UNIVERSIDADE ESTADUAL DE CAMPINAS

INSTITUTO DE BIOLOGIA

EDER AUGUSTO CHILQUILLO TORRES

FILOGENIA DO GÊNERO *LADENBERGIA* KLOTZSCH (RUBIACEAE: CINCHONEAE) E TAXONOMIA ATUALIZADA DAS ESPÉCIES QUE OCORREM NOS ANDES TROPICAIS

PHYLOGENY OF THE GENUS *LADENBERGIA* KLOTZSCH (RUBIACEAE: CINCHONEAE) AND UPDATED TAXONOMY OF THE SPECIES OCCURRING IN THE TROPICAL ANDES

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Dissertação apresentada ao Instituto de Biologia da Universidade Estadual de Campinas como parte dos requisitos exigidos para a obtenção do Título de Mestre em Biologia Vegetal

Dissertation presented to the Institute of Biology of the University of Campinas in partial fulfillment of the requirements for the degree of Master in Plant Biology.

ESTE ARQUIVO DIGITAL CORRESPONDE À VERSÃO FINAL DA DISSERTAÇÃO DEFENDIDA PELO ALUNO EDER AUGUSTO CHILQUILLO TORRES E ORIENTADO PELO DR. ANDRÉ OLMOS SIMÕES.

Orientador: ***Prof. Dr. André Olmos Simões***

CAMPINAS

2016

Agência(s) de fomento e nº(s) de processo(s): Não se aplica.

Ficha catalográfica
Universidade Estadual de Campinas
Biblioteca do Instituto de Biologia
Mara Janaina de Oliveira - CRB 8/6972

C439f

Chilquillo Torres, Eder Augusto, 1985-
Filogenia do gênero *Ladenbergia* Klotzsch (Rubiaceae: Cinchoneae) e taxonomia atualizada das espécies que ocorrem nos Andes tropicais / Eder Augusto Chilquillo Torres. – Campinas, SP : [s.n.], 2016.

Orientador: André Olmos Simões.
Dissertação (mestrado) – Universidade Estadual de Campinas, Instituto de Biologia.

1. Botânica - América Latina – Classificação. 2. Filogenia. 3. Áreas de endemismo. 4. Taxonomia vegetal. 5. Rubiacea. I. Simões, André Olmos,1975-. II. Universidade Estadual de Campinas. Instituto de Biologia. III. Título.

Informações para Biblioteca Digital

Título em outro idioma: Phylogeny of the genus *Ladenbergia* Klotzsch (Rubiaceae: Cinchoneae) and updated taxonomy of the species ocurring in the tropical Andes
Palavras-chave em inglês:
Plants - Latin America – Classification
Phylogeny
Areas of endemism
Plant taxonomists
Rubiaceae
Área de concentração: Biologia Vegetal
Titulação: Mestre em Biologia Vegetal
Banca examinadora:
André Olmos Simões [Orientador]
Carla Poleselli Bruniera
Maria Fernanda Aguiar Calió
Data de defesa: 25-02-2016
Programa de Pós-Graduação: Biologia Vegetal

Campinas, 25 de fevereiro de 2016.

COMISSÃO EXAMINADORA

Prof.(a) Prof. André Olmos Simões (Orientador)

Prof.(a). Dra. Carla Poleselli Bruniera

Prof.(a) Dra. Maria Fernanda Aguiar Calió

Os membros da Comissão Examinadora acima assinaram a Ata de Defesa, que se encontra no processo de vida acadêmica do aluno.

DEDICATÓRIA

A minha querida família, professores, amigos

e a todas as pessoas que lutam dia a dia por seus sonhos.

AGRADECIMENTO

Ao Programa de Pós-Graduação em Biologia Vegetal do Instituto de Biologia da UNICAMP. À Programa de Bolsas "Beca Presidente da Republica" (PRONABEC-PERU) pela bolsa de mestrado. À CONCYTEC pelo auxílio na pesquisa. Ao Missouri Botanical Garden pela bolsa Gentry outorgada durante meu mestrado.

Ao laboratório de Taxonomia Vegetal do departamento de Biologia Vegetal do Instituto de Biologia da UNICAMP, por disponibilizar as instalações, equipamentos, materiais e técnicos de seus laboratórios para o desenvolvimento deste estudo. Ao Herbário UEC pelo suporte e colaboração durante minha pesquisa.

Ao Prof. Dr. André Olmos Simões, pela orientação e disponibilidade em todo momento em que este trabalho foi realizado. Obrigado pela sua dedicação, pela sua aposta em minha persona e pelas oportunidades concedidas que têm contribuído para minha formação profissional.

À Dra. Rosemeri Morokawa, pela paciência e motivação durante a fase de laboratório, analises de resultados e escrita envolvidas durante o mestrado. Obrigado também pela disponibilidade constante e pelas sugestões proporcionadas durante o trabalho.

À Dra. Charlotte Taylor pela motivação e colaboração constante. Obrigado por me permitir conhecer um pouco mais das Rubiaceae neotropicaes e surpreender-me dia a dia com toda essa diversidade de plantas.

À Dra. Joaquina Albán por iniciarem neste mundo das Rubiaceae e por ensinar-me a ver como nossas pesquisas podem ajudar ao desarrolho e crescimento do pais.

Ao Grupo de pesquisa de Cinchoneae: Carla Maldonado, Nina Ronsted, Alexandre Antonelli, Claes Persson, Alessandra Márquez, Ruy Alves, Charlotte Taylor e Joaquina Albán, pela colaboração constante.

Aos herbários e seus respectivos curadores, pelas facilidades durante minha visita, empréstimos e doações de exsicatas concedidas ao herbário UEC, indispensáveis para este estudo: CR, F, G, HOXA, INB, MO, MOL, NY, R, RB , UB, USJ, USM, CEN, COL, K, MA, P, QCA, QCNE, US.

Aos membros da pre-banca e banca de mestrado: Dr. Jomar Jardim, Dra. Maria Fernanda Aguiar Calió, Dra. Luiza Kinoshita, Dra. Carla Poleselli Bruniera por toda sua ajuda e colaboração.

Aos professores que contribuíram para minha formação durante o mestrado: João Semir, Maria do Carmo Amaral, Fernanda Aguiar Calió, Sandra Carmelo Guerreiro, Ingrid Koch, Samantha Khoeler e Lucia G. Lohmann.

Aos pesquisadores e pessoal técnico do Missouri Botanical Garden em St. Louis, EUA pela ajuda durante minha estadia. Obrigado a Olga Martha Montiel, Charlotte Taylor, John Prusky, Rosa Ortiz, Alba Arbelaez, Roy Gereau, Ronald Liesner, Carmen Ulloa, Zacchary Rogers, James Solomon, Mary Stiffler, Kathy Hurlbert e Dawn Trog.

A meus amigos e professores do Museu de Historia Natural da UNMSM em Lima, Peru pela colaboração e disposição de ajuda em tudo momento. A galera do departamento de Etnobotanica por ser minha segunda família.

Aos meus colegas e amigos de bancada, em especial a Nallaret Dávila por sua ajuda constante, pela motivação e por toda essa força nos momentos críticos da tese, a Gustavo Shimizu pela ajuda constante, a Suzana Costa pelas dicas e motivação, pelos mapas e traduções, a Marcelo Monge, João do Carmo, Rafael Barboza, Fernanda Cabral, Natali Bordon, Andreza Pereira, Zé Junior, Edimar Lopez, Alexandre Zuntini, Elisa Candido e André Vito Scatigna pela motivação e colaboração.

Ao povo do café da UNICAMP: Nallaret Dávila, João do Carmo, Marcela Firens, Maria Fernanda Calió, Juliana Amaral pela disposição, colaboração e essa alegria sempre.

A Elluz Huamán, por sempre confiar em mim, por sua alegria e motivação constante. Por me ensinar a nunca desistir na vida e a lutar por meus sonhos.

A meus queridos: Bracco, Dana, Junior, Fuan, Fuana, Petra e Scottinho.

A meus amigos da vida: Carlos Salvador, Auxi Zuñiga, Edu Torres e Maria Chipz por estar sempre conmigo. A meus amigos peruanos residentes em Campinas, Brasil: Tomas, Gatusso, Rikin, Pepo, Pablo, Melissa, Rene, Lú e Jas por sempre alegrarem os dias com suas ocorrências.

A minha turma de mestrado: Nathália Streher, Amanda Mesquita, Aninha Alencar pela colaboração sempre. Somos mestres.

A todos aqueles que me ajudaram em viagens de coleta, nas visitas aos herbários, durante os processos experimentais, na discussão de metodologias e de resultados, nas questões burocráticas, ou em qualquer outro aspecto deste trabalho. Agradeço imensamente a todos.

RESUMO

Ladenbergia Klotzsch é um gênero que apresenta uma distribuição predominante nos Andes tropicais. Na atualidade se reconhecem 34 espécies ao longo de toda sua distribuição. Pertence à tribo Cinchoneae e se encontra relacionado ao gênero *Remijia*, em virtude de suas semelhanças morfológicas. Estudos moleculares prévios sustentam sua monofília, não obstante, é necessária uma amostragem maior para corroborar essas hipóteses. O presente trabalho tem como objetivo principal inferir as relações filogenéticas das espécies do gênero *Ladenbergi*a, assim como esclarecer problemas taxonômicos pontuais a respeito de algumas espécies distribuídas nos Andes tropicais. Foram utilizados 03 marcadores moleculares (ITS, *trn*L, *rps*16). O alinhamento das sequências de DNA foi feito com o programa Geneious v.8.1.3. As análises filogenéticas foram realizadas pelo uso de abordagens de parcimônia e inferência bayesiana com os programas PAUP v. 4.0 e Mr. Bayes v. 3.2.4, tendo como grupos externos os gêneros da tribo Cinchoneae. Foram amostradas em total 18 especies do gênero: 12 procedentes dos Andes de Colômbia, Equador, Peru e Bolívia, 03 espécies registradas na Amazônia do Brasil, Peru e Bolívia e 03 espécies registradas na América Central. As análises corroboram a monofilia de *Ladenbergia* e a sua relação com *Remijia*, indicando que as espécies andinas não constituem um grupo monofilético e que possivelmente as mesmas se agrupam em vários clados. Além disso, se propõe as siguientes hipóteses sobre as relações de algumas especeis dentro do gênero, como: *L. hexandra* e *L. cujabensis*, espécies que ocorrem no cerrado e sudeste do Brasil; *L. amazonensis* e *L. graciliflora*, espécies restritas a habitats amazônicos; *L. carua* e *L. bullata*, espécies que habitam os Andes tropicales do sul; *L. riveroana* e *L. stenocarpa*, espécies que ocorrem em habitats com solos de arenisco nos Andes Centrales do Sul e *L. oblongifolia* espécie ampliamente distribuída nos Andes a qual se relaciona com *L. heterophylla*, *L. pavonii* e *L. dwyeri* as quais se distribuiem em os Andes do Norte e America Central. Com isto se descarta a formação do clado "Lambertiana" proposto por Andersson. A abordagem taxonômica aqui apresentada mostra um tratamento taxonômico detalhado que considera 18 espécies que ocorrem nos Andes Tropicais, inclui descrições, chave taxonômica e aspectos ecológicos das espécies do gênero *Ladenbergia*. Foram esclarecidas alguns problemas taxonômicos correntes nestas espécies mas também se apontam outros problemas de delimitação, como é o caso de *L. heterophylla* e especies afines (*L. obovata*, *L. epiphytica* e *L. dwyeri*) e *L. crassifolia* e seus morfotipos presentes a longo de sua distribuição. À luz dos nossos resultados, um maior amostragem de táxons é necessário, o qual permita a obtenção de uma filogenia mais completa para o gênero. Além disso, novas regiões precisam ser exploradas que permita proporcionar uma melhor resolução das relações no nível de espécie.

Por outra parte seria interessante dar início a estudos anatômicos, citológicos e ecológicos que forneçam informações ao respeito do desenvolvimento, biologia reprodutiva e habitat onde ocorrem as espécies de *Ladenbergia*, o que ajudaria a ter uma visão completa sobre o grupo e permita melhorar o entendimento das espécies.

Palavras-chaves: neotrópico, sistemática, endemismo, taxonomia, *Remijia*.

ABSTRACT

Ladenbergia Klotzsch is a genus that occurs mainly at the tropical Andes. Currently 34 species are recognized to the genus. The genus belongs to the tribe Cinchoneae and is closely related to *Remijia* due to morphological similarities. Previous molecular studies confirm the monophyletic status of the genus; even though a better sampling is necessary. The present work has as main goal to infer the phylogenetic relationships of *Ladenbergi*a's species, and to clarify taxonomic problems of species from the tropical Andes. We used three molecular markers (ITS, *trn*L, *rps*16). We peformed the alignment of DNA sequences with the software Geneious v.8.1.3. The phylogenetic analysis were done through the parsimony and Bayesian inference approach using the software PAUP v. 4.0 and Mr. Bayes v. 3.2.4, respectively, and with the other genus of Cinchoneae as outgroup. We sampled 18 species of *Ladenbergia*: 12 from the Andes of Colombia, Ecuador, Peru e Bolivia; 03 from Amazon of Brazil, Peru e Bolivia; and 03 from the Central America. The analysis shows *Ladenbergia* as a monophyletic group and its close relationship with *Remijia*, stating that Andean species are not a monophyletic group and possibly cluster in many clades. Additionally, it was possible to hypothesize the relationship of species of the genus: *L. hexandra* and *L. cujabensis*, species from the Cerrado biome and southeast Brazil; *L. amazonensis* and *L. graciliflora*, species restricted to amazon habitats; *L. carua* and *L. bullata*, species from the south tropical Andes; *L. riveroana* and *L. stenocarpa*, species from habitats of *arenisca* soils of Central and South Andes; and *L. oblongifolia* species broadly distributed at the Andes and related to *L. heterophylla*, *L. pavonii* and *L. dwyeri*, species that occurs at the northern Andes and Central America. These results disagree with the clade "Lambertiana" proposed by Andersson (1997). We provide a detailed taxonomic treatment of 18 species of *Ladenbergia* Klotzsch from the tropical Andes, with descriptions, identification keys and ecological comments. We clarified some taxonomical problems but also highlight other circumscription problems, as the *L. heterophylla* and allied species (*L. obovata*, *L. epiphytica* and *L. dwyeri*) and *L. crassifolia* and its geographical morphotypes. According to our results, there is still need a better sampling effort to generate a complete phylogeny to the genus. Other DNA regions must be tested to improve the resolution of relationships at species level. Anatomical, cytological and ecological studies could add information about the development, reproductive biology and habitats of occurrence of *Ladenbergia*'s species, helping to form a full view of the group and better acknowledge of species.

