalcante, P. & Silva, M. 1520 (2).

Cerón, C. & Factos, M. 7485 (9).

Cid, C.A. 3999 (23).

Cid, C.A. et al. 8282 (7); 8391 (11).

Cid, C.A. & Nelson, B.W. 01 (31); 2872 (25); 2964 (7).

Cid, C.A. & Rosa, A. 2945 (7).

Cid Ferreira, C.A. 9506 (28).

Cid Ferreira, C.A. et al. 5329 (5); 9506 (28); 10018 (26.4); 10601 (22).

Coelho, L. et al. 401 (22).

Coelho, L.S. et al. 90 (20).

Cordeiro, M.R. 782 (7).

Cornejo, X. & Bonifaz, C. 6247 (26.3).

Daly , D.C. et al. 1179 (2); 1411 (2); 6160 (10); 7772 (26.1); 8329 (20); 9994 (7); 9996 (21); 10512 (22).

Davidson, C. 5236 (11).

Dick, C. 82 (13).

Dionizia et al. 119 (7).

Ducke, A. s.n. (IAN 50550) (2); (RB 35441) (2); (RB 18300) (7); (RB 13028) (13); (INPA 14959) (16); (INPA 15594) (16), (RB 23985) (16); (RB 141607) (16); (RB 19491) (16); (RB 35439) (26.2); (SP 444901) (16); (RB 18290) (26.1); (RB 35440) (26.1).

Ducke, A. 1045 (26.1); 1456 (11); 1785 (15).

Egler, S.G. et al. 1495 (20); (SP 330807), (20).

Ek et al. 1027 (8).

Equipe de resgate 1287 (5).

Ferreira, A.J.C. e Equipe s.n (2).

Ferreira H. 61 (12).

Fiaschi, P. et al. 3460 (19).

Forero, E. et al. 6343 (15).

Freitas, C.A.A. et al. 69 (23).

Freitas, M.A. et al. 455 (28).

Fróes, R.L. 26241 (7); 23702 (26.1); 28329 (15).

Gentry, A. et al. 27466 (27); 36547 (26.2).

Gentry, A. & J. Brand, M. 36924 (24).

Gentry, A. & Ortiz, R. 74198 (10).

Gomes, J.V. 10 (16).

Gomes, M. & Miranda, S. 325 (7).

Goulding, M. 1415 (12).

Grández, C. 1077 (1).

Grández, C. et al. 4913 (10).

Grijalva, A. et al. 600 (3).

Haber, W. & Zuchowski, W. 11612 (3).

Herrera, G. & Chacón, A. 2674 (18).

Ho, R.C. & Madrid, J. 45 (18).

Holdridge, L.P. 2536 (18).

Jaramillo, J. et al. 12138 (10).

Killip. E.P. & Smith, A.C. 2844 (26.1); 28179 (26.2).

Kukle, P. 18 (28); 93 (13).

Kuhlmann, J. 270 (16).

Kuhlmann, J.G. 1955 (2).

Lima, H.C. et al. 2092 (2).

Lima, L. 549 (23).

Little, E.L. et al. 522 (5).

Lobato, LC.B. et al. 1333 (16); 1952 (16).

Lombardi, J.A. et al. 7109 (19).

Lowrie, S.R. et al. 499 (11).

Medeiros, H. 486 (11).

Medeiros, H. et al. 204 (22); 388 (12); 787 (1); 788 (7); 824 (12).

Miller, R. et al. 605 (20).

Monteiro, O.P. 147 (13).

Monteiro, R.S. 306 (25).

Mori, S. et al. 14901 (8).

Nascimento, J.R. & Oliveira, J.G. 515 (13).

Nee, M. 34575 (7); 42333 (13); 344338 (5).

Neill, D. et al. 8335 (9).

Neill, D. & Dendrology course 15334 (6).

Nelson, B. 689 (25); 744 (11).

Oliveira, A.A. et al. 207 (20); 225 (28); 305 (26.2).

Oliveira, E. 753 (2); 2933 (28); 2881 (26.2).

Oliveira, P.P. 264 (19).

Ortiz, A. et al. 17 (26.3).

Paixão J.L. et al. 1250 (19).

Palacios, W. et al. 9674 (17); 9691 (17).

Pereira, J.B.S. et al. 01 (31).

Pereira, M.J.R. & Equipe s.n. (INPA 174074) (13).

Pena B.B. 436 (12).

Pennington, T.D. et al. 16103 (4).

Pipoly, J. et al. 18394 (18).

Pires, J.M. 9955 (30); 9956 (30); 13110 (25); 51293 (8).

Prance, G.T. 8644 (12).

Prance, G.T. et al. 2426 (11); 2428 (26.1); 2441 (1), 8411 (12), 8646 (12), 8704 (16); 12467 (15); 22713 (29); 22716 (28), 23002 (20); 23841 (26.2); P 25386 (25); P 25594 (13); P 25796 (7); P 26406 (20).

Pruski, J. et al. 3476 (22).

Quinet, A. 1198 (5).

Quizhpe, W. et al. 740 (6).

Ramos, J.F. 1634 (2).

Ramos, J. & Lima, E.F. 1510 (25); 1579 (2).

Ramos, J. & Mota, G. (26.1).

Ribamar, J. & Ramos, J. 212 (28).

Ribeiro, J.E.L.S. et al. 1231 (13); 1741 (13); 1800 (23).

Ribeiro J.E.L.S. & Assunção P.A.C.L. 1964 (26.2).

Rimach Y., M. 6707 (1).

Rodrigues, W. 2060 (5).

Rodrigues, W. & D. Coelho 5593 (13).