Keywords: neotropic, systematic, endemic, taxonomy, *Remijia*.

SUMÁRIO

INTRODUÇÃO GERAL

1. Rubiaceae

Rubiaceae é a quarta família mais diversa das Angiospermas (Robbrecht 1988), com cerca de 620 gêneros e 13.100 espécies (Govaerts *et al.* 2006), embora estimativas indiquem uma riqueza de 16.000 espécies. (Davis *et al.* 2009). Sua distribuição é cosmopolita, mas principalmente pantropical, com cerca de 5.000 espécies e 200 gêneros na região neotropical (Govaerts *et al.* 2006, Davis *et al.* 2009, Delprete & Jardim 2012).

Estudos sistematicos demonstram que Rubiaceae corresponde a um táxon monofilético, grupo-irmão do clado formado pelas demais famílias da ordem Gentianales, das quais se distingue por ausência de floema interno, presença de ovário ínfero, simpetalia precoce, estrias de Caspary e dados moleculares (Erbar 1991, Struwe *et al.* 1994, Bremer 1996, Backlund *et al.* 2000, APGIII 2009). A diversidade das formas de vida é variada e inclui ervas de pequeno porte, subarbustos, arbustos, lianas e árvores; flores com diversos tipos de adaptações a uma ampla variedade de polinizadores e diversos tipos de frutos e sementes com diferentes formas de dispersão (Bawa & Beach, 1983, Robbrecht 1988, Mendoza *et al.* 2004).

A classificação de Rubiaceae em subfamílias foi objeto de vários estudos (Schumann 1891, Verdcourt 1958, Bremekamp 1966, Robbrecht 1988, Bremer *et al.* 1995, Bremer 1996, Robbrecht & Manen 2006, Bremer & Eriksson 2009), divergindo de autor para autor. Segundo Robbrecht (1988), o reconhecimento de subfamílias em Rubiaceae é necessário, devido ao fato de que a classificação e evolução de uma família tão diversa só poderão ser entendidas a partir de uma classificação principal aplicável, na qual várias tribos são agrupadas em subfamílias naturais que eventualmente indicarão prioridades a serem consideradas para pesquisa taxonômica detalhada.

Schumann (1891) foi o primeiro a nomear subfamílias em Rubiaceae. Este reconheceu apenas duas subfamílias (Cinchonoideae e Coffeoideae), circunscritas com base apenas no número de óvulos por lóculos do ovário. Esta classificação foi criticada por autores posteriores, que argumentaram com base no maior número possível de caracteres, tanto morfológicos quanto anatômicos, citológicos, palinológicos e

ecológicos (Verdcourt 1958, Bremekamp 1966, Robbrecht 1988) (Tabela 1). Com o advento das filogenias moleculares a partir da última década do século XX, estudos corroboram a existência de três grandes clados, reconhecidos como três subfamílias, Cinchonoideae, Ixoroideae e Rubioideae (Bremer & Jansen 1991, Bremer *et al.* 1995, Bremer 1996, Bremer & Manen 2000, Rova *et al*. 2002, Bremer & Eriksson 2009).

Tabela 1. Classificações tradicionais de Rubiaceae baseados em dados morfológicos.

Subfamílias consideradas dentro de Rubiaceae		
Verdcourt (1958)	**Bremekamp (1966)**	**(Robbrecht 1988)**
1.Cinchonoideae	1. Cinchonoideae	1. Cinchonoideae
2. Rubioideae	2. Rubioideae	2. Rubioideae
3. Guettardoideae	3. Guettardoideae	3. Antirheoideae
	4. Ixoroideae	4. Ixoroideae
	5. Hillioideae	
	6. Gleasonioideae	
	7. Pomazotoideae	
	8. Urophylloideae	

As três subfamílias em Rubiaceae representam três grandes clados com alto suporte (Bremer & Eriksson 2009): (1) Cinchonoideae compreende cerca de 1.500 espécies, representada principalmente por pequenas árvores e arbustos, com prefloração da corola imbricada ou valvar e distribuição pantropical; (2) Ixoroideae, com ca. 4.100 espécies, são árvores ou arbustos, com prefloração da corola variável, geralmente contorta para a esquerda, apresentação secundária de pólen comum, e distribuição pantropical e pan-subtropical; e (3) Rubioideae, a mais diversa com 7.475 espécies, representada por ervas, arbustos e árvores que apresentam ráfides (cristais de oxalato de cálcio) em suas estruturas, com prefloração da corola valvar, tricomas articulados, com distribuição ampla, principalmente tropical ou subtropical, mas com algumas espécies no Mediterrâneo e regiões temperadas.

A estimativa de tempo de divergência da família é de 90 Milhões de anos (Ma), inferindo-se que a divergência de cada subfamília corresponda, por sua vez, a cerca de 85 Ma para Rubioideae, 73 Ma para Ixoroideae e 73 Ma para Cinchonoideae (Bremer & Eriksson 2009). Segundo Raven & Axelrod (1974), Rubiaceae figura entre os táxons que se dispersaram da África a região Neotropical durante o Cretáceo tardio, depois do

rompimento da Gondwana, através de cadeias de ilhas ao longo do então estreito Oceâno Atlântico.

Gentry (1982) aceitou a hipótese de Rubiaceae ter se originado na região neotropical, propondo dois centros de diversificação, nos Andes e América Central. Bremer & Eriksson (2009) sugerem que o Sudeste da Ásia é o berço da família, devido a que os generos mais antigos: *Coptosapelta* (86.6 Myr) e *Luculia* (80.3 Myr) ocorrem nessa região, mesmo que estes dois gêneros apareçam em uma politomia juntamente com Rubioideae e o clado formado por Cinchonoideae e Ixoroideae. Em contrapartida, Antonelli *et al.* (2009) sugerem um centro de origem boreotropical para a família, em florestas laurasianas, a partir das quais se dispersou utilizando o corredor de terra do Atlântico Norte ("North Atlantic Land Bridge") para chegar aos neotrópicos durante Paleoceno tardio ou começo do Eoceno.

De acordo com Delprete & Jardim (2012), a metade das espécies e um terço dos gêneros de Rubiaceae ocorrem nos neotrópicos, onde ocupam vários tipos de hábitats em diferentes regiões biogeográficas. Segundo Davis *et al.* (2009), das 20 regiões mais diversas para a família (baseadas no número de espécies), oito encontram-se nos neotrópicos (1° Colômbia, 2° Venezuela, 4° Norte do Brasil, 6° Sudeste do Brasil, 7° Peru, 8° Equador, 15° Cuba e 17° Panamá); em diversidade relativa (log número espécies/área) oito (1° Venezuela, 2° Colômbia, 3° Cuba, 9° Equador, 11° Panamá, 13° Sudeste do Brasil, 15° Costa Rica e 19° Peru); e em número bruto de espécies endêmicas, sete (5° Cuba, 6° Sudeste do Brasil, 7° Colômbia, 8° Venezuela, 14° Nordeste do Brasil, 17° Peru e 18° Panamá).

2. *Ladenbergia* Klotzsch

Ladenbergia Klotzsch pertence à tribo Cinchoneae (subfamília Cinchonoideae), estabelecida em 1830 por De Candolle, baseada na presença de frutos capsulares biloculares e sementes aladas abundantes (Robbrecht 1988). Estudos recentes baseados em dados morfológicos (Andersson & Persson 1991, Andersson 1995b) e moleculares (Andersson & Antonelli 2005) sustentam a monofília da tribo. Em sua circunscrição clássica (Andersson 1995b), Cinchoneae é constituída por oito gêneros: *Cinchona*, *Joosia*, *Ladenbergia*, *Remijia*, *Cinchonopsis*, *Stilpnophyllum*, *Pimentelia* e *Maguireocharis*. Segundo Andersson & Antonelli (2005), um nono gênero, *Ciliosemina*,

deve ser reconhecido em Cinchoneae, a partir de *Remijia pedunculata* (H. Karst.) Flueck, pois apresenta um padrão morfológico diferente (inflorescência corimbosa e sementes ciliadas ou fimbriadas) e não se encaixa dentro dos outros gêneros da tribo (inflorescência tirsoide ou cimosa e sementes inteiras, laciniadas ou denticuladas).

Atualmente são reconhecidas 35 espécies em *Landerbergia* (Taylor & Gereau 2010), embora estima-se que novas espécies ainda não foram descritas (Andersson 1997). Suas espécies são reconhecidas por apresentar o seguinte conjunto de características (Mendoza *et al.* 2004): inflorescências terminais, flores heterostílicas de antese noturna, corolas alvas com lobos que apresentam uma porção terminal e marginal em forma de cunha minutamente papilosa e cápsulas septicidas longas portando sementes aladas numerosas. O gênero apresenta uma distribuição geográfica que compreende desde Costa Rica até o sul da Bolívia (Andersson 1997).

Andersson (1992) propõe subdivisões fitogeográficas para Rubiaceae na região neotropical, sendo que *Ladenbergia* pode ocorrer nas seguintes áreas: Sul da América Central, Norte da Área do Chocó, Sul da Área do Chocó Área de Llanos-Magdalena, Bacia do rio Napo - Marañon, Sudoeste Amazônico, Oeste Amazônico, Escudo das Guianas, Amazônia Central, Leste Amazônico, Sudeste do Brasil, Planalto Brasileiro e Andes Tropicais onde concentram-se a maioria das espécies do gênero (Andersson 1997). Baseado no número de especies, o centro de diversificação de *Ladenbergia,* poderia ser os habitats de arenito nos Andes do Equador e Peru, áreas recentes que teriam ter surgido simultaneamente (Luebert & Weigend 2014) e que apresentam uma alta taxa de diversificação de espécies (Pitman *et al*. 2012).

Após a descrição do gênero por Klotzsch (1846), outros autores trouxeram importantes contribuições à sua taxonomia (Weddell 1848; Weddell 1849; Weddell 1865; Osorio 1874; Standley 1921; Standley 1930; Standley 1931a; Standley 1931b; Standley 1936; Steyermark 1974; Dwyer 1980; Andersson 1994; Andersson 1997; Steyermark 2004; Taylor & Gereau 2010). O tratamento sistemático mais completo e atual de *Ladenbergia* foi proposta por Andersson (1997). Nesta obra, é apresentada uma revisão taxonômica, na qual o autor reconhece 34 espécies, sendo sete novas para a ciência, uma análise filogenética baseada em caracteres morfológicos e uma análise biogeográfica combinada à filogenia morfológica. A análise filogenética resultou em topologias pouco sustentadas, evidenciada pela presença de clados não

resolvidos ou com valores de suporte baixos, provavelmente devido ao baixo número de caracteres informativos e homoplásicos em relação ao número maior de táxons estudados.

Os resultados de Andersson (1997) permitiram a visualização de um grado basal constituído por quatro espécies: *L. acutifolia* (Ruiz & Pavon.) Klotzsch, *L. discolor* K. Schum., *L. klugii* L. Andersson e *L. ferruginea* Standl. Essas espécies são caracterizadas por apresentar flores pequenas e distribuição no sudeste do Peru. Outro resultado é um grupo de espécies com certa afinidade morfológica que se agruparam em um clado denominado Lambertiana, constituído por oito espécies (*L. amazonensis* Ducke, *L. lambertiana* (Mart.) Klotzsch, *L. chapadensis* S. Moore, *L. graciliflora* K. Schum., *L. pittieri* Standl., *L. cujabensis* Klotzsch, *L. paraensis* Ducke e *L. stenocarpa* (Lamb.) Klotzsch), ocorrentes principalmente na floresta amazônica, escudo das Guianas e no escudo Brasileiro, sendo *L. stenocarpa* a única espécie com uma distribuição andina.

3. Andes Tropicais

Os Andes Tropicais são um dos 25 "hotspots" de biodiversidade reconhecidos no mundo. Além de abrigar grande variedade de biomas, contém cerca de 30.000 espécies de plantas vasculares (cerca de 10% das espécies do planeta) e apresentam um alto nível de endemismo, produto de seu isolamento geográfico (Barthlott et al 2005, Brummitt & Lughadha, 2003, Kreft & Jetz 2007, Mittermeier et al. 1998, 1999, 2011). O hotspot compreende cadeias de montanhas úmidas e secas com até 6000 m.s.n.m. e terras baixas das florestas úmidas tropicais no lado noroeste e sudeste (Richter et al 2009).

O zoneamento da vegetação dos Andes tropicais é difícil e controverso, pois a região apresenta uma vegetação contínua englobando desde as ladeiras andinas nas terras baixas até áreas mais altas, as quais se encontram adjacentes as vertentes oeste e leste dos Andes e que mostram padrões florísticos heterogêneos devido a características abióticas diferentes (WWF & IUCN, 1994-1997).

Andersson (1995a), considera 18 espécies de *Ladenbergia* na região dos Andes Tropicais, que por sua vez é subdividido em Andes do Norte, Andes Centrais do Norte e Andes do Sul. Os Andes e as terras baixas tem como linha de separação os 1000 m de

altitude em toda sua amplitude. Estas unidades são biogeograficamente significativas e guardam relação com os padrões de distribuição das Rubiaceae e outros grupos neotropicais (Struwe *et al.* 2009, Weigend *et al*. 2010, Symmank *et al.* 2011). Os Andes do Norte incluem áreas desde a Serra Nevada de Santa Marte (Colômbia), a Serra de Perija e a Cordilheira de Mérida (Venezuela) no norte até o limite sul nos departamentos de Cauca e Huila no sul da Colômbia. Os Andes Centrais estendem-se até o limite sul dos departamentos de Piura e Amazonas no norte do Peru, tendo como área limite no sul a zona de Amotape-Huancabamba, a qual é considerada uma barreira biogeográfica (Weigend 2002, 2004; Weigend et at, 2005). Finalmente, os Andes do Sul, incluem as zonas andinas restantes de Peru, Bolívia e norte de Argentina.

Andersson (1997), baseado em padrões de distribuição de *Ladenbergia* sugere quatro áreas de endemismo dentro dos Andes tropicais (incluindo a zona pré-montana, 500-1000 m.s.n.m.): seis espécies são endêmicas dos Andes do Norte (noroeste de Venezuela e Serra Nevada de Santa Marta no norte e ca 1°S) - *L. obovata* L. Andersson, *L. magdalenae* L. Andersson, *L. pittieri* Standl., *L. pauciflora* L. Andersson, *L. undata* Klotsch, *L. lehmanniana* L. Andersson; uma espécie endêmica dos Andes Centrais do Norte (ca. 1°S até a deflexão de Huancabamba) - *L. stenocarpa*; três espécies endêmicas ao Andes Centrais do Sul (desde a deflexão de Huancabamba ate o 11°S) - *L. klugii* L. Andersson, *L. acutifolia*, *L. discolor*; três espécies endêmicas dos Andes do Sul (11°S no Peru até o centro da Bolivia) - *L. carua* (Wedd) Standl., *L. bullata* (Wedd) Standl., *L. ferruginea*). Somente *Ladenbergia oblongifolia* (Humb. ex Mutis) L. Andersson apresenta ampla distribuição nos Andes, e observa-se uma diferenciação morfológica entre as populações que ocorrem no norte, centro e sul dos Andes (Andersson 1994).

O soerguimento dos Andes é considerado um dos eventos mais importantes na história biogeográfica da biota neotropical (Hoorn *et al*., 2010) e talvez seja responsável por quase metade da biodiversidade da região (Gentry 1982). Devido à sua localização geográfica no continente sul-americano, os Andes atuaram como um corredor (Young & Reynel 1997, Hensold 1999, Weinged 2004, Antonelli *et al*., 2009, Luebert *et al*., 2009 e Pinto & Luebert 2009), promovendo o intercâmbio Norte-Sul de elementos bióticos, bem como uma barreira (Schulte *et al*., 2000, Flores & Roig-Juñent

2001, Pirie *et al*., 2006 e Roig-Juñent *et al*., 2006), gerando um processo de vicariância interna tanto ao leste-oeste, e também como promotor de especiação (Vuilleumier 1971, Simpson 1975, Gentry 1982, Luteyn 2002, Weigend 2002, von Hagen and Kadereit 2003, Bell & Donoghue 2005, Hughes & Eastwood 2006, Moore & Donoghue 2007 e Scherson *et al*., 2008), por meio da disponibilização de novos ambientes de alta altitude durante a sua formação.

Além do soerguimento dos Andes, mudanças climatológicas e de condições hidrológicas em um nível continental também influenciaram a história evolutiva dos grupos de espécies que ficaram fora da cadeia montanhosa dos Andes (Hartley, 2003; Blisniuk et al, 2005; Antonelli *et al*., 2009; Hoorn et al., 2010).

Supõe-se que o soerguimento dos Andes também propiciou a radiação de *Landebergia* e que a origem do gênero é recente (Antonelli *et al.* 2009). Andersson (1997) sugere que a possível área ancestral seria os Andes Centrais do Sul e o habitat seria a floresta pré-montana, indicando que o gênero se originou em áreas de menor altitude, quando ainda os Andes tropicais eram baixos, com posteriores dispersões para os Escudos das Guianas e Brasileiro e para áreas mais altas dos Andes. Isso implicaria considerar os Andes como uma fonte de biodiversidade para toda a América do Sul (Antonelli et al., 2009).

Outra hipótese propõe a origem de *Ladenbergia* em terras mais antigas, como os Escudos das Guianas e Brasileiro, seguida pela colonização dos Andes, padrão já relatado em outros grupos taxonômicos (Croizat 1976; Givnish *et al*. 2007; Givnish *et al*. 2011) e que indicaria que a biodiversidade dos Andes representa uma segunda radiação da flora neotropical.

JUSTIFICATIVA

Rubiaceae apresenta uma grande diversidade taxonômica e ecológica, tornando-se um grupo modelo para estudos ecológicos, evolutivos e biogeográficos (Antonelli *et al.* 2009, Bremer 2009). No entanto, muitos grupos taxonômicos ainda não foram estudados ao nível infratribal ou infragenérico (Bremer 2009, Delprete & Jardim 2012). Assim, Bremer (2009) e Bremer & Eriksson (2009) chamam atenção para o fato de que mais de 200 gêneros reconhecidos não foram avaliados durante a análise filogenética da família como um todo, o que é fundamental para se ter um panorama amplo das relações dentro da família, o qual pode ser utilizado para estudos futuros.

Ladenbergia (Cinchoneae: Rubiaceae) é um gênero neotropical, que apresenta um padrão de distribuição de espécies centrado nos Andes Tropicais, conta com uma sinopse taxonômica feita por Andersson (1997), a qual mostra um abordagem geral e constitue um ponto de partida no conhecimento das especies do gênero. Embora os resultados tinham sido superficiais devido a protólogos antigos, curtos e pouco compreensíveis, o qual somados às poucas coletas realizadas nas areas de ocorrência resultaram em um inadequado conhecimento das espécies

Adicionalmente, se o gênero tem origem recente (Antonelli *et al.* 2009), muitas espécies se encontram em processo de especiação, o que leva a muitas espécies serem morfologicamente semelhantes ou se distinguirem com base em caracteres questionáveis, apresentado uma variação gradual e/ou relacionados com o habitat de coleta dos indivíduos, o que dificulta o entendimento da delimitação das espécies (Andersson 1994; Andersson 1997; Steyermark et al. 2004).

Por outro lado, existe o risco de que algumas espécies de *Ladenbergia* se encontrem em uma situação vulnerável, causada principalmente pela retirada de seu córtex e madeira em virtude de sua similaridade morfológica com espécies do gênero *Cinchona* as quais são amplamente comercializadas por suas propriedades medicinais e alto nível de alcaloides. Estudos farmacológicos têm demostrado a presença de compostos derivados de alcaloides em algumas espécies de *Ladenbergia*, o que explicaria, ao menos em parte, a diminuição de suas populações em ambiente natural (Holker et al. 1964; Okunade et al. 2001; Cosenza et al. 2013).

Neste contexto, a geração de uma hipótese filogenética, combinada com um tratamento taxonômico atualizado para as espécies andinas e classificação interna de *Ladenbergia* permitirá um estudo sistemático deste interessante grupo de plantas neotropicais, contribuindo para o conhecimento mais aprofundado dos processos de diversificação e evolução da flora neotropical.

OBJETIVOS

Dadas as considerações expostas acima, a presente tese de mestrado tem como objetivos gerais:

- Inferir as relações filogenéticas infragenéricas de *Ladenbergia* (Cinchoneae: Rubiaceae) e sua relação com outros gêneros da tribo Cinchoneae a partir de caracteres moleculares (ITS, *trn*L, *rps*16); e
- Fornecer um tratamento taxonômico atualizado para as espécies andinas de *Ladenbergia.*

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CAPÍTULO 1

Towards a Phylogeny of *Ladenbergia* (Rubiaceae: Cinchoneae): A Preliminary Hipothesis Based on Nuclear and Chloroplast DNA Sequences

Journal: to be submitted to Systematic Botany

Abstract

Ladenbergia is a Neotropical genus, belonging to the tribe Cinchoneae (Rubiaceae). It comprises more than 35 species, of which nearly 18 occur in the tropical Andes. This paper reports a preliminary phylogenetic analysis of nuclear (ITS) and chloroplast (*trn*L and *rps*16 introns, and *trn*L-*trn*L intergenic spacer) nucleotide sequences from 18 species of *Ladenbergia* and allied genera. The phylogenetic hypothesis indicates that *Ladenbergia* is monophyletic and closely related to *Remijia*. Phylogenies based in chloroplast data sets were mostly uninformative, while the ITS region showed a greater support of relationships within *Ladenbergia*. Two main clades and five sub-clades within *Ladenbergia* are well supported. Our analyses provide no support for the previously proposed classifications. This work is an important step in elucidating relationship of *Ladenbergia* and it contributes to the understanding of the phylogenetic relationships within the Cinchoneae tribe.

Keywords: Andes, bayesian inference, Neotropics, parsimony, *Remijia*.

Introduction

The Neotropical genus *Ladenbergia* Klotzsch has about 35 species of trees and shrubs (Taylor & Gereau, 2010). It occurs in the south Central America, Venezuela, Colombia, Brazil, Ecuador, Peru and northern Bolivia, mainly in lowlands, pre-montane and montane life zones (Andersson, 1997). The genus is defined by a suite of characters including terminal inflorescence with white, heterostilyc, nocturnal flowers, salverform corollas with five to seven valvate lobes adaxially ridged and marginally papillose-tomentose and septicidal capsular fruits having numerous flattened seeds (Andersson 1994, 1997, Taylor & Gereau 2010). The species' pollination syndrome is sphingophily, and the flowers are visited by the Shingidae, Hymenoptera and Trochilidae (Wolff 2005).

Recent studies suggest the monophyly of *Ladenbergia* (Andersson 1995, Rova et al 2002, Andersson & Antonelli 2005; Mann & Bremer, 2010; Mann et al 2012), the genus belongs to the tribe Cinchoneae, which in the current circumscription includes the following genera: *Cinchona* L., *Joosia* H. Karst., *Remijia* DC., *Cinchonopsis* L. Andersson, *Stilpnophyllum* Hook. f., *Pimentelia* Wedd., *Maguireocharis* Steyerm. and *Ciliosemina* Antonelli (Andersson & Antonelli, 2005). However, the position of *Ladenbergia* within the tribe is uncertain.

Steyermark (1972) based in morphological patterns suggested a close relationship between *Cinchona, Remijia and Ladenbergia*. Andersson (1995), based in the corolla ridged shape and indument of corolla lobes, proposes *Remijia* as sister to *Ladenbergia*. Rova et al. (2002), based on molecular analysis of *trnL*-F region and considering a single species of *Ladenbergia,* suggested a relationship between *Cinchona* and *Ladenbergia*. Andersson & Antonelli (2005), based in five loci (ITS region, *mat*K and *rbc*L genes, *rps*16 intron and *trnL*-F regions) and considering five species of *Ladenbergia,* mentioned that the relationship between the "crown group" (*Ladenbergia*, *Cinchona* and *Remijia*) are unclear, because of the weak support found in their analysis. However, Mann & Bremer (2010) based in nrDNA (ITS) and cpDNA markers (*rbc*L, *ndh*F, *trn*T-L-F region, *atp*B-*rbc*L spacer and *rps*16 intron) and considering three species of *Ladenbergia* suggested a relationship between *Ladenbergia* and *Ciliosemina*.

Ladenbergia has a great taxonomic interest because it represents a recent neotropical group (Antonelli *et al.* 2009) under constant speciation processes which has led to a poor understanding of the taxonomy of its species. Moreover, because of its morphological resemblance to the genus *Cinchona,* which is a genus of economic importance and widely exploited and commercialized, its populations are potentially at risk.

Early taxonomic treatments considered species of *Ladenbergia* under *Cinchona* (Vahl 1797, Ruiz et al 1801, Lambert 1821, Lindley 1838, Tafalla 1989), *Cinchona* section *Cascarilla* Endl. (Endlicher 1837) and *Buena* Pohl (Pohl 1826). However the genus as such was described by Klotzsch (1846), who recognized 25 species divided in

two sections: a) *Buena* (Pohl) Klotzsch, with four species and *Cascarilla* (Endl.) Klotzsch, with twenty-one species (Table 1).

Subsequently, Weddell (1848; 1849) not accept completely the creation of the *Ladenbergia* proposed by Klotzsch, due to an inconsistency with a nomenclatural rule of the Laws Code that prevailed at the time, which states that if one section becomes genus, the old name must be maintained, so decided to consider *Cascarilla* (Endl.) Wedd. as a name for the genus and not *Buena* Pohl because it could cause confusion with the genus *Cosmibuena* Ruiz & Pav. In the other hand, he circumscribes *Ladenbergia* (Klotzsch) Wedd. to comprise only one definitely included species (*Ladenbergia dichotoma* Wedd.) and two tentatively included ones (*Ladenbergia moritziana* Klotzsch and *Ladenbergia schomburgkii* Wedd.).

Table 1. Klotzsch (1846) and Weddell (1849, 1869) taxonomic proposal for *Ladenbergia* Klotzsch.

Klotzsch (1846)		**Weddell (1849)**		**Weddell (1869)**	
Section	**Species**	**Section**	**Species**	**Section**	**Species**
***Buena* Pohl**	*Ladenbergia undata*	***Carua* Wedd.**	*Cascarilla undata*	***Eubuena* Wedd.**	*Buena undata*
	Ladenbergia roraimae		*Cascarilla roraimae*		*Buena roraimae*
	Ladenbergia hexandra		*Cascarilla hexandra*		*Buena hexandra*
	Ladenbergia macrocarpa		*Cascarilla riedeliana*		*Buena riedeliana*
***Cascarilla* Endl.**	*Ladenbergia moritziana*		*Cascarilla heterophylla*		*Buena heterophylla*
	Ladenbergia schomburgkii		*Cascarilla pavonii*		*Buena pavonii*
	Ladenbergia dissimiflora		*Cascarilla lambertiana*		*Buena lambertiana*
	Ladenbergia cujabensis		*Cascarilla gaudichaudiana*		*Buena gaudichaudiana*
	Ladenbergia firmula		*Cascarilla citrifolia*		*Buena citrifolia*
	Ladenbergia lambertiana		*Cascarilla calycina*		*Buena calycina*
	Ladenbergia bergeniana		*Cascarilla bullata*		*Buena bullata*
	Ladenbergia macrocnemia		*Cascarilla carua*		*Buena carua*
	Ladenbergia magnifolia	***Pseudoquina* Wedd.**	*Cascarilla magnifolia*	***Cascarilla* (Endl.) Wedd.**	*Buena magnifolia*
	Ladenbergia dichotoma		*Cascarilla nitida*		*Buena nitida*
	Ladenbergia caduciflora		*Cascarilla stenocarpa*		*Buena stenocarpa*
	Ladenbergia tenuiflora		*Cascarilla acutifolia*		*Buena acutifolia*
	Ladenbergia denuiflora		*Cascarilla riveroana*		*Cascarilla riveroana*
	Ladenbergia stenocarpa	***Calyptria* Wedd.**	*Cascarilla macrocarpa*	***Calyptria* Wedd.**	*Buena macrocarpa*
	Ladenbergia acutifolia		*Cascarilla calyptrata*		*Buena calyptrata*
	Ladenbergia cava	***Muzonia* Wedd.**	*Cascarilla muzonensis*	***Muzonia* Wedd.**	*Buena muzonensis*
	Ladenbergia ovalifolia		*Cascarilla hookeriana*		*Buena hookeriana*

In the circumscription of Weddell (1849), he accepted 21 species divided in four sections based in morphological characters: *Pseudoquina* Wedd., with free stipule at base, multiflore panicle, corolla submembranaceous with lobes margins lacinate and papillose; *Carua* Wedd., with free stipules or fused at base, multi or pauciflora panicle, corolla more or less coriaceous, corolla lobes completely papillose; *Calyptria* Wedd. with pauciflora panicle and stipules completely fused; and *Muzonia* Wedd. with flower clustering in elongate panicle and subcapitate and free stipules or fused at base.

Finally Weddell (1869) moves all species of *Cascarilla* to *Buena* noting that this genus cannot be confused with *Cosmibuena* because they have a different floral morphology. He maintains two sections of the early proposal (Weddell 1849): *Calyptria* Wedd. and *Muzonia* Wedd. Proposes two new sections here: *Cascarilla* (Endl.) Wedd. (includes *Pseudoquina* Wedd.) and *Eubuena* Wedd. (includes sections as *Buena* Klotzsch and *Carua* Wedd).