Rodrigues, W. & Osmarino 6842 (13).

Rodrigues, W. & Loureiro 7132 (28).

Rosa, N.A. & Coelho, L. 570 (22).

Rosário, C.S. & M.R. Santos 721 (23).

Rubio, D. et al. 1268 (3).

Salomão, R.P. 1181 (2).

Santos, A. et al. 154 (23); 163 (10); 199 (25); 202 (15).

Santos, M.R. 98 (26.2).

Santos, T.S. 1226 (19).

Silva, M.G. 6476 (26.1).

Silva, M.F.F. et al. 360 (25).

Silva, N.T. 425 (23).

Silveira, M. et al. 987 (21).

Silverstone-Sopkin, P. et al. 9048 (17).

Scolnik, R. et al. 19S005 (7).

Sothers et al. 66 (14).

Sothers, C.A. & Assunção, P.A.C.L. 850 (23).

Souza, S.A.M. et al. 545 (20).

Setz, E. s.n. (UEC 43755) (13); (UEC) (13).

Silva, M.F. & pessoal da botânica 757 (15).

Silva, M.G. 6213 (12).

Silveira, M. et al. 700 (12); 1060 (7).

Spichiger, R. & Loizeau, P. A. 4501 (1).

Teixeira, L.O.A. et al. 622 (23); 739 (5).

Tello 201 (21).

Tipaz, G. et al. 1309 (3); 1362 (3).

Tirado, M. et al. 247 (4).

Thomas, W. et al. 4119 (25); 4950 (16).

Valenzuela, L. et al. 9295 (29).

Vásquez, R. et al. 12138 (10); 30711 (26.4).

Vásquez, R. & Jaramillo N. 3422 (26.1); 4477 (11); 13092 (9).

Vicentini, A. et al. 727 (20).

Vieira, G. et al. 289 (16).

Vieillescazes, A. 487 (8).

Appendix II. Numerical list of species.

1. *N. acreana*
2. *N. caloneura*
3. *N. capirensis*
4. *N. chiguila*
5. *N. concinna*
6. *N. francisci*
7. *N. glabra*
8. *N. guianensis*
9. *N. herrerensis*
10. *N. humilis*
11. *N. imitans*
12. *N. inaequalis*
13. *N. insculptula*
14. *N. jamariensis*
15. *N. krukovii*
16. *N. macrophylla*
17. *N. meridionalis*
18. *N. naga*
19. *N. oblongifolia*
20. *N. pauciflora*
21. *N. pseudonaga*
22. *N. riparia*
23. *N. stipularis*
24. *N. straminea*
25. *N. ternstroemiiflora*
26. *N. ulei,*
27. *N. velutina*
28. *N. sp1*
29. *N. sp2*
30. *N. sp3*
31. *N. sp4*

Capítulo 3 – Estudos biogeográficos

Patterns of biogeographic regionalization and biogeographical history of *Naucleopsis* (Moraceae) from Neotropics and comments from allied genera

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ABSTRACT

Aim *Naucleopsis* ranges from Honduras to the State of Rio de Janeiro, in Brazil, and most species belong to the Amazon region, mainly in lowland tropical moist forest. In this study, we used a time-calibrated molecular phylogeny to perform ancestral-area reconstructions for the terminals analyzed, in order to: (1) infer its area of origin; (2) test whether vicariance played a role in the history of lineages occupying the Neotropical region; (3) infer the ages of lineages diversification.

Locations South and Central America.

Methods Our study focused in analysis of DNA sequence data from the plastidial *trnL-F* and nuclear FA03310 markers of 28 terminals from Moraceae, of which nine from *Naucleopsis.* We used bayesian inference and divergence time estimation method implemented in the program BEAST 2.1.0. Ancestral areas were reconstructed through statistical dispersal–vicariance analysis (S-DIVA) using the program RASP v. 3.2.

Results and main conclusions Our analyses focusing *Naucleopsis* and the results suggest that the genus was originated during Oligocene (ca. 32.91 Mya), in Boreal-South Brazilian region (Amazon rainforest). The Andean uplift presumably has played an important role in the diversification of the major lineage (*Naucleopsis* core clade) in *Naucleopsis* by several likely ways, during the Miocene (ca. 16,09 Mya). Environmental and geologic change during late Miocene and Pliocene (ca. 7.44–4.78 Mya) might have driven to diversification of recent lineages of the genus. Divergence time estimation is also provided for the main accession of Castilleae Neotropical analyzed.

Keywords Amazon rainforest, biogeography, Castilleae, *Naucleopsis*, Neotropical flora.

INTRODUCTION

The Neotropical region (tropical America) comprises about 90,000 plant species, representing 37% of the world's total (Richardson *et al*., 2001). This region is the most rich of species on Earth (Antonelli & Sanmartín, 2011). Many mechanisms have been proposed to have played a role in the historical assembly and evolution of neotropical biodiversity (Antonelli & Sanmartín, 2011).

Recent studies have focused on better understanding the origin of contemporary plant diversity in the Neotropics (Pennington and Dick, 2004; Dick *et al*., 2007; Särkinen *et al*., 2007; Trénel *et al*., 2007). The Gondwanan vicariance was thought to be originated from the diversity of tropical South America (Gentry, 1993) followed by a long period of isolation, coined "splendid isolation" (Simpson, 1980).

Four major geologic events were mentioned as being responsible for the high diversity thrusters in Neotropics by Burnham & Graham (1999): isolation between South America and Africa, uplift and physigraph change, closure of the Isthmus of Panama, and quaternary climate fluctuations.

These events were corroborated for many botanical studies suggesting that the Andean uplift was crucial for the evolution of Amazonian landscapes and ecosystems, and that current biodiversity patterns were rooted deep in the pre-Quaternary (Vuilleumier, 1971; Muller, 1972; Gentry, 1982; Granville, 1982; Prance, 1982; Frailey *et al*., 1988; Colinvaux, 1989; Hildebrand *et al*., 1991; Coates *et al*., 1992; Pitman *et al*., 1993; Romaniuc-Neto, 1998; Tada *et al*., 2003; Iturralde-Vinent, 2006; Clement, 2008; Hoorn *et al*., 2010; Rossetti *et al*., 2013).

Moraceae is cosmopolitan and comprised of 37 genera and about 1150 species (Berg, 2001). The family is heavily represented in tropical moist forest at low altitudes and one of the greatest diversity of species occurs within the Amazon region.

Molecular phylogenies (Sytsma *et al*., 2002, Datwyler & Weiblen; 2004; Clement & Weiblen, 2009), have corroborated the taxonomic affiliation of the Castilleae within the Moraceae. *Naucleopsis* Miq. is the largest genus of Castilleae. The genus is a monophyletic lineage strongly supported (Bootstrap [BP] = 100 and Bayesian posterior probability [PP] = 1.0) within of Castilleae tribe included in Moraceae (Chapter 1). The genus includes 31 species (Chapter 2), occurring ranges from Honduras to the southeast of Brazil, in Rio de Janeiro. The greatest diversity of species occurs mainly in terra firme forest (non-inundated). It is recognized by being usually trees, dioecious, rarely monoecious. Leaves coriaceous to chartaceous, always entire and mostly glabrous. Stipules fully amplexicaul, free, caducous or rare persistent in the internodes along leafy twigs. Staminate inflorescences up to 10 together, inner involucral bracts covering the flowers before anthesis. Pistillate inflorescence mostly solitary, ovary entirely immersed in the receptacle and flowers with distinct to indistinct perianth.

Castilleae Neotropical is an interesting model for biogeography and evolutionary studies, due to its phylogenetic relationship with Castilleae paleotropical, patterns of biogeographic regionalization in Neotropical region, and remarkable morphological diversity. Also, the study with focus in *Naucleopsis* aims to provide a time-calibrated molecular phylogenetic tree and ancestral area reconstructions to evaluate historical biogeography of the genus.

MATERIAL AND METHODS

Taxon sampling

We included 28 accessions (25 taxa) in this study. The ingroup comprised all neotropical genera that have been placed in Castilleae in the most recent circumscriptions (Datwyler & Weiblen, 2004; Zerega *et al.*, 2005; Clement, 2008; Clement & Weiblen, 2009; Zerega *et al.*, 2010). Thus, the ingroup has one accession of *Poulsenia* (1 taxon), two of *Castilla* (1), two of *Pseudolmedia* (2 taxa), five of *Perebea* (4), one of *Maquira* (1), three of *Helicostylis* (3), and nine of *Naucleopsis* (8).

Outgroup taxa belong to other tribes of Moraceae, such as Ficeae (3 taxa of *Ficus*), Maclureae (1 taxon of *Maclura*) and Moreae (1 taxon of *Sorocea*) as recognized in the most recent accounts of the tribes of Moraceae (Datwyler & Weiblen, Clement & Weiblen, 2009).

Taxa sampled, voucher information, and GenBank accession numbers for the three datasets are listed in Appendix 1.

DNA extraction, sequencing and editing

Leaf samples were collected either in silica gel or from herbarium sheets (Appendix 2). Genomic DNA was extracted with approximately 20 mg of dried leaf tissue using a modified CTAB (cetyltrimethylammonium bromide) method (Weiblen, 2000). Amplification of the *trnL-F* region utilized external primers “c” and “f,” and the internal primers “d” and “e” were also employed for amplification from herbarium specimens (Taberlet *et al.*, 1991). Thermal cycling conditions for amplification of the *trnL-F* region were: 94°C for 10 min followed by 32 cycles of 94°C for 45 sec, 57°C for 30 sec, 72°C for 1 min 30 sec, and a final extension of 74°C for 7 min.

PCR amplification of the nr FA03310 DNA region was achieved in one fragment using FA FA03310 forward (5'-GCGGGTATAAGAAGGGAACC-3') and FA03310 reverse (5'- GGTGCATTGACCACCTTGAT-3') an exon-primed intron-crossing (EPIC) marker designed specifically for *Ficus* from Yao *et al*. (2013). Amplification of FA03310 included about 25 µl volume ReadyMixTM Taq PCR Reaction Mix with MgCl2 (Sigma-Aldrich), 1mg/ml de BSA (bovine serum albumin), 20 µM of each primer and ~50 ng of genomic DNA. Thermal cycling conditions for amplification of the FA03310 region were: 94°C for 10 min followed by 36 cycles of 94°C for 45 sec, 54°C for 30 sec, 72°C for 1 min 30 sec, and a final extension of 74°C for 7 min.

PCR products were sent to Magrogen Inc. South Korea (Seoul), where they were purified and subsequently sequenced in both directions using the same PCR primers.

Complementary DNA sequences were assembled for each accession using Geneious® 8.0.2 (Kearse *et al*., 2012; Biomatters, 2015). Multiple-sequence alignment was performed using Clustal W (Chenna *et al*., 2003) followed by manual optimization. Manual alignment and optimization were performed in Geneious® 8.0.2.