Standley (1921) does not accept the proposals of Weddell and recognized the circumscription by Klotzsch (1846), possibly because this is not clear according to the nomenclature code, which indicates, what a typification of a genus cannot be recognized by means of exclusion of species.

Andersson (1997) in his cladistic analysis based on morphological characters mentions that Weddell's classification is not very successful because the recognized sections are paraphyletic groups characterized by plesiomorphic features. In contrast, Andersson (1997) suggested a basal grade restricted to the eastern foothills of the Andes (*L. acutifolia*, *L. discolor*, *L. ferruginea* and L. *klugii*), characterized by a combination of plesiomorphic traits such as small flowers with small calyx, small and thin-walled capsules and small seeds. Also, they suggested one informal group denominated Lambertiana (*L. amazonensis*, *L. lambertiana*, *L. chapadensis*, *L. graciliflora*, *L. pittieri*, *L. cujabensis*, *L. paraensis* and *L. stenocarpa*), supported mainly by leaf anatomical features and distributed predominately in the Amazon basin. Andersson's proposal is questionable due to the small number of characters compared to the number of species analyzed and high number of homoplasies that may result in

a topology slightly supported after successive reweighting of characters.

This paper aims to propose a preliminar phylogenetic hypothesis based on nuclear (ITS region) and chloroplast (*trn*L-*trn*L-*trn*F intergenic spacer and *rps*16 intron) nucleotide sequences of *Ladenbergia*. The main goals of this study are: (1) to corroborate the monophiletic status of *Ladenbergia* based on a broader sampling*;* (2) to clarify a which is the position of the *Ladenbergia* within of Cinchoneae tribe*;* (3) to test whether previous grouping proposed by Klotzsch (1846), Weddell (1849, 1969) and Andersson (1997) represent monophyletic groups.

Materials and Methods

Taxon Sampling– We sampled 18 species of *Ladenbergia* (ca. 52 % the genus), used as ingroup, of which 14 were represented by two or more individuals from localities in Panama, Colombia, Ecuador, Peru and Bolivia, witch showed intraspecific morphologic variation. We obtained sequences of the genus *Isertia, Cephalanthus, Uncaria, Sabicea* and *Luculia* from Genbank (Appendix 1).

DNA Isolation and PCR Amplification– We extracted the total DNA from leaf material dried in silica gel (Chase & Hills, 1991) or from herbarium specimens following the NucleoSpin Plant II Kit (Macherey-Nagel, Duren, Germany) protocol. The ITS region (ITS1, the 5.8S coding region and ITS2), *trn*L – *trn*L – *trn*F intergenic spacer and *rps*16 region were amplified with the primer 18S 1830 forward and 26S 25 revers (Nickrent *et al.* 1994), primer c' and f' (Taberlet *et al*. 1991) and primer pair rpsF/rpsR2 (Oxelman *et al*., 1997). PCRs for the ITS were conducted in a reaction mixture as follows: 12.5 µl Go Taq Green Master Mix (Promega, USA), 1.5 µl of each primer, 1.5 µl of DNA, 2 µl of BSA, 4 µl of DMSO. PCR reactions for the chloroplast were prepared as follows: 12.5 µl Go Taq Green Master Mix (Promega, USA), 2 µl of each primer, 1.5 µl of DNA, 3 µl of Nucleasa, 4 µl of BSA. PCR conditions were: For the ITS amplification, the following PCR cycle program was used: initial denaturation at 94 °C for 3 minutes followed by 35 cycles of 94 °C for 30 sec, 1 minute annealing at 50 °C, and 1 minutes with 30 sec elongation at 72 °C; and a final elongation of 5 minutes at 72 °C; For trnL- *trn*L - *trn*F intergenic spacer, the following PCR cycle program was used: initial denaturation at 95

°C for 5 minutes followed by ramp with gradient of temperature: Stage 1 with 4 cycles 95°C for 30 sec, 54 °C for 40 sec and 72°C for 1 minute and 15 sec.; Stage 2 with 4 cycles 95°C for 30 sec, 52 °C for 40 sec and 72°C for 1 minute and 15 sec. and Stage 3 with 35 cycles 95°C for 30 sec, 49 °C for 30 sec and 72°C for 1 minute and 15 sec.; For *rps*16 region, the following PCR program was used: initial denaturation at 95 °C for 2 minutes followed by 33 cycles of 95 °C for 30 sec, 1 minute annealing at 49.5 °C, and 2 minutes elongation at 72 °C; and a final elongation of 7 minutes at 72 °C. All PCR products were purified using a QIAquick purification kit (Qiagen Corp.).

Sequencing and Alignment– Sequencing reactions were performed in the Center of Molecular Biology and Genetics (CBMEG) (UNICAMP, Brazil) using BigDye Terminator v 3.1 kit (Applied Biosystems Inc., Framingham, Massachusetts; following the manufacturer's instructions, except that quarter reactions were used). The sequencing reaction condition were performed as follows: 01 cycle at 96 °C for 1:30 minutes, followed by 30 cycles at 96 °C for 12 sec., 50 °C for 6 sec and 60 °C for 4 minutes, and subsequent storage at 14 °C. Sequenced reactions were purified with 5 µl EDTA 125mM, adding 80 µl ethanol at 80 %, centrifuged by 45 min at 4000 rpm/25 °C, add 150 µl ethanol at 70 % and centrifuged by 15 minutes, followed by denaturation at 95 °C for 5 min with posterior cooling for 5 minutes. Automatic Sequencing was run using an ABI 3700 automated sequencer. The obtained sequences were edited in Genious R9 (Kearse et al., 2012), automatically aligned in Mafft (Katoh and Standley 2013) online version and aligned manually using Mesquite v. 2.75 (Maddison and Maddison, 2003).

Incongruence Testing and Combined Data Analysis– We constructed a combined data matrix of ITS, *trn*L – *trn*L - *trn*F intergenic spacer and *rps*16 and found out the congruence of the datasets in Partition Finder (Lanfeor et al. 2012). Given an alignment of predefined data blocks (in this case, the three-gene dataset), this program selects both the best-fitting partition scheme and models of molecular evolution for each partition.

Phylogenetic Analyses– All datasets were analyzed using maximum parsimony (MP) and Bayesian inference (BI) methods. MP was performed in PAUP 4.0b10 (Swofford 2000) using heuristic searches. All characters were treated as equally weighted and unordered, and gaps were treated as missing data. Bootstrap (BS) was performed to assess support for branches in MP (1 000 full heuristic replicates) being considered significant values ≥ 75%. Strict consensus tree was used to summarize all the trees found in the analysis of MP. Modeltest v. 3.06 (Posada and Crandall 1998; Posada and Buckley 2004) was used to determinate the substitution model that best fit the sequences datasets. The parameters of the best model under the Bayesian Information Criteria (BIC) were used BI analysis. BI analyses were performed in MrBayes v. 3.1.2 (Huelsenbeck and Ronquist 2001). Model parameters for the substitution model were specified and each analysis was conducted with two independent runs with four (one heated and three cold) Markov Chain Monte Carlo (MCMC) chains for twenty million generations starting from a random tree. After discarding 25 % of the saved trees was discarded as burn in. Majority rules consensus trees were produced using Tree Anotator v. 1.7.4 (Drummond et al. 2012) and exported to Figtree 1.4.0 (Rambaut, 2015) for visualization and edition. Posterior probabilities (PP) for each node were calculated; values ≥ 0.95 were considered strongly supported (Alfaro et al. 2003; Huelsenbeck & Rannala, 2004).

Results

Data Matrices–Fifteen species of *Ladenbergia* were sampled with ITS region and 43 sequences were obtained. Aligned sequences have a length of 726 base pairs (bp). Sixteen species of *Ladenbergia* were sampled with *rps*16 region and 48 sequences were obtained. Aligned sequences have a length of 893 bp. Eighteen species of *Ladenbergia* were sampled with *trn*L region and 52 sequences were obtained. Aligned sequences of the have a length of 1036 bp.

The combined dataset was separated using the software Partition Finder into two partitions, ITS and two plastid DNA genes, thus reducing model complexity compared with partitioning by gene. Despite the incongruence between the

chloroplast and nuclear markers, a total evidence analysis was performed to test whether the clades obtained with the individual datasets would remain. Sequences analysis revealed that the region ITS is more variable compared to sequences of *trn*L and *rps*16 and present a larger number of informative characters. The combined dataset included only taxa with sequences for all three markers, total of 2721 bp, from which 386 were potentially informative characters (Table 2).

Table 2. Statistics from parsimony analysis of different data sets including consistency index (CI) and retention index (RI). The CI values listed are excluding uninformative characters.

Description	ITS	trnL	rps16	Combined data set
Number taxa sampled	16	18	15	49
Parsimony informative characters	204	84	71	386
Variable characters	49	65	57	239
Tree lenghts	546	178	163	1102
CI	0.66	0.87	0.86	0.73

Phylogenetic Analysis and Relationships– Our Maximum Parsimony (MP) analysis with chloroplast markers (*trn*L and *rps*16) was uninformative and shows weak resolution at the generic level, among genus within tribe Cinchoneae and also poor resolution at the species level (Fig 1). In this analysis, nor the monophyletic status of *Ladenbergia* is corroborated (*trn*L: BS= 73% and *rps*16:BS=64%) neither the position of *Ladenbergia* within the tribe Cinchoneae.

Similarly Bayesian Inference (BI) analysis of each chloroplast dataset with different substitution model (*trn*L: GTR + I + G and *rps*16: HKY + G) yielded low resolution,as in MP analysis. The BI of the combined chloroplast data showed the genus as monophyletic (PP=1) (Fig 2) but the species level relationship is not completely resolved. But some well-supported relationships between *Ladenbergia*'s species can be observed, the clade comprising *L. riveroana* and *L. stenocarpa* (PP=1) and the clade comprising *L. bullata* and *L. carua* (PP=1).

The MP analysis based on the ITS region show *Ladenbergia* as monophyletic (BS= 86%), and the relationship between species are more resolved (Figure 3A). Four well-supported clades can be delimited in this analysis. The first composed by Amazon species only: *L. amazonensis* + *L. graciliflora* (BS = 99%); the second comprising Andean species only: *L. bullata*, *L. carua*, *L. riveroana* and *L. stenocarpa* (BS = 100%); a third clade with Andean and central American species: *L. oblongifolia*, *L. pavonii*, *L. heterophylla* and *L. dwyeri* (BS = 90%), and a the fourth clade with species from southeastern Brazil, Guiana Shield and Andes: *L. hexandra*, *L. cujabensis*, *L. paraensis*, *L. lambertiana*, *L. crassifolia*, *L. bullata*, *L. klugii* and *L. macrocarpa* (BS=85%)

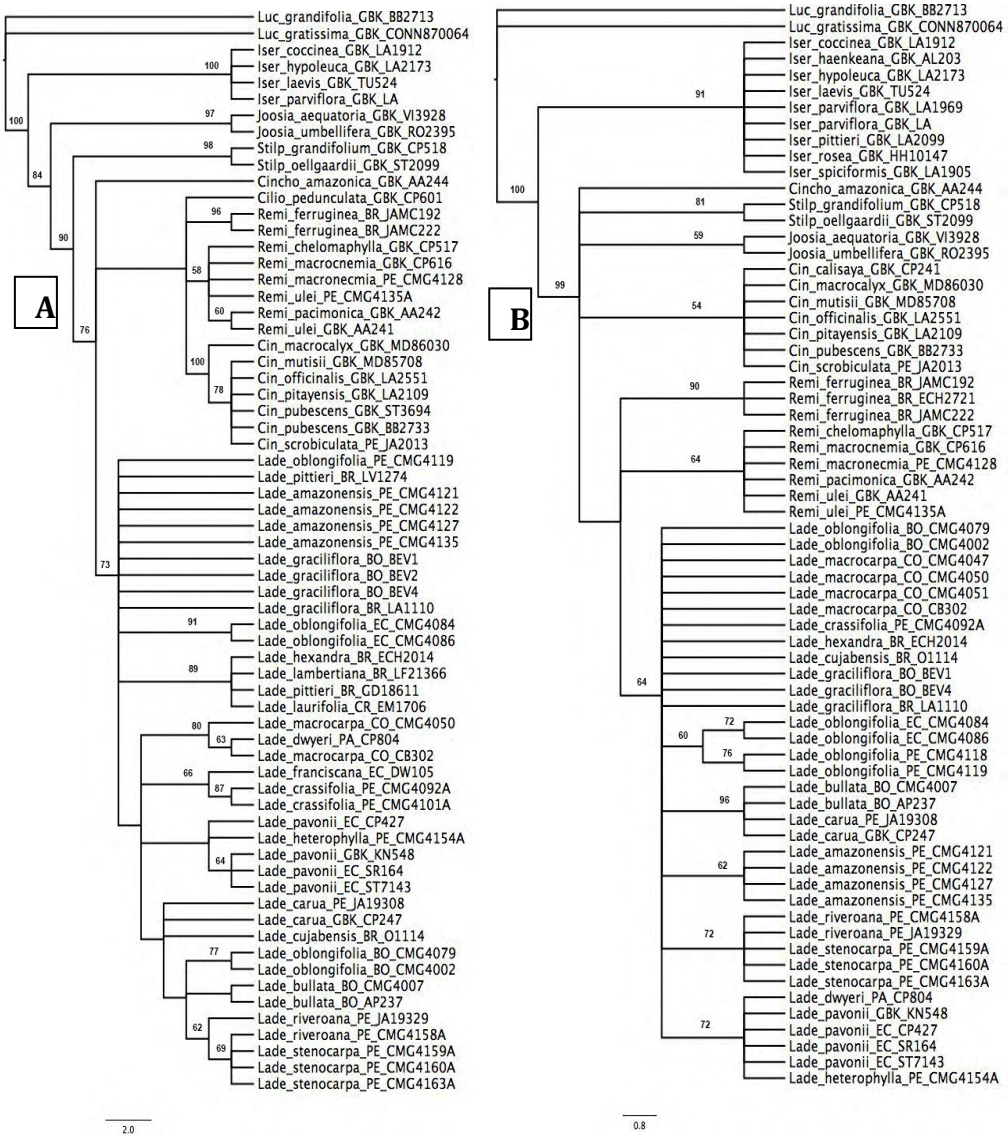

Fig. 1. Strict consensus tree for cdDNA obtained with MP. **A.** *Trn*L (CI = 0.87 and RI = 0.93). **B.** *rps*16 (CI = 0.86 and RI = 0.92). The numbers above the branches are MP bootstrap values based on 1,000 replicates.

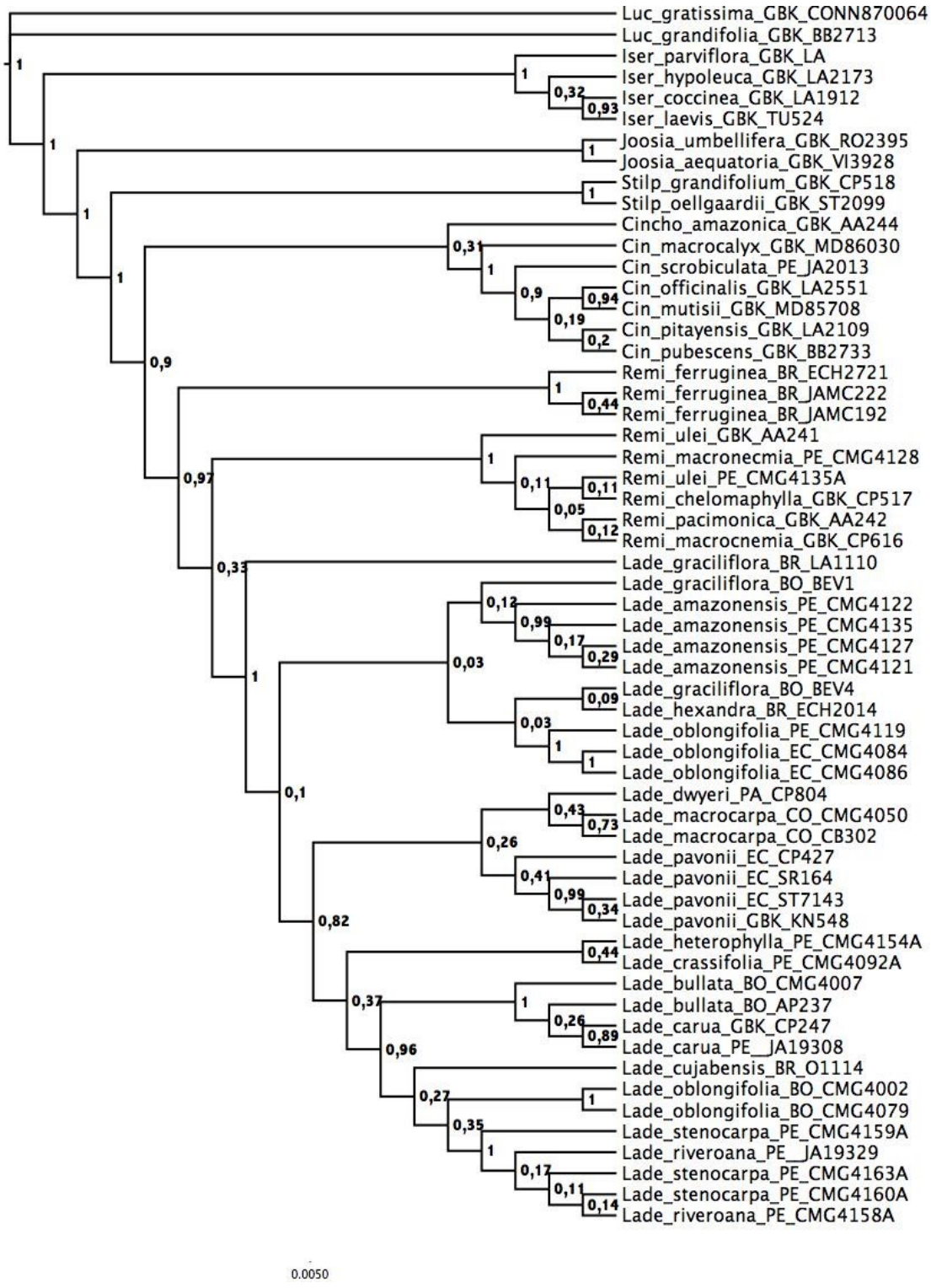

Fig. 2. **A.** Majority rule consensus tree obtained by Bayesian Inference (BI) for chloroplast combined data (trnL/rps16), numbers above the branches are the posterior probability values.

The BI analysis based on ITS region followed the GTR + G model. This analysis shows *Ladenbergia* (PP= 1) as a clade and as sister to *Remijia* (PP=0.87) (Fig 2B). One main clade (PP=0.98) with species distributed in Andean, Brazilian territory and Guiana Shield in *Ladenbergia* was observed, and two sub-clades are well supported: 1) *L. hexandra* + *L. cujabensis* + *L. paraensis* and *L. lambertiana* (PP=1); species that ocurr in the southeastern Brazil, Brazilian territory and Guiana Shield; 2) *L. crassifolia* + *L. bullata* + *L. klugii* and *L. macrocarpa* (PP=0.98), from southern Central Andes to southern tropical Andes.

Other possibly main clade (PP=0.77) with species distributed in Amazon, Andean and Central America was observed, and four sub-clades are well supported: 1) *L. amazonensis* and *L. graciliflora* (PP=1), from the Amazon basin 2) *L. carua* and *L. bullata* (PP=0.96), that occurs in the southern tropical Andes; 3) *L. riveroana* and *L. stenocarpa* (PP=1), from southern Central Andes; and (4) *L. oblongifolia* (widespread in the Andes) + *L. pavonii* + *L. heterophylla* and *L. dwyeri* (PP=1), that ocurrs in the souther the Central America.

The analysis based on the total evidence data (nDNA and cdDNA region) (Fig 4) confirm the monophyly of *Ladenbergia* (PP=1) and *Remijia* as its sister group (PP=0.99). Two main clades appears in this analysis but they are different from those of the ITS region analysis. Some subclades found in the ITS region analysis also appears at this analysis: clade comprising *L. graciliflora* and *L. amazonensis* (PP=1); and the clade composed by *L. bullata*, *L. carua*, *L. riveroana* and *L. stenocarpa*; *L. oblongifolia*, *L. dwyeri*, *L. pavonii* and *L. heterophylla* (PP=1).

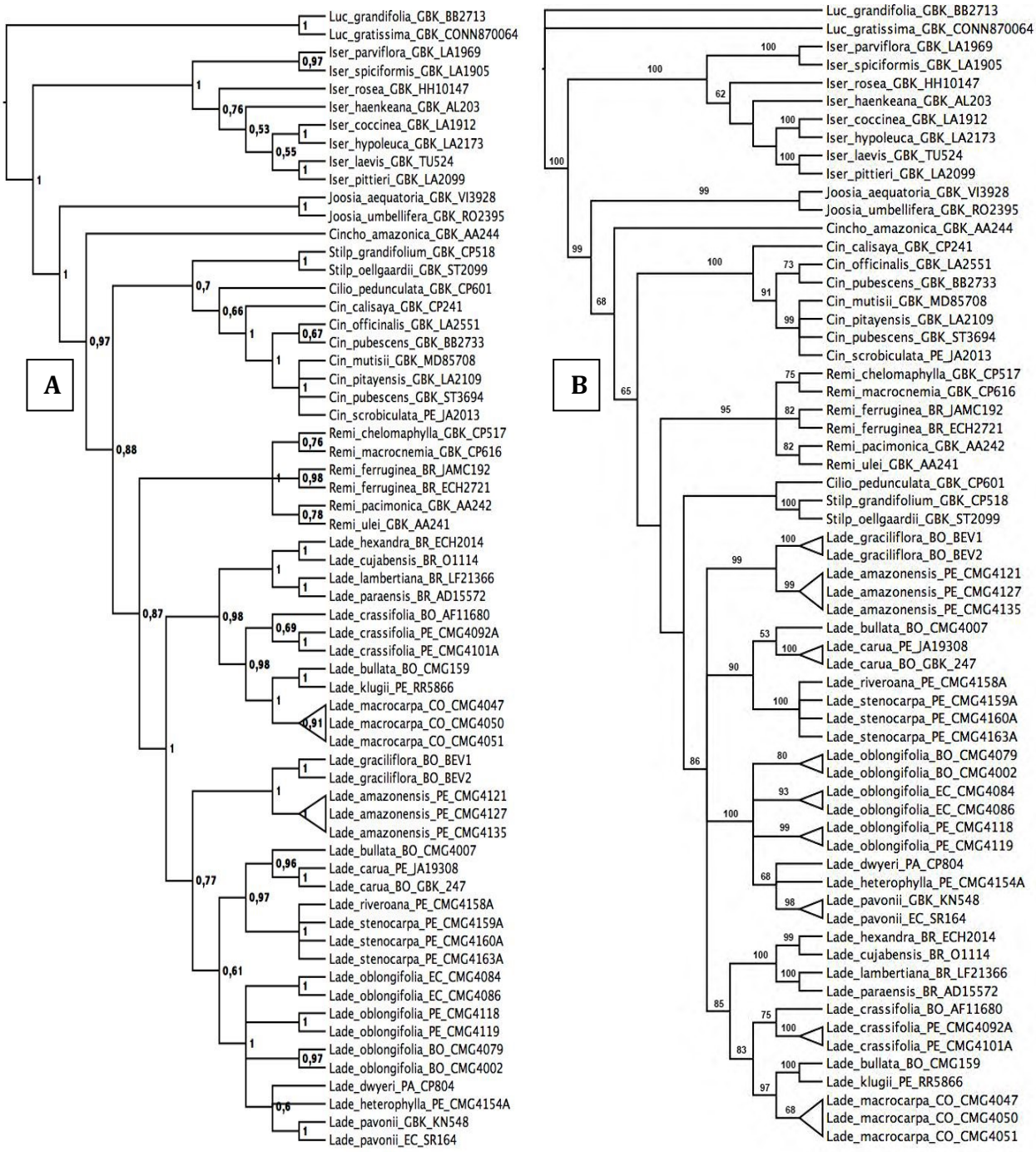

Fig. 3. **A.** Majority rule consensus tree obtained with the Bayesian Inference (BI) for ITS. Numbers above the branches are BI posterior probabilities. **B.** Strict consensus tree obtained with Maximum Parsimony for ITS (CI = 0.66 and RI = 0.87). The numbers above the branches are MP bootstrap values based on 1,000 replicates.

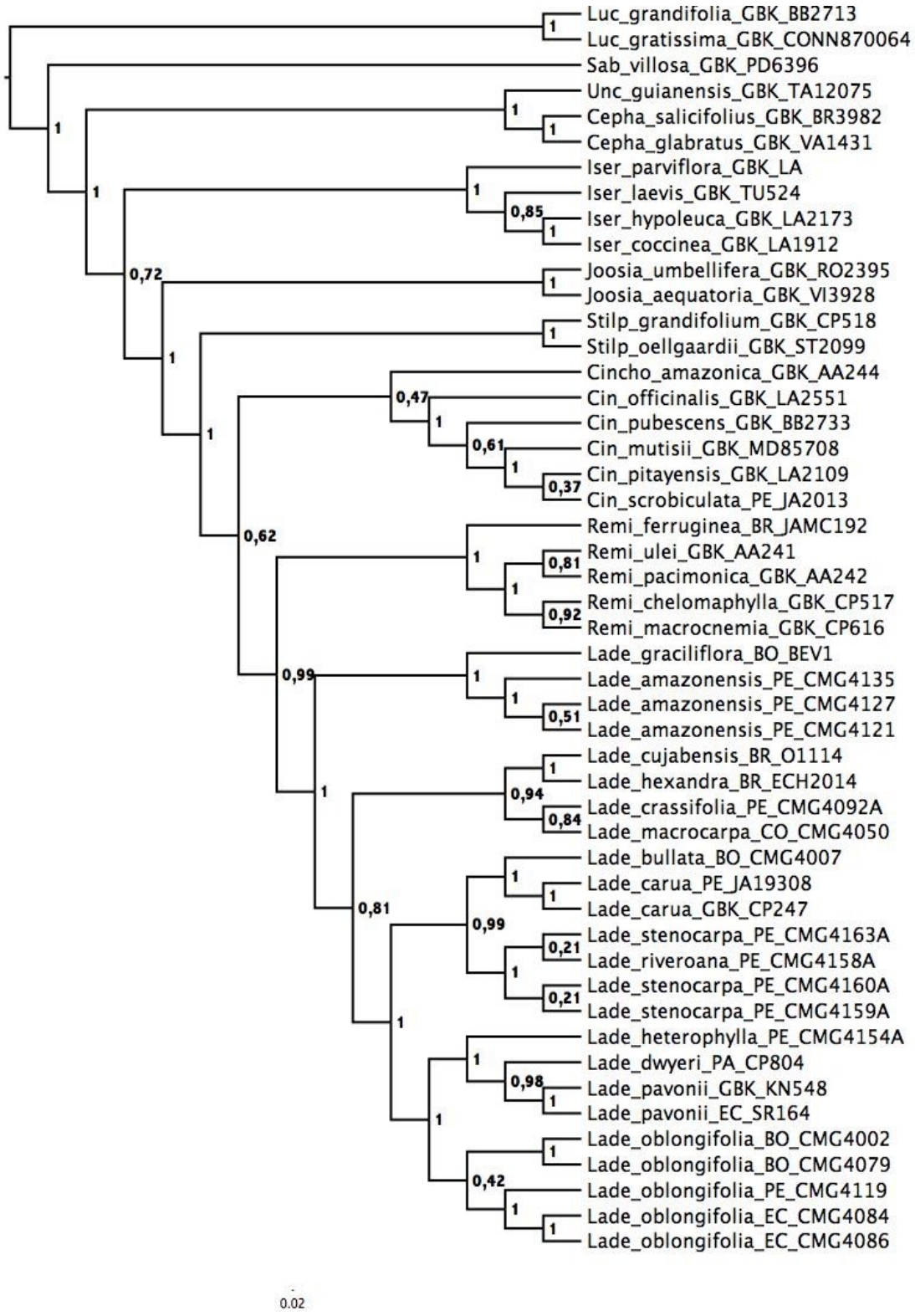

Fig. 4. Majority rule consensus tree obtained with Bayesian Inference (BI) based on the combined ITS/trnL/rps16 data set. Numbers above the branches are posterior probability values.

Discussion

This study represents the first comprehensive phylogenetic molecular study of *Ladenbergia* to date. Our samplings of eighteen species of *Ladenbergia* included in this phylogeny are morphologically distinct and represent the morphological diversity of the genus.

Our results with the ITS region only and the combined dataset support the monophyly of *Ladenbergia*, confirming previous inferences with a reduced number of species sampled (Andersson 1995, Andersson & Antonelli 2005, Rova et al 2002, Mann & Bremer 2010, Mann et al 2012). The *trn*L and *rps*16 regions do not provide sufficient variation to clarify infrageneric relationships of *Ladenbergia*. Futures studies applying more variable DNA regions with extensive sampling may be valuable.

Also we confirm the positioning of *Ladenbergia* within the Cinchoneae tribe and its close relationship to *Remijia*, which was suggested by Andersson (1994, 1997) based on the shape and indumentum of the corolla lobes.