Pattern of biogeographic regionalization

The data matrix of geographic distribution were obtained from Moraceae database, using FileMaker Pro 14.4, in which were analyzed approximately 40000 herbarium specimens of Moraceae from several herbaria of the world. In *Naucleopsis*, our analyses were based on about 2000 herbarium specimens from 19 herbaria and multiple field trips, which resulted in Revision of *Naucleopsis* (Chapter 2).

The pattern of biogeographic regionalization was based in Morrone (2014), as well as the coding of biogeographical regions character states, which reflect patterns of endemism in *Naucleopsis*. The regions correspond to domains proposed by Morrone (2014) and are: Mesoamerican; Pacific; Boreal Brazilian; South Brazilian; Chacoan; Parana (Figure 1 B).

Estimation of divergence times

We implemented a Bayesian relaxed model to determine divergence times for the three regions (pt *trnL-F*, and nr FA03310) dataset using BEAST v.2.1.0 (Bouckaert *et al*., 2013; Bouckaert *et al*., 2014). A likelihood ratio test for rate constancy was performed using PAUP* 4.0b10 (Swofford, 2002) and results indicated that the gene region was not evolving in a clock-like manner. Based on the hierarchical likelihood ratio tests - hLRT (Posada & Buckley, 2004), combined data sets were evaluated for the appropriate model of molecular evolution using ModelTest v. 3.7 (Posada & Crandall, 1998). With BEAUti 2 (Bouckaert *et al*., 2013) we created the input file with nucleotide substitution HKY + G (pt *trnL-F*, and nr FA03310) using a gamma distribution with four rate categories, under an uncorrelated lognormal relaxed clock model (Drummond *et al*., 2006), and a Yule process of speciation (Gernhard *et al*., 2008) was employed as prior.

Markov Chain Monte Carlo (MCMC) analysis was run for 10 million generations and sampled every 10000th generation. Convergence of the chains was checked using Tracer v.1.6.0 (Rambaut *et al*., 2013). All trees obtained prior to convergence were discarded and trees were summarized in a maximum clade credibility tree under 95% highest posterior density (HPD) in TreeAnotator v.2.0.3 (Rambaut & Drummond, 2013). The final tree was viewed using FigTree v.1.4.2 (Rambaut, 2014).

Sorocea, *Maclura* and *Ficus* were constrained as outgroup taxa and node priors for the root.

The root node was set to a minimum age of 60 Mya based on fruits fossils of *Ficus* (Collison, 1989) and a maximum age of 199 Mya based on the oldest known angiosperm fossil (Bell *et al*., 2010).

Biogeographical Reconstructions and coding of biogeographical regions character states

We performed the biogeographic analyses with RASP v. 3.2 (Reconstruction Ancestral State in Phylogenies; Yu *et al*., 2012) using statistical dispersal–vicariance analysis (S-DIVA; Yu *et al*., 2010) to reconstruct the biogeographical history of *Naucleopsis*. For these analyses, we used the maximum clade credibility tree under 95% HPD of TreeAnotator v.2.0.3 from results of BEAST v.2.1.0.

S-DIVA analyses were performed in RASP v. 3.2 using default parameters. Additionally, we set six max areas at each node, and selected the two boxes (allow extinction, allow reconstruction, and use ancestral range of condensed trees).

The regions that correspond to biogeographical regionalization proposed by Morrone (2014) are: (A) Mesoamerican; (B) Pacific; (C) Borel Brazilian; (D) South Brazilian; (E) Chacoan; (F) Parana.

RESULTS

Patterns of biogeographic regionalization and diversity of *Naucleopsis*

Naucleopsis is a neotropical genus of Moraceae traditionally included in Castilleae (Berg 1977). The center of diversity of genus is the Amazon region, mainly in terra firme forest at low altitudes often up to 450 meters.

Based on biogeographic regionalization proposed by Morrone (2014) and on maps from revision of *Naucleopsis* (Chapter 2) we considered six patterns of biogeographic regionalization for *Naucleopsis*: Neotropical, Mesoamerican-Pacific, Pacific, Boreal, Boreal-South and South Brazilian.

Neotropical pattern (Figure 1 A, B).

It is characterized by species with wide distribution, comprising areas between north of South America (8ºN and 79ºW) to east of Brazil (28ºS and 34ºW). This pattern includes three biogeographical regions from Morrone (2014): Parana, Boreal and South Brazilian (Figure 1 B). It corresponds to the distribution of only one species: *Naucleopsis oblongifolia*.

The largest concentration of this species occurs in terra firme forests of the Amazon Basin and in dense ombrophilous forest of the Atlantic forest of the coastal region from Bahia to Rio de Janeiro, in Brazil.

Mesoamerican-Pacific pattern (Figure 1 A, B).

It comprises south of Mexico (18ºN) up to northeast of Ecuador (1º50’S) and includes the Mesoamerican and Pacific dominions (Figure 1 B). *Naucleopsis naga* and *N. capirensis* present this pattern of biogeographic regionalization, occurring in tropical moist at an elevation of up to 2000 m above sea level.

Pacific pattern (Figure 1 A, B).

It includes Costa Rica, Panama, north of Colombia (up to ca. 2º30’N), northwest of Venezuela (up to ca. 7º20’N), west of Ecuador, and Colombia (76º20’W to 80º50’W). This pattern is related to the Pacific dominion (Figure 2B) from Morrone (2014), except by

Galapagos Islands and Trinidad province, in which *Naucleopsis* does not occur. It corresponds to the distribution of four species: *Naucleopsis chiguila, N. straminea, N. ulei* subsp. *puberula* and *N. meridionalis*. These species are distributed in lowland moist evergreen forest, at an elevation of up to 700 m above sea level, with the exception of *N. meridionalis*. This species is often distributed on the western slopes of the Andes from Antioquia (Colombia) to Azuay (Ecuador), at an elevation of about 800 to 2100 m above sea level.

Boreal Brazilian pattern (Figure 1 A, B).

This pattern corresponds to the Boreal Brazilian dominion (Figure 1 B) from Morrone (2014). It included eigth countries (Brazil, French Guiana, Suriname, Guyana, Venezuela, Colombia, Ecuador, and Peru) between the coordinates in about 9º40’N (Delta Amacuro, Venezuela) to 4º30’S (Amazonas, Peru), and 42ºW (Maranhão, Brazil) to 78ºW (Amazonas, Peru). This pattern comprises six species: *Naucleopsis francisci, Naucleopsis herrerensis, N. guianensis, N. ulei* subsp. *amara, N. velutina* and *N. sp1*. These species occur mostly in lowland of terra firme Amazonian rainforest, rare varzea, at an elevation of up to 450 m above sea level. Some species are endemic and rarely found in nature, such as: *N. francisci* and *N. velutina* (see conservation status in Chapter 2).

Boreal-South Brazilian pattern (Figure 1 A, B).

This pattern comprises two biogeographical regions from Morrone (2014): Boreal and South Brazilian dominions (Figure 1 B). This pattern comprises a great diversity of *Naucleopsis* with 16 species (ca. 50% of total): *Naucleopsis acreana, N. caloneura, N. concinna, N. glabra, N. humilis, N. imitans, N. insculptula, N. krukovii, N. sp2, N. pauciflora, N. pseudonaga, N. riparia, N. stipularis, N. ternstroemiiflora, N.* sp3 and *N.*

ulei subsp. *ulei*. These species occur mostly in lowland of terra firme forest Amazonian rainforest, often in riparian forest, less often in varzea forest, at an elevation of up to 600 m above sea level.

South Brazilian pattern (Figure 1 A, B).

This pattern comprises the regions from Morrone (2014): Boreal and South Brazilian dominions (Figure 1 B). This pattern comprises five species: *Naucleopsis ulei* subsp. *subandina*, *N. inaequalis*, *N. jamariensis*, *N. macrophylla* and *N. sp4*. These species occur mostly in lowland of terra firme Amazonian rainforest, often in riparian forest, less often in varzea forest, at an elevation of up to 450 m above sea level. However, *Naucleopsis ulei* subsp. *subandina* occur sometimes in montane forest, at an elevation of about 800 to 1500 m above sea level.

Divergence Time Estimation

Our divergence time analyses (Figure 2 A; Table 1) suggest that the earliest diverging contemporary lineages in Moraceae arose to approximately 89.32 Mya during the Late Cretaceous, age Coniacian (node 1 with 95% HPD, 78.89–94.74 Mya) (Table 1). The estimate age for the family is similar to Zerega *et al*. (2005) and within of the estimates ages for Rosales (100.76–101.33 Mya) from Magallón & Castilho (2009).

The analyses indicated lineages in Castilleae arose to approximately 41.16 Mya during the Eocene, age Bartonian (node 2 with 95% HPD, 60.42-25.05 Mya) (Table 1). The estimate age for the tribe is similar to Clement (2008). Within the tribe emerge two main lineages: *Castilla - Poulsenia* clade (node 3) and *Pseudolmedia, Perebea, Maquira, Helicostylis, Naucleopsis* clade (node 4). The node 3 emerges to ca. 17.28 Mya (32.19-13.86 Mya) (Table 1) during Miocene. The node 4 arose to ca. 35 Mya (46.01-22.78 Mya)

Figure 1 A. Diversity and geographic distribution of *Naucleopsis*. B. Biogeographic regionalization adapted from Morrone (2014): Mesoamerican (red); Pacific (green); Boreal Brazilian (orange); South Brazilian (yellow); Chacoan (purple); Parana (blue); Regions without register of *Naucleopsis* (gray).

(Table 1) during Eocene. Within the node 4, *Naucleopsis* is more closely related to *Helicostylis* and *Maquira*, and these lineages diverging to about 34.02 Mya (45.06-22.17 Mya) during the Eocene, age Priaborian (node 6).

The lineages in *Naucleopsis* diverged probably during Oligocene, age Rupelian to ca. 32.91 Mya (node 8 with 95% HPD, 53-21 Mya). The first lineage diverging in *Naucleopsis* is *N. humilis.* The major *Naucleopsis* lineage is *Naucleopsis* core clade, diverging to about 16.09 Mya during Miocene. This clade includes two lineages: *Naucleopsis imitans* clade and *Naucleopsis* eucore clade. Among the lineages, *Naucleopsis* eucore clade is the oldest, emerging during Miocene to about 14.08 Mya (21.62-8.53 Mya). This *Naucleopsis imitans* clade arose to ca. 10.65 Mya, during Miocene. The node 11 includes one lineage interesting within this group, where all species present conspicuously distinct perianth, fruiting perianth very thick and, presenting a significant reduction in the number of free pseudo-tepals. This type of perianth may be related to direction of diversification in this lineage. Some collectors mention that the fruits are eaten by animals (Berg 1972). Our field observations revealed that the fruits of *Naucleopsis oblongifolia* are colored (yellowish) when ripe. In addition, we observed that they were eaten by small mammals.

Biogeographical Reconstructions

Ancestral area reconstructions based on S-DIVA from RASP analyses indicated that the earliest divergences and the most recent common ancestor (MRCA) in *Naucleopsis* arose in the Boreal-South Brazilian region (Figure 2) with 98% of frequency (node 8; Table 1). The split between the major lineages in *Naucleopsis* (nodes 9) of S-DIVA analyses suggest colonization of South Brazilian region in nodes 9-11 (Figure 2), and of Parana region in nodes 11 and 15 (Figure 2). Our reconstruction in *Naucleopsis oblongifolia* clade (node 15) presented the most widespread MRCA, probably because of the recent distribution.