The previous conclusion of Anderson (1997) that Weddell's classification comprises polyphyletic/paraphyletic groups is confirmed. We also discard the Lambertiana group proposed by Anderson (1997), because in our analysis species belonging to this group are positioned in different clades and related to other species with Andean distribution.

The basal placement of *Ladenbergia amazonensis* in our total evidence analysis agrees with Andersson (1997), Andersson & Antonelli (2005) and Mann & Bremer (2010). Nevertheless, it is not entirely clear in the ITS only analysis if *L. amazonesis* is positioned in a basal position. But this could be an artifact of the topology including more terminals. Unfortunally, most of the species that was proposed by Anderson (1997) as basal grades was not sampled here and it was not possible to infer their position. We obtained ITS sequences to just one of the species of the basal grade, *L.*

klugii, and its position was not basal but close to species that occurs in the northern Andes.

The close relationship between *L. amazonensis* and *L. graciliflora* is also observed in morphological characters and geographical distribution. These species share the following morphological characters: flowers with thin tubes, toothed calyx, hirsute styles and thin fruits; and both genus occur in Amazon biome. Due to such morphological similarities, Andersson (1997) included these species in the Lambertiana group. The clade formed by *L. hexandra*, *L. cujabensis*, *L. lambertiana* and *L. paraensis* are not morphologically similar but share a biogeographic pattern including species that occur from southeastern Brazil to Brazilian and Guyana Shields. It is important to notice that this clade is related to a Andean clade, so there is a disjunction pattern which could be explained with mechanisms and processes of long distance dispersal.

The Andean clade composed by *L. crassifolia, L. bullata, L. klugii* and *L. macrocarpa* has a considerable morphological variation between each of the species. *Ladenbergia macrocarpa* and *L. crassifolia* form a species complex based on morphology, but according to BI analysis based on the ITS region, *L. macrocarpa* were closely related to *L. bullata* and *L. klugii*. At the total evidence analysis these species were in the same clade, probably due to the lower number of terminals. Studies with greater sampling of these species is necessary to establish the relationship between *L. macrocarpa* and *L. crassifolia.*

The Andean clade ((*L. bullata*, *L. carua)*(*L. riveroana* and *L. stenocarpa))*, which is distributed in suthern and central Andes, are morphologically related, respectively. *Ladenbergia bullata* and *L. carua* share pauciflora inflorecences, large flowers and fleshy fruits. While *L. riveroana* and *L. stenocarpa* share multiflora inflorescences, small flowers and slender fruits.

Ladenbergia oblongifolia, a species widely distributed in the Andes and morphologically distinct, is related to species of a species complex (*L. heterophylla, L. pavonii and L. dwyeri*) that occur from North Andes to Central America, which agrees to the mentioned by Mann & Bremer (2010).

Final Remarks

Here we present the first documented molecular study of the genus *Ladenbergia* including more than 50% of all currently recognized species. The ITS region provide sufficient information to clarify some relationships at infrageneric level.

In this paper, we confirm the monophyly of *Ladenbergia* under a analysis including more taxa and highlight the genus *Remijia* as its sister-group. We reject Andersson's proposal (1997) that Amazon species form a monophyletic group. Additionally, our analysis corroborates with notes of Anderson (1997) pointing out the classification proposed by Weddell (1849) as unnatural sections.

Our data suggest some clades and relationships within *Ladenbergia*: (*L. amazonensis* and *L. graciliflora*); ((*L. hexandra*, *L. cujabensis*) and (*L. lambertiana*, *L. paraensis*)); ((*L. carua*, *L. bullata*) and (*L. stenocarpa*, *L. riveroana*)) and ((L. oblongifolia and (*L. dwyeri*, *L. heterophylla*, *L. pavonii*)).

It is still interesting to see whether more exhaustive sampling and additional genetic evidence (i.e. other nuclear or cpDNA regions) will support the exhibited hypothesis developed in this study.

Acknowledgments

This study was supported by University of Campinas (UNICAMP) and Programa Nacional de Becas de Peru (PRONABEC). We are grateful to Dr. Claes Persson, Joaquina Alban and Alessandra Marquez for providing many samples of leaf tissue. The curators from herbaria MO, NY, F, UEC generously let us take samples from their collections, for which we are most grateful. We are deeply grateful with Carla Maldonado and Nina Ronsted for providing DNA sequences of the tribe Cinchoneae's representatives and to Gustavo Shimizu and Nállarett Dávila for their assistance at the molecular laboratory.

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Appendix. Sequences used in cladistics analyses, together with data an origin of sequenced material and Genbank accession numbers (in order taxon, origin, voucher, Genbank accessions number: ITS, *Rps*16 and *TrnL*-F.

Taxon	Voucher	Herbarium	Collection Country	Sequences / Accesion Number Genbank		
				ITS	Rps16	TrnL
Ladenbergia bullata (Wedd.) Standl.	Maldonado, *159*	MO	Bolivia	x		
Ladenbergia bullata (Wedd.) Standl.	Maldonado, *4007*	LPB	Bolivia	x	x	x
Ladenbergia macrocarpa (Vahl) Klotzch	Maldonado, *4047*	GB	Colombia	x	x	x
Ladenbergia macrocarpa (Vahl) Klotzch	Maldonado, *4050*	GB	Colombia	x	x	x
Ladenbergia macrocarpa (Vahl) Klotzch	Maldonado, *4051*	GB	Colombia	x	x	x
Ladenbergia macrocarpa (Vahl) Klotzch	Persson, *302*	GB	Colombia			x
Ladenbergia macrocarpa (Vahl) Klotzch	Andersson et al., *2103*	GB	Colombia	x	AF242971	AF152683
Ladenbergia crassifolia (Pav. ex DC.) Standl.	Maldonado, *4086*	USM	Ecuador	x	x	x
Ladenbergia crassifolia (Pav. ex DC.) Standl.	Maldonado et al., *4092A*	USM	Ecuador	x	x	x
Ladenbergia crassifolia (Pav. ex DC.) Standl.	Maldonado et al., *4101A*	USM	Peru	x		x
Ladenbergia crassifolia (Pav. ex DC.) Standl.	Maldonado et al., *4102A*	USM	Peru	x	x	x
Ladenbergia crassifolia (Pav. ex DC.) Standl.	Fuentes, *11680*	MO	Bolivia	x		
Ladenbergia franciscana C.M. Taylor	Wolff, *158*	MO	Ecuador		x	x
Ladenbergia oblongifolia (Humb. ex Mutis) L. Andersson	Maldonado, *4002*	LPB	Bolivia	x	x	x
Ladenbergia oblongifolia (Humb. ex Mutis) L. Andersson	Maldonado, *4079*	GB	Bolivia	x	x	x
Ladenbergia oblongifolia (Humb. ex Mutis) L. Andersson	Maldonado, *4084*	GB	Ecuador	x	x	x
Ladenbergia oblongifolia (Humb. ex Mutis) L. Andersson	Maldonado, *4096*	GB	Ecuador	x	x	x
Ladenbergia oblongifolia (Humb. ex Mutis) L. Andersson	Maldonado, *4098*	GB	Ecuador		x	x
Ladenbergia oblongifolia (Humb. ex Mutis) L. Andersson	Maldonado, *4099*	GB	Ecuador	x	x	x
Ladenbergia oblongifolia (Humb. ex Mutis) L. Andersson	Maldonado, *4100*	GB	Ecuador	x	x	x
Ladenbergia oblongifolia (Humb. ex Mutis) L. Andersson	Maldonado et al., *4118*	USM	Peru	x	x	
Ladenbergia oblongifolia (Humb. ex Mutis) L. Andersson	Maldonado et al., *4119A*	USM	Peru	x	x	x
Ladenbergia amazonensis Ducke	Maldonado et al., *4121*	USM	Peru	x	x	x
Ladenbergia amazonensis Ducke	Maldonado et al.,	USM	Peru	x	x	x

	4122					
Ladenbergia amazonensis Ducke	Maldonado et al., *4127*	USM	Peru	x	x	x
Ladenbergia amazonensis Ducke	Maldonado et al., 4135	USM	Peru	x	x	x
Ladenbergia heterophylla (Wedd.) Standl.	Maldonado et al., *4154A*	USM	Peru	x	x	x
Ladenbergia riveroana (Wedd.) Standl.	Maldonado et al., *4158A*	USM	Peru	x	x	x
Ladenbergia riveroana (Wedd.) Standl.	Alban, *19329*	USM	Peru		x	x
Ladenbergia stenocarpa (Lamb.) Klotzsch	Maldonado et al., *4159A*	USM	Peru	x	x	
Ladenbergia stenocarpa (Lamb.) Klotzsch	Maldonado et al., *4160A*	USM	Peru	x	x	x
Ladenbergia stenocarpa (Lamb.) Klotzsch	Maldonado et al., *4161A*	USM	Peru	x	x	x
Ladenbergia stenocarpa (Lamb.) Klotzsch	Maldonado et al., *4163A*	USM	Peru	x	x	x
Ladenbergia stenocarpa (Lamb.) Klotzsch	Homeier, *4832*	MO	Ecuador	x		
Ladenbergia stenocarpa (Lamb.) Klotzsch	Homeier, *4706*	MO	Ecuador		x	
Ladenbergia klugii L. Andersson	Rojas et al., *5866*	MO	Peru	x		
Ladenbergia carua (Wedd.) Standl.	Beck, *29508*	MO	Bolivia	x		
Ladenbergia carua (Wedd.) Standl.	Persson & Gustafsson, *247*	GB	Bolivia	AY538364	AY538435	AY538461
Ladenbergia graciliflora K. Schum.	Escobari, *1*	LPB	Bolivia	x	x	x
Ladenbergia graciliflora K. Schum.	Escobari, *2*	LPB	Bolivia	x	x	x
Ladenbergia graciliflora K. Schum.	Escobari, 4	LPB	Bolivia		x	x
Ladenbergia graciliflora K. Schum.	Sasaki et al. 2241	K	Brasil	x		x
Ladenbergia graciliflora K. Schum.	Laneto et al., *1110*	UB	Brasil		x	x
Ladenbergia cujabensis Klotzsch	Santos et al., *708*	UB	Brasil			x
Ladenbergia cujabensis Klotzsch	Martinelli, *18333*	CEN	Brasil		x	x
Ladenbergia hexandra (Pohl) Klotzsch	Chilquillo, E80	USM	Brasil	x		x
Ladenbergia carua (Wedd.) Standl.	Alban, *19308*	USM	Peru	x	x	x
Ladenbergia pavonii (Lamb.) Standl.	Persson, *427*	GB	Ecuador		x	x
Ladenbergia pavonii (Lamb.) Standl.	Delprete, *6404*	UPS	Ecuador			AM117369
Ladenbergia pavonii (Lamb.) Standl.	Knudsen, *548*	GB	Ecuador	AY538367	AY538437	AY538463
Ladenbergia pavonii (Lamb.) Standl.	Raponen, 164	GB	Ecuador	x	x	x
Ladenbergia pavonii (Lamb.) Standl.	Stahl et al., *7143*	GB	Ecuador		x	x
Ladenbergia pavonii (Lamb.) Standl.	Stahl et al., *2866*	GB	Ecuador		x	
Ladenbergia pittieri Standl.	Valverde, *1274*	MO	Venezuela			x
Ladenbergia bullata (Wedd.) Standl.	Apaza, *237*	MO	Bolivia		x	x
Ladenbergia cujabensis Klotzsch	Oliveira et al., *1114*	NY	Brasil	x	x	x
Ladenbergia hexandra (Pohl) Klotzsch	Chilquillo, E94	UEC	Brasil	x	x	x
Ladenbergia lambertiana (A. Braun ex Mart.) Klotzsch	Froes, *21366*	NY	Guyana		x	x
Ladenbergia lambertiana (A. Braun ex Mart.) Klotzsch	Froes, *21337*	NY	Guyana	x	x	

Ladenbergia pittieri Standl.	Davidse et al., *18611*	GB	Venezuela		x	x
Ladenbergia laurifolia Dwyer	Montenegro, *1706*	MO	Costa Rica			x
Cinchona calisaya Wedd.	Persson & Gustafsson, *241*	GB	Peru	AY538352	AF242927	AY538447
Cinchona hirsuta Ruiz & Pav.	Weigend, *5784*	GB	Peru	AY538368	AY538438	AY538464
Cinchona nitida Benth.	Maldonado et al., *4109*	USM	Peru	x	x	x
Cinchona officinalis L.	Andersson & Nilsson, *2551*	GB	Peru	GQ852117	GQ852387	GQ852483
Cinchona pitayensis (Wedd.) Wedd.	Andersson et al. *2109*	GB	Peru	AY763888	AF242928	AY763819
Cinchona pubescens Vahl	Ståhl, *3694*	GB	Peru	AY538356	AF004035	AY538451
Cinchona scrobiculata Bonpl.	Alban, E81	USM	Peru	x	x	x
Cinchona scrobiculata Bonpl.	Alban, E34	USM	Peru	x	x	x
Remijia chelomaphylla G.A. Sullivan	Persson, *517*	GB	Ecuador	AY538369	GQ852435	GQ852539
Remijia macrocnemia (Mart.) Wedd.	Persson & Grandez, *616*	GB	Peru	GQ852152	GQ852436	GQ852540
Remijia macrocnemia (Mart.) Wedd.	Maldonado et al., *4128*	USM	Peru	x	x	x
Remijia macrocnemia (Mart.) Wedd.	Maldonado et al., *4131*	USM	Peru	x	x	x
Remijia ferruginea (A. St.-Hil.) DC.	Chilquillo, *2721*	UEC	Brasil	x	x	x
Remijia ferruginea (A. St.-Hil.) DC.	Carmo, *192*	UEC	Brasil	x	x	x
Remijia ferruginea (A. St.-Hil.) DC.	Carmo, *222*	UEC	Brasil		x	x
Remijia pacimonica Standl.	Antonelli, *242*	GB	Brasil	AY538372	AY538443	AY538472
Remijia ulei K. Krause	Antonelli, *241*	GB	Brasil	AY538374	AY538445	AY538474
Remijia ulei K. Krause	Maldonado et al., *4135A*	USM	Peru		x	x
Ciliosemina pedunculata (H. Karst.) Antonelli	Persson et al, 601	GB	Peru	AY538373	AY538444	AY538473
Stilpnophyllum oellgaardii L. Andersson	Ståhl, 2099	GB	Ecuador	AY538376	AF243026	AY538477 3
Stilpnophyllum grandifolium L. Andersson	Persson, 518	GB	Ecuador	AY538375	AY538446	AY538476
Cinchonopsis amazonica (Standl.) L. Andersson	Antonelli, 244	GB	Brasil	AY538357	AY538428	AY538452
Joosia aequatoria Steyerm.	Vivar et al, 3928	GB	Ecuador	AY538360	AY538432	AY538457
Joosia umbellifera H. Karst.	Rova et al, 2395	GB	Panama	AY538361	AY538433	AY538458
Isertia parviflora Vahl				GQ852141	DQ448603	GQ852520
Isertia spiciformis DC.				DQ448612	DQ448606	
Isertia rosea Spruce ex K. Schum.				KP204855	KP204857	
Isertia haenkeana DC.				DQ448607	DQ448601	
Isertia coccinea (Aubl.) Vahl				GQ852140	GQ852405	AF152689
Isertia hypoleuca Benth.				DQ448608	IHAF004059	AF152688
Isertia laevis (Triana) B.M. Boom				AY538359	AY538431	AY538456
Isertia pittieri (Standl.) Standl.				DQ448610	DQ448604	AM117365
Luculia grandifolia Ghose				AJ346896	DQ662205	DQ662149
Luculia gratissima (Wall.) Sweet				EU145344	EU817448	EU817472

CAPÍTULO 2

A new species of *Ladenbergia* (Rubiaceae: Cinchoneae) from Andean tepui in Northeastern Peru

Journal: to be submitted to Phytotaxa

Abstract. *Ladenbergia shawii* Chilquillo (Rubiaceae) is a new species from the Andean tepuis on the boundary of Loreto and San Martin departments in Peru. This new species is morphologically similar to *L. moritziana* and *L. pauciflora*, which are distributed in the Andean regions of Venezuela and Colombia respectively. *Ladenbergia shawii* can be distinguished from these by the inflorescence resembling an umbelliform cyme with a short peduncle and three sessile flowers; hypanthium puberulous outside; small and deeply lobed calyx; and hirsute style. *Ladenbergia shawii* is only known from the Cordillera Escalera, Loreto, Peru.