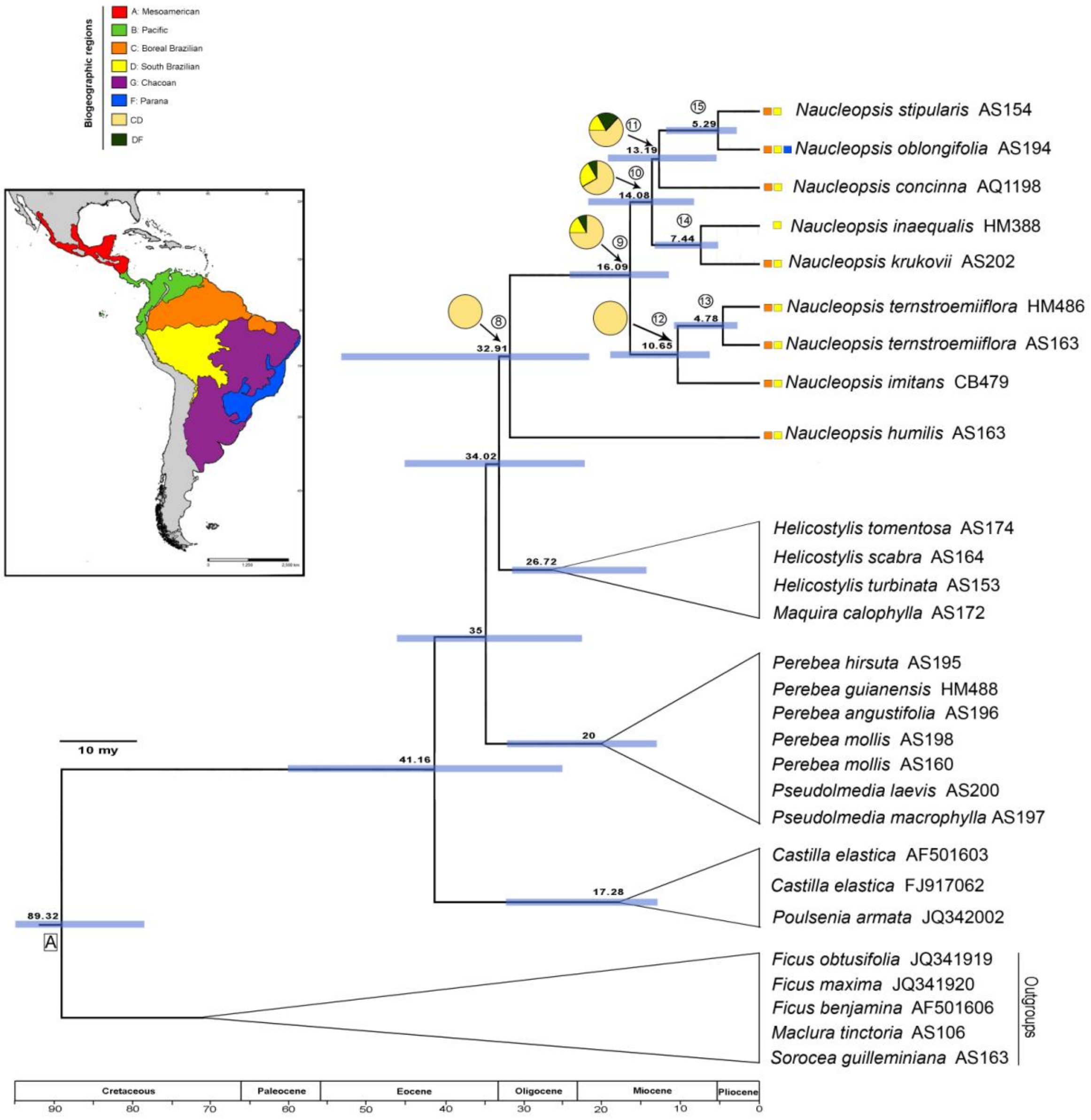

Figure 2. Chronogram resulting from the BEAST analysis of the combined sequence data (*trnL-F*and FA03310) of Castilleae (Moraceae), with focus in *Naucleopsis*. Bars represent the 95% high posterior density credibility interval for node ages, and numbers above or below branches are age of nodes. Pie graphs report relative probabilities from the statistical dispersal-vicariance analysis (S-DIVA) of the RASP analyses overlaid onto the maximum clade credibility chronogram from BEAST. Calibration points are indicated by A within square. Nodes 1–15 within circles are discussed in the text. Biogeographic regions from Morrone (2014).

However, all MRCA of these major lineages (nodes 9–15) appear strongly associated to Boreal-South Brazilian region.

DISCUSSION

Our biogeographic reconstruction corroborates a Boreal-South Brazilian origin in *Naucleopsis*, between the Andes and lowland Amazonia, during the Oligocene and/or Late Eocene (Figure 2, node 8, ca. 32.91 Mya).

The Andean uplift has probably played a central role in the diversification of the major lineages in *Naucleopsis* (nodes 8–15) by several likely ways, mostly during the Late Oligocene and Miocene (ca. 25,56–11,31 Mya). The split between the lineages in the nodes 10 and 12 of *Naucleopsis* arose maybe in the gradual uplift of the Eastern Cordillera creates a huge watershed forming the Pebas system (Burnham & Graham, 1999; Wesselingh *et al.*, 2002; Antonelli *et al.*, 2009; Hoorn *et al.*, 2010) that might have been a geographical barrier between these lineages, during the Middle Miocene (nodes 9).

Diversification of lineages (nodes 9-15) suggests colonizations of the Boreal-South and South Brazilian, during the late Oligocene and early Pliocene. Some geological events such as uplift of the Northern Andes, formation of Acre system and the increasing nutrient deposition in western Amazonia (Hoorn *et al.*, 2010; Antonelli & Sanmartín, 2011) were perhaps important ways for colonization of these areas.

Most part of the recent lineages of *Naucleopsis* arose during Miocene (nodes 10) (ca. 21.62–8.53 Mya) that was probably driven by the periods of intensified Andean uplift, the draining of wetland in Amazonia and climate fluctuations including the glacial climates (Burnham & Graham, 1999; Hoorn *et al.*, 2010). Parana region was likely colonized during the late Pliocene and early Pliocene (ca. 12.76–3.02) Mya, *Naucleopsis oblongifolia* clade, node 15).

The refuge theory of Pleistocene (Haffer, 1969; Vuilleumier, 1971; Granville, 1982; Andrade-Lima, 1982; Prance, 1982) might be also correlated with the contemporary pattern of biogeographic regionalization in *Naucleopsis*.

Our analyses reinforce the importance of geological and climatic events in the diversification of lineages in the Neotropical region, such as Andean Orogeny and climatic fluctuations.

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Table 1. Age estimates from BEAST analyses and ancestral state reconstruction from RASP analyses. HPD: highest posterior density; S-DIVA: statistical dispersal–vicariance analysis.

Node number and major clades	Age estimate and 95% HPD	Probababilities for nodal reconstruction
		S-DIVA
Node 1 – Moraceae	89.32 Mya 78.89–94.74 Mya	Not shown
Node 2 – Castilleae	41.16 Mya 60.42–25.05 Mya	Not shown
Node 3 – *Castilla* and *Poulsenia* clade	17.28 Mya 32.19–13.86 Mya	Not shown
Node 4 – *Pseudolmedia*, *Perebea*, *Maquira*, *Helicostylis* and *Naucleopsis* clade	35 Mya 46.01–22.78 Mya	Not shown
Node 5 – *Pseudolmedia* and *Perebea* clade	20 Mya 32.49–13.04 Mya	Not shown
Node 6 - *Maquira*, *Helicostylis* and *Naucleopsis* clade	34.02 Mya 45.06–22.17 Mya	Not shown
Node 7 – *Maquira* and *Helicostylis* clade	26.72 Mya 32.28–14 Mya	Not shown
Node 8 – *Naucleopsis*	32.91 Mya 53–21 Mya	CD: 0.98; DF: 0.02
Node 9 - *Naucleopsis* core clade	16.09 Mya 24.56–11.31 Mya	CD: 0.75; D: 0.18; DF: 0.07
Node 10 - *Naucleopsis eucore* clade	14.08 Mya 21.62–8.53 Mya	CD: 0.69; D: 0.24; DF:0.07

Table 1. Continued

Node number and major clades	Age estimate and 95% HPD	Probababilities for nodal reconstruction
		S-DIVA
Node 11 - *Naucleopsis concinna* clade	13.19 Mya 19.18–7.62 Mya	CD: 0.56; DF: 0.26; D: 0.18
Node 12 - *Naucleopsis imitans* clade	10.65 Mya 18.59–6.43 Mya	CD: 1.00
Node 13 - *Naucleopsis ternstroemiifolia* clade	4.78 Mya 10.94–2.17 Mya	CD: 1.00
Node 14 - *Naucleopsis krukovii* clade	7.44 Mya 13.66–5.06 Mya	CD: 0.67; D: 0.33
Node 15 - *Naucleopsis oblongifolia* clade	5.29 Mya 12.76–3.02 Mya	CD: 0.62; DF: 0.33; F: 0.05;

Appendix I. Specimens, voucher and GenBank accession number for taxa included in this study.

Species, collection voucher specimen (Herbarium), GenBank accession for nuclear FA03310 /plastid *trnL-F*. (GenBank numbers will be added after acceptance of manuscript)

Taxa/	**Voucher/ GenBank accession**	**Markers**
ingroup		
Naucleopsis caloneura	AY686819	26S
Naucleopsis concinna	A. Quinet 1198	FA03310 and *trnL-F*
Naucleopsis guianensis	AY686828	26S
Naucleopsis humilis	A. Santos 163	FA03310 and *trnL-F*
Naucleopsis imitans	C. C. Berg 479	FA03310 and *trnL-F*
Naucleopsis inaequalis	H. Medeiros 388	FA03310 and *trnL-F*
Naucleopsis krukovii	A. Santos 202	FA03310 and *trnL-F*
Naucleopsis krukovii	AY686784	26S
Naucleopsis naga	AY686841	26S
Naucleopsis oblongifolia	A. Santos 194	FA03310 and *trnL-F*
Naucleopsis ternstroemiiflora	A. Santos 163	FA03310 and *trnL-F*
Naucleopsis ternstroemiiflora	H. Medeiros 486	FA03310 and *trnL-F*
Naucleopsis ternstroemiiflora	AY686821	26S
Naucleopsis stipularis	A. Santos 154	FA03310 and *trnL-F*
Naucleopsis ulei	AY686791	26S