Keyword: Cahuapanas, cordillera of Andes, endemic, neotropics, taxonomy,

Introduction.

The Neotropical Rubiaceae genus *Ladenbergia* Klotzsch includes ca. 35 species (Andersson, 1997; Taylor & Gereau 2010) and belongs to the Tribe Cinchoneae (Andersson & Persson, 1991; Andersson 1995b; Andersson & Antonelli, 2005). Its species occur mostly in South America, with few reaching Central America (Andersson 1992, 1997, Lorence et al. 2012). *Ladenbergia* is centered in the northern and central Andes (Andersson 1995a, 1997), and 14 of its species are found in the Andes of Peru.

Plants of *Ladenbergia* are shrubs, small trees or large trees, and their distictive characters include well developed interpetiolar stipules that are held erect and flatly pressed tother in bud; terminal inflorescences; 5- or 6-merous corollas that are thick-textured, salverform, white, and have tubes distinctly longer than the lobes and densely puberulent outside but glabrous inside or shortly pubescent above the stamen

attachment; corolla lobes that are valvate in bud with the distal part ridge-shaped and papillose-puberulent; capsules that are septicidal with variously basipetal or acropetal dehiscence; and numerous flattened seeds with winged margins (Andersson, 1994, 1997).

Ladenbergia is similar to *Cinchona* L., and these were widely confused until Andersson (1995b) clarified their distinctions. These genera are similar vegetatively, in inflorescence form, and in fruit, but differ in their flowers: *Cinchona* has pale to deep pink or purple-red corollas that are densely pubescent in the throat, while *Ladenbergia* has white corollas that are glabrous or shortly puberulous in the throat.

The new species described here was discovered during botanical exploration by the Rapid Biological Inventories (RAPD) program of The Field Museum, which inventories the biota and evaluates the conservation significance of the selected high-priority sites suggested for preservation. The site where this new species was discovered, in the Cordillera Escalera (Pitman et al., 2014), is one of several areas recently explored by this project for the first time in northeastern Peru. The Cordillera Escalera represents an unusual formation of sedimentary rock that outcrops in an area composed mainly of volcanic rock. Very little is known biologically about these mountains because of their difficult accessibility.

The Cordillera Escalera is one of several relatively young flat-topped mountains composed of sedimentary rocks, and specifically of sandstone, that are located east of the main Eastern Cordillera of the Andes in Peru and southern Ecuador; several similar formations are found as as isolated sandstone mountains in western Amazonia in Colombia and Ecuador and as sandstone outcrops in the Cordillera Oriental of Colombia and Venezuela. These areas differ floristically from their surrounding regions, apparently due to their distinct substrate. They do have some of the floristic identity of their local region, but they also show marked floristic affinities with the tepui formations in the Guayana Highlands of eastern Venezuela and Guyana (Ulloa & Neill 2006, Neill et al. 2014). Based on this these scattered sandstone formations in the western Amazon basin have sometimes been grouped together into their own region, the "Andean tepuis" (Neill et al. 2014). One characteristic of the flora of these Andean tepuis is a notable level of endemism, presumably due to their distinct substrates and geographic isolation.

Methods

This study is based on standard taxonomic methods, and is part of a comprehensive revisionary study of *Ladenbergia*. Illustrations were drawn with the aid of detailed photographs that were taken with a Celestron 44314 FlipView Handheld LCD Microscope. Terminology of the leaf indumentum was adapted from Andersson (1998).

Taxonomic Treatment

Ladenbergia shawii Chilq., sp. nov.- TYPE: PERU. Loreto. Cordillera Escalera, Provincia Datem del Marañon. Distrito Cahuapanas, Field Museum Inventario Rapido Campamento Alto Cahuapanas. 76°50'20.4" W, 5°39'51.8" S, 1028 m.s.n.m., 29 Sep 2013, *M. Rios, T. Mori, D. Neill, L. Torres and C. Vriesendorp 3531* (holotype: F; isotypes: USM; AMAZ "n.v."; ECUAMZ "n.v.").

Ladenbergia fosteri is is distinguished from other *Ladenbergia* species by its umbelliform inflorescence with only three flowers, with these sessile or subsessile and covered by the bract, along with its deeply lobed calyx with the lobes acute and glabrous inside and its pilose style.

Shrubs, 5 m tall. Young branches glabrous or sparsely puberulous, with trichomes ferrugineous. Stipules shortly fused at the base, oblong in the basal portion with upper part acuminate, glabrous to puberulous, 1-1.2 cm x 0.45-0.5 cm; petioles 0.3-0.45 cm long, glabrous to sparsely puberulent; leaf blades plane, thick in texture when fresh, chartaceous when dry, 1.3-6.4 x 0.9-2.1 cm, narrowly elliptic to obovate (length/width 2.1-2.9), acute at base, acute to acuminate at apex, adaxial surface matte to subnitid and glabrous, abaxial surface glabrous, margins revolute, tuft domatia absent, secondary veins 5-7 pairs, weakly brochidodromous, slightly to strongly sulcate above, prominent beneath, tertiary venation just weak above, weakly evident below with opposite-percurrent arrangement. Inflorescence terminal, in a strongly congested umbelliform cyme, flowers 3, bracts 0.6-0.75 cm long, peduncle 0.4-0.45 cm long.

Flowers 6-merous, nocturnal, strongly fragant, sessile to subsessile with pedicels 0.5-1.5 mm long; bracteoles 0.18-0.21 cm long; hypanthium obconical, pilosulose to tomentulose, 3-3.5 x 2.7-3 mm, calyx limb 4-4.5 mm long, deeply lobed, lobes acute to obtuse, 3.9-4.3 mm long, glabrous to sparsely puberulous outside, glabrous inside, colleters not seen; corolla salverform, fleshy, white or flushed with pink on the tube base, tube 16-18 mm long, hirtellous outside, inside villous in upper half and glabrous in lower half, lobes 10-13 mm long, ridged part glabrous to puberulous, central part hirtellous; filaments 0.8-1.2 mm long and attached ca. 10-12 mm above base of corolla tube (ca. 70 % of tube length), anthers 3-3.5 mm; style ca. 16 mm long, rather sparsely hirsute in lower half, glabrous or puberulous in upper half, stigmatic lobes ca. 3.2 mm long. Capsules woody, oblong-cylindrical, externally puberulous, 25-28 x 4.5-5.5 mm, endocarp 0.5-0.6 mm thick. Seeds oblong-fusiform, 11-13 x 4-5 mm, with wings marginally fimbriate.

Distribution and Habitat- *Ladenbergia shawii* is only know from the type collection, from southwestern Loreto in northeastern Peru (Figure. 1). This species is known from a group of small mountains of the Cushabatay formation. These mountains are locally called "Cahuapanas", and situated along the northern margin of the Alto Mayo Valley, between the departments of San Martin and Loreto (Stallard and Lindell 2014). These mountains are lacks traces of human activities and its range at their highest to 1000--1500 m. Their are vegetated with shrubland or low dense chaparral (Figure. 2), with the dominant woody plants 1.5-3 m tall on the plateau areas as and dominated by *Bonnetia paniculata* Spruce ex Benth. (Bonnetiaceae), *Dacryodes uruts-kunchae* Daly, M. C. Martinez & D. A. Neill (Burseraceae), *Graffenrieda emarginata* (Ruiz & Pav.) Triana (Melastomataceae) and *Parkia nana* D. A. Neill (Fabaceae) (Neill et al. 2014).

Etymology- The species name is dedicated at Peruvian ethnic group Shawi, which inhabit the Escalera mountain range and along its history have played a crucial role in the management and conservation of the area where the specie was collected.

Phenology- Collected with flowers and fruits in September.

Conservation status-This species is only known for one specimen from one site in a large, poorly explored area. In consequence, it is not possible to determine its conservation status, and we here categorize it as Data Deficient (DD) according to the IUCN (2014) categories.

Ladenbergia shawii is unique in the genus in its combination of unusual characters: stipules that are shortly fused at the base, narrowly elliptic thick-textured leaf blades, terminal three-flowered inflorescences with short peduncles and sessile to subsessile flowers, well developed the bracts, corolla tube that are villous inside in upper half, and sparsely hirsute styles.

Ladenbergia shawii is similar to *L. pauciflora* L. Andersson of premontane forests of the Colombian Andes, and to *L. moritziana* of montane forests of northern Venezuela, which share inflorescence arrangement and morphology of the leaf. However, these last two species can both be separated of *L. shawii* by characters of the inflorescences, flowers and leaves, as outlined in Table 1).

Table 1. Morphological differences between *Ladenbergia shawii*, *Ladenbergia pauciflora* and *Ladenbergia moritziana*.

	L. shawii	*L. pauciflora*	*L. moritziana*
Inflorescence	Congested	Congested	Lax
Number of flowers/inflorescence	3	7-12	12-20
Flower position	Sessile to Subsessile	Sessile to Subsessile	With developed pedicels
Inflorescence bracts	Present	Present	Absent
Corolla tube length	16-18 mm	55-60 mm	25-35 mm
Style pubescence	Hirtellous	Hirtellous	Glabrous
Fruit length	25-28 mm	60-80 mm	30-40 mm
Geographical distribution	Andean Peru	Andean Colombia	Cordillera de la Costa in Venezuela
Leaf shape	Elliptic	Ovate to Rounded	Elliptic

Leaf size	1-1.2 x 0.45-0.5 cm	8.5-19 x 4.9-8.8 cm	6-17 x 2.5-11cm
Leaf Indumentum	abaxial surface glabrous	abaxial surface hirtellous	abaxial surface glabrous

Key to Distinguish *Ladenbergia shawii* from *L. pauciflora* and *L. moritziana*

1. Inflorescence lax, dichasial, without bracts; style glabrous……***L. moritziana***

1. Inflorescence congested, umbelliform, with bracts; style hirsute.

2. Inflorescence with 3 flowers; corollas with shorter tube, 16-18 mm long; fruits 25-28 mm long….***L. shawii***

2. Inflorescence with ca. 10 flowers; corollas with longer tubes, 50-60 mm long; fruits 60-80 mm long….***L. pauciflora***

Acknowledgments. We thank the Missouri Botanical Garden, Programa Nacional de Becas y Creditos Educativos del Peru (PRONABEC), and Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil (CNPq) for financial assistance. We thank the curators of F, G, GB, MO, MOL, NY, and USM for access to specimens. Thanks also go to John Pruski, Christine Niezgoda, Nancy Hensold, Robin Foster and David Neill for collaboration and motivation for my research; to RAPD Team of The Field Museum for access to collections, photos, and information respect at habitat; to Klei Souza for the excellent illustration and to Rosemeri Morokawa, Suzana Costa, Gustavo Shimizu, Nállarett Dávila and Elluz Huáman for the help with the revision of the articl

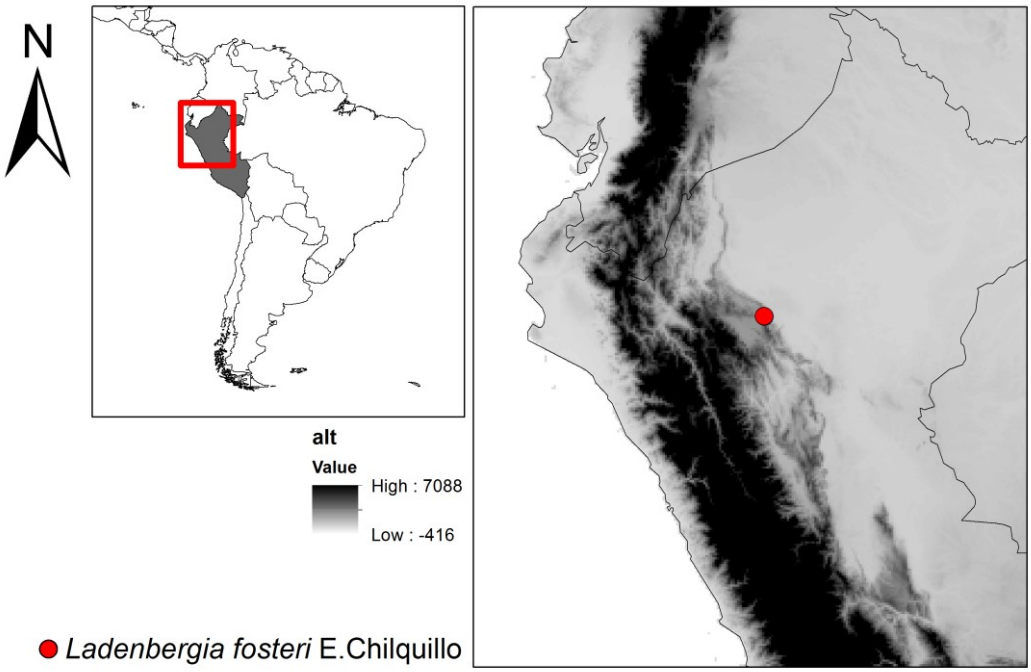

Fig 1. Upper Left: Peru and South America. Map enlarged of eastern slopes of Andes in Peru where *Ladenbergia shawii* Chilq. occur.