Castilla elastica	AF501603	*trnL-F*
Castilla elastica	FJ917062	*trnL-F*
Castilla elastica	AY686823	26S
Castilla elastica	AY686830	26S
Antiaris toxicaria	AY686858	26S
Antiaropsis decipiens	AY686834	26S
Helicostylis scabra	A. Santos 164	FA03310 and *trnL-F*
Helicostylis pedunculata	AY686816	26S
Helicostylis tomentosa	AY686839	26S
Helicostylis tomentosa	A. Santos 174	FA03310 and *trnL-F*
Helicostylis turbinata	A. Santos 153	FA03310 and *trnL-F*
Maquira calophylla	A. Santos 172	FA03310 and *trnL-F*
Maquira costaricana	AY686801	26S
Mesogyne insignis	AY686840	26S
Perebea angustifolia	A. Santos 198	FA03310 and *trnL-F*
Perebea angustifolia	AY686843	26S
Perebea guianensis	H. Medeiros 488	FA03310 and *trnL-F*
Perebea hirsuta	A. Santos 195	FA03310 and *trnL-F*
Perebea humilis	AY686842	26S
Perebea longepedunculata	AY686826	26S
Perebea mollis	A. Santos 198	FA03310 and *trnL-F*
Perebea mollis	A. Santos 160	FA03310 and *trnL-F*
Perebea rubra	AY686844	26S
Perebea xanthochyma	AY686857	26S

Pseudolmedia laevis	A. Santos 200	FA03310 and *trnL-F*
Pseudolmedia laevigata	AY686845	26S
Pseudolmedia macrophylla	AY686792	26S
Pseudolmedia macrophylla	A. Santos 197	FA03310 and *trnL-F*
Poulsenia armata	JQ341920	*trnL-F*
Poulsenia armata	EU422992	26S
Sparattosyce dioica	AY686856	26S
outgroup		
Ficus benjamina	AF501606	*trnL-F*
Ficus insipida	AF165390	26S
Ficus maxima	JQ341920	FA03310
Ficus obtusifolia	JQ341919	FA03310
Maclura tinctoria	A. Santos 106	FA03310 and *trnL-F*
Sorocea guilleminiana	A. Santos 163	FA03310 and *trnL-F*
Cannabis sativa	AY686773	26S

VI. Conclusão e considerações finais

A presente tese apresenta o estudo mais amplo envolvendo dados moleculares biogeográficos e taxonômicos para a tribo Castilleae, enfatizando as espécies de *Naucleopsis*.

Os resultados das análises filogenéticas de Castilleae contribuíram com dados importantes para uma melhor circunscrição deste grupo, corroborando com as propostas atuais relacionadas aos gêneros *Palmolmedia* e *Ogcodeia* e a posição incerta do gênero *Perebea*. As análises com foco em *Naucleopsis* ajudaram corroborar a monofilia da linhagem do gênero, inserida na tribo Castilleae.

O tratamento taxonômico de *Naucleopsis* inicialmente considerou as 23 espécies até o momento reconhecidas mais recentemente na literatura (Berg 2001, Berg & Homeier 2010). Entretanto, outras duas foram restabelecidas, uma nova combinação e um novo status são propostos e mais quatro foram incluídas no tratamento como espécies novas para o grupo. Reinterando a importância deste estudo taxonômico para o grupo.

Os ensaios biogeográficos indicaram que o *Naucleopsis* tenha emergido durante o Oligoceno (ca. 32-35 mya), na região amazônica. Estas primeiras linhagens teriam surgido com inflorescências pistiladas com pseudo-tépalas livres e perianto indistinto no receptáculo. As linhagens subsequentes foram colonizando regiões em direção à mata atlântica, com situações morfológicas intermediárias entre perianto distinto e indistinto no receptáculo. Com uma linhagem específica para grupo com perianto conado, partido no ápice.

Estes grupos com diversificações mais recentes apresentam também frutos mais carnosos e adocicados com cores mais atrativas. Observações de campo também revelaram que *Naucleopsis obolongifolia*, ocorrente atualmente na mata atlântica seja dispersada pelo consumo de seus frutos adocicados por pequenos mamíferos na mata.

Há ainda, poucos estudos sobre as formas de polinização e dispersão para *Naucleopsis*. Entretanto, há alguns estudos e relatos de campo que sugerem a polinização por insetos (*Thrips*) para *Castilla* e *Helicostylis.* Observações também feitas por Berg (1972) indicariam que as brácteas involucrais não apenas serviriam para proteção das flores, mas também como abrigo para o polinizador.

Os resultados aqui apresentados sugerem que as linhagens que se diversificaram mais recentemente teriam uma redução do número de brácteas involucrais e um maior espessamento, adocicamento e coloração do perianto em frutificação.

Este trabalho contribuiu com dados importantes para elucidação da circunscrição de Castilleae e a resolução de diversos problemas taxonômicos em *Naucleopsis*, bem como para uma melhor compreensão dos padrões de distribuição biogeográfica deste grupo. Entretanto, a reconstrução de uma filogenia ainda mais robusta para o gênero através da incorporação de um maior número de caracteres moleculares informativos, ou ainda com o sequenciamento do genoma completo, contribuiria com mais dados importantes para uma melhor resolução do parentesco entre suas espécies.

O desenvolvimento desse trabalho demandou um estudo amplo dos demais representantes da tribo Castilleae e ficou evidente a necessidade da revisão e ampliação dos estudos moleculares e biogeográficos para os outros gêneros neotropicais da tribo (*Castilla*, *Helicostylis*, *Perebea*, *Pseudolmedia*, *Maquira* e *Poulsenia*).

Consideramos que os objetivos propostos nesta tese foram atingidos, com considerável contribuição na compreensão da evolução espaço-temporal de *Naucleopsis* e Castilleae.

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