Fig 2. Natural habitat of *Ladenbergia shawii* Chilq. (Photos: RAPDs Team Field Museum Chicago).

Fig 3. Line drawing of *Ladenbergia shawii* Chilq. A. Flowering branch. B. Detail of the inflorescence peduncle. C. Dorsal view of the bracteole. D. Ventral view of the bracteole. E. Flower. F. Detail of the inside the flower. G. Style. H. Fruit. I. Seed.

Fig 4. Inflorescence of *Ladenbergia shawii* Chilq., frontal view (Photos: RAPDs Team Field Museum Chicago).

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CAPÍTULO 3

Updated Taxonomy of *Ladenbergia* Klotszch (Rubiaceae, Cinchoneae) in the Tropical Andes

Journal to be submitted to Annals of the Missouri Botanical Garden

ABSTRACT

Ladenbergia Klotszch is a Neotropical genus distributed from Costa Rica to Bolivia; most of the species are centered in the tropical Andes. This genus presents a large morphological variability at species level. We provide an updated taxonomic treatment for species of *Ladenbergia* distributed in the tropical Andes. This study was based on herbarium material and fieldwork collections. As a result a total of 18 species are recognized for the tropical Andes. We provide a taxonomic history of the genus and discussion about the delimitation of species, taxonomic description, illustrations, identification key, ecological details, and maps of distribution for Andean species. Also two species were synonymized (*L. ferruginea* and *L. franciscana*) and lectotypifications are made for seven species.

Key words: South America, synonymy, lectotype, distribution, dubious species.

INTRODUCTION

Ladenbergia Klotszch is a Neotropical genus of Rubiaceae (tribe Cinchoneae). It is distinguished by cymose terminal inflorescences, salverform white corollas with five to seven valvate lobes and septicidal capsular fruits bearing numerous flattened seeds (Taylor & Gereau, 2010). The genus occurs in wet forests at low and high elevations from southern Central America to southeastern Brazil (Andersson, 1997).

Species of *Ladenbergia* were early treated under *Cinchona* L. because of their morphological similarity (Ruiz et al. 1801, Lambert 1821, De Candolle 1830, Lindley 1838). However the genus as such was described by Klotzsch (1846), who recognized 25 species within of *Ladenbergia* divided in two sections: 1) *Buena* (Pohl) Klotzsch, with four species and 2) *Cascarilla* (Endl.) Klotzsch, with twenty-one species.

Subsequently, Weddell (1848; 1849) not accept completely the creation of the *Ladenbergia* proposed by Klotzsch, due to an inconsistency with a nomenclatural rule of the Laws Code, so decided to consider *Cascarilla* (Endl.) Wedd. as a name for the genus and not *Buena* Pohl because it could cause confusion with the genus *Cosmibuena* Ruiz & Pav. In the other hand, he circumscribes *Ladenbergia* (Klotzsch) Wedd. to comprise only one definitely included species (*Ladenbergia dichotoma* Wedd.) and two tentatively included ones (*Ladenbergia moritziana* Klotzsch and *Ladenbergia schomburgkii* Wedd.).

In the circumscription of Weddell (1849), he accepted 21 species in *Ladenbergia* divided in four sections based in morphological characters: *Pseudoquina* Wedd., with free stipule at base, multiflore panicle, corolla submembranaceous with lobes margins lacinate and papillose; *Carua* Wedd., with free stipules or fused at base, multi or pauciflora panicle, corolla more or less coriaceous, corolla lobes completely papillose; *Calyptria* Wedd. with pauciflora panicle and stipules completely fused; and *Muzonia* Wedd. with flower clustering in elongate panicle and subcapitate and free stipules or fused at base.

Finally Weddell (1869) moves all species of *Cascarilla* to *Buena* noting that this genus cannot be confused with *Cosmibuena* because they have a different floral morphology. He maintains two sections of the early proposal (Weddell 1849): *Calyptria* Wedd. and *Muzonia* Wedd. and proposes two new sections: *Cascarilla* (Endl.) Wedd. (includes *Pseudoquina* Wedd.) and *Eubuena* Wedd. (includes sections as *Buena* Klotzsch and *Carua* Wedd).

Standley (1921) does not accept the proposals of Weddell and recognized a creation of *Ladenbergia* under the circumscription made by Klotzsch (1846), possibly because this is not clear according to the nomenclature code, which indicates, what a typification of a genus cannot be recognized by means of exclusion of species. At the same time, a series of local floristic treatments was written including *Ladenbergia*.

Standley (1930) in the Rubiaceae of Colombia recognized nine species of *Ladenbergia*. Standley (1931a) in the Rubiaceae of Bolivia recognized three species of which *Ladenbergia sericea* Standl. were described as new. Standley (1931b) in the Rubiaceae of Venezuela recognized seven species of which *Ladenbergia lucens* Standl. were described as new. Standley (1936) in the Rubiaceae of Peru recognized fifteen species. Steyermark (1974) in the Flora of Venezuela recognized eight species. Dwyer (1980) in the Flora of Panama recognized three species of which *Ladenbergia laurifolia* Dwyer were described as new. Burger & Taylor (1993) in the Flora of Costa Rica recognized three species. Andersson (1994) in the Flora of Ecuador recognized 09 species of which *Ladenbergia rubiginosa* L. Andersson were described as new. Steyermark (2004) in the Flora of the Venezuelan Guayana recognized three species and one possible new species, which were not formally described by lack of fertile material.

The only treatment for the entire genus was made by Andersson (1997), who consider 34 species and described seven new species for the genus: *L. dwyeri*, *L. nubigena* (Panama); *L. klugii* (Peru); *L. lehmanniana*, *L. magdalenae*, *L. obovata* and *L. pauciflora* (Colombia). It mentioned here that several more species are represented in herbaria, but that the material is incomplete for a formal description.

New collections of *Ladenbergia* and allied genera from the last two decades, after Andersson (1997) synopsis, particularly those made by the Missouri Botanical Garden projects and the Field Museum of Chicago Inventories allowed further understanding of some poorly known species, at the same time revealed many taxonomic problems in other *Ladenbergia*'s species.

The present taxonomic treatment aims to clarify nomenclatural and taxonomic problems, and delimit at species of *Ladenbergia* Klotszch occurs in the tropical Andes.

MATERIAL AND METHOD

This treatment is mainly based on the analyses of herbarium collections and some fieldwork exploration. The study was concentrated on material from the Andes, all available material from the following herbaria (those personally visited are indicated with an asterisk): CR*, F*, G, HOXA*, INB*, MO*, MOL*, NY*, R*, RB*, UB, UEC*, USJ*, USM*, CEN, COL (photos only), K (photos only), MA (photos only), P (photos only), QCA (photos only), QCNE (photos only), US (photos only) was studied. We analyzed about 1500 herbarium specimens, which correspond to ca. 1200 collections. Some nomenclatural types were revised through the JSTOR Plant initiative (http://plants.jstor.org/) and species names were revised on TROPICOS Database (http://tropicos.org/Home.aspx).

Information about habit, phenology and ecological preferences derive mostly from voucher labels, but also come from direct field observations. Vegetative and reproductive characters were studied on dry material using dissecting microscope at magnifications up to 30 X. Flowers and seeds were boiled in water before detailed study. Measurements of vegetative parts were taken with an ordinary office ruler; with an accuracy of 1 mm. Measurements seeds were taken with aid of ocular micrometer, with an accuracy of 0.1 mm. All measurements presented in descriptions are based on mature material.

Descriptions of vegetative and reproductive structures are given mainly with terminology proposed by Stearn (1983). Leaf shapes are described according to the Systematic Association chart of simple symmetrical plane shapes (as reproduced by Stearn, 1983). Terminology for leaf texture and indumentum follow Anderson (1998). Terminology of the inflorescence forms follows Taylor (2014) with reference to Andersson (1995).

We provide a taxonomic delimitation of *Ladenbergia*'s species occurring in the tropical Andes. Geographical delimitation of the tropical Andes were considered according to Andersson (1995). Distribution maps were elaborated using QGIS v.2.12.2 (QGIS Development Team, 2009) with geographical information from herbarium collections.

GENERAL MORPHOLOGY OF *LADENBERGIA*

Habit. Species of *Ladenbergia* are shrubs, or more commonly trees up to 30 m tall and 20 cm in diameter at breast height (dbh). The largest dimensions are recorded for *L. oblongifolia*, *L. riveroana*, *L. macrocarpa* and *L. amazonensis*.

Ladenbergia cujabensis, *L. fosteri*, *L. crassifolia* and *L. lambertiana* are shrubs and some of these species are known from very few collections. *Ladenbergia epiphytica* and *Ladenbergia pauciflora* are occasionally described as epiphytic shrub, however new collections show that these species are trees (Devia 1132, Tyson et al 4425, Gentry et al 55286).

Stipules. The stipules are interpetiolar, entire, obtusely triangular to tongue-shaped, with colleters inside. They are membranaceous or coriaceous in texture and held flat, back-to-back in bud (Fig 1A, 1B). Three shapes of stipules can be distinguished: ovate to elliptic, roundish and oblong (Fig 1C, 1D, 1E). According to the degree of fusion can be distinguish four types: fused only at base, fused at 1/2 forming a sheath, fused at ¾ of its length and fused throughtout (Fig 1F, 1G, 1H). The stipular margin is revolute or plane. The variation in texture, shape and fusion of stipules seems to be taxonomically important.

Leaves. The leaves of *Ladenbergia*, like those of most Rubiaceae, are decussate, stipulate, subsessile to petiolate and entire-margined. Some species have both arrangements, opposite and ternate (*L. macrocarpa*, *L. crassifolia*). Also leaves of vegetative shoots seem to be usually larger than those of flowering shoots. The variation in size and form of leaf blade in *Ladenbergia* is wide between species (Fig 2). Generally the leaf blade are: elliptic, ovate, obovate, oblong, orbicular or roundish. The variation of the form the apex and the base of the leaves are characters taxonomic valuables.

Some species present domatia in the abaxial side of leaf blade. The presence of domatia is correlated with state of the growth the plant and it is more evident in younger individuals. Detailed studies are necessary to examine if these attributes have relevance within the genus taxonomic.

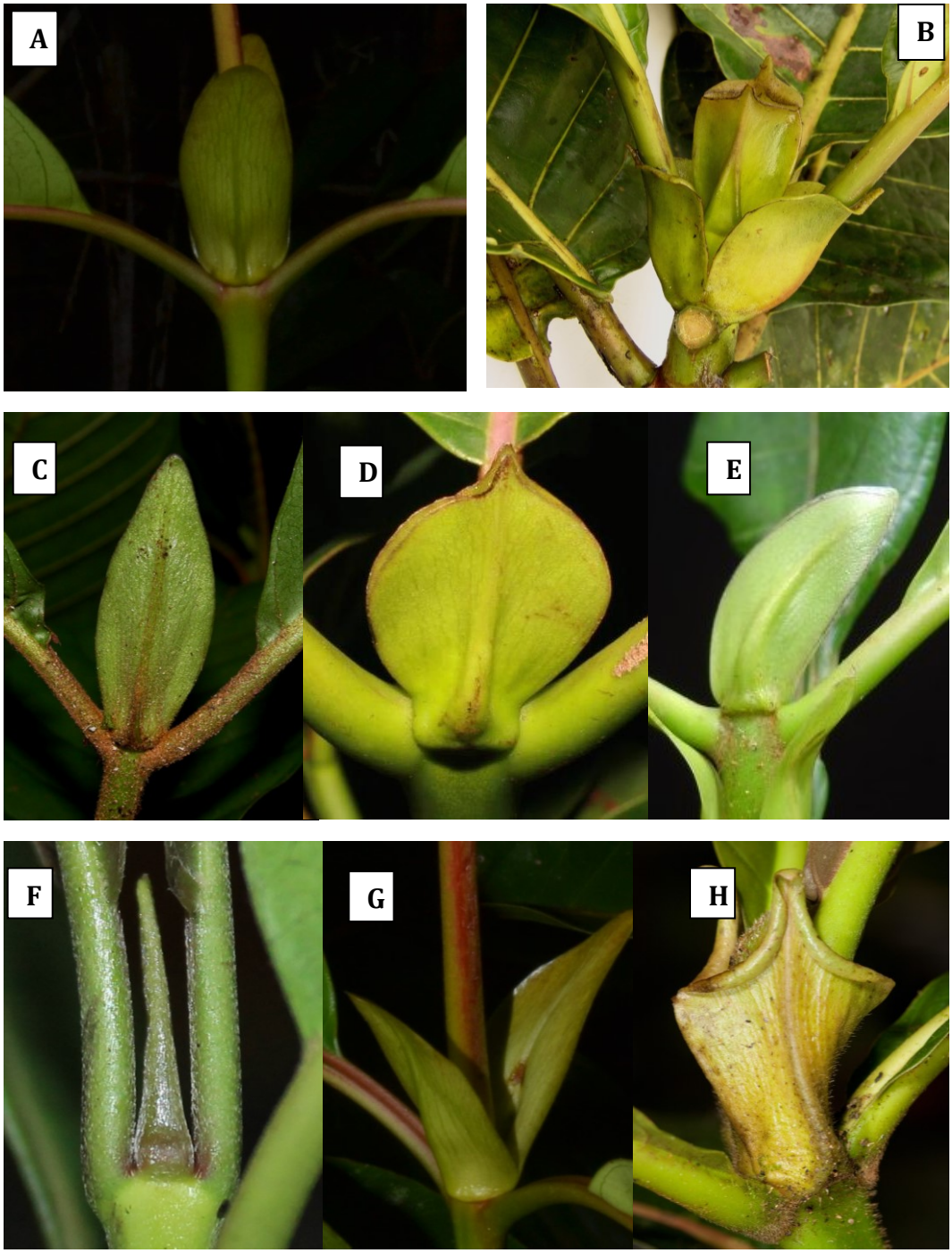

Fig 1. Texture of stipules in *Ladenbergia*. A. Membranaceous in *L. discolor*. B. Coriaceous in *L. epiphytica* (Photos: Robin Foster and Rolando Perez). Stipule Shape. C. Ovate to Elliptic in *L. klugii*. D. Roundish in *L. oblongifolia.* E. Oblong in *L. bullata* (Photos: Eder Chilquillo, Jhon Janovec and Alfredo Fuentes). Fusion and Stipular margin in *Ladenbergia*. A. Caliptrate in *L. crassifolia*. B. Fused only at base and plane margin in *L. discolor.* C. Fused at ½ forming a sheath and revolute margin in *L. heterophylla* (Photos: Eder Chilquillo, Robin Foster and Paola Pedraza).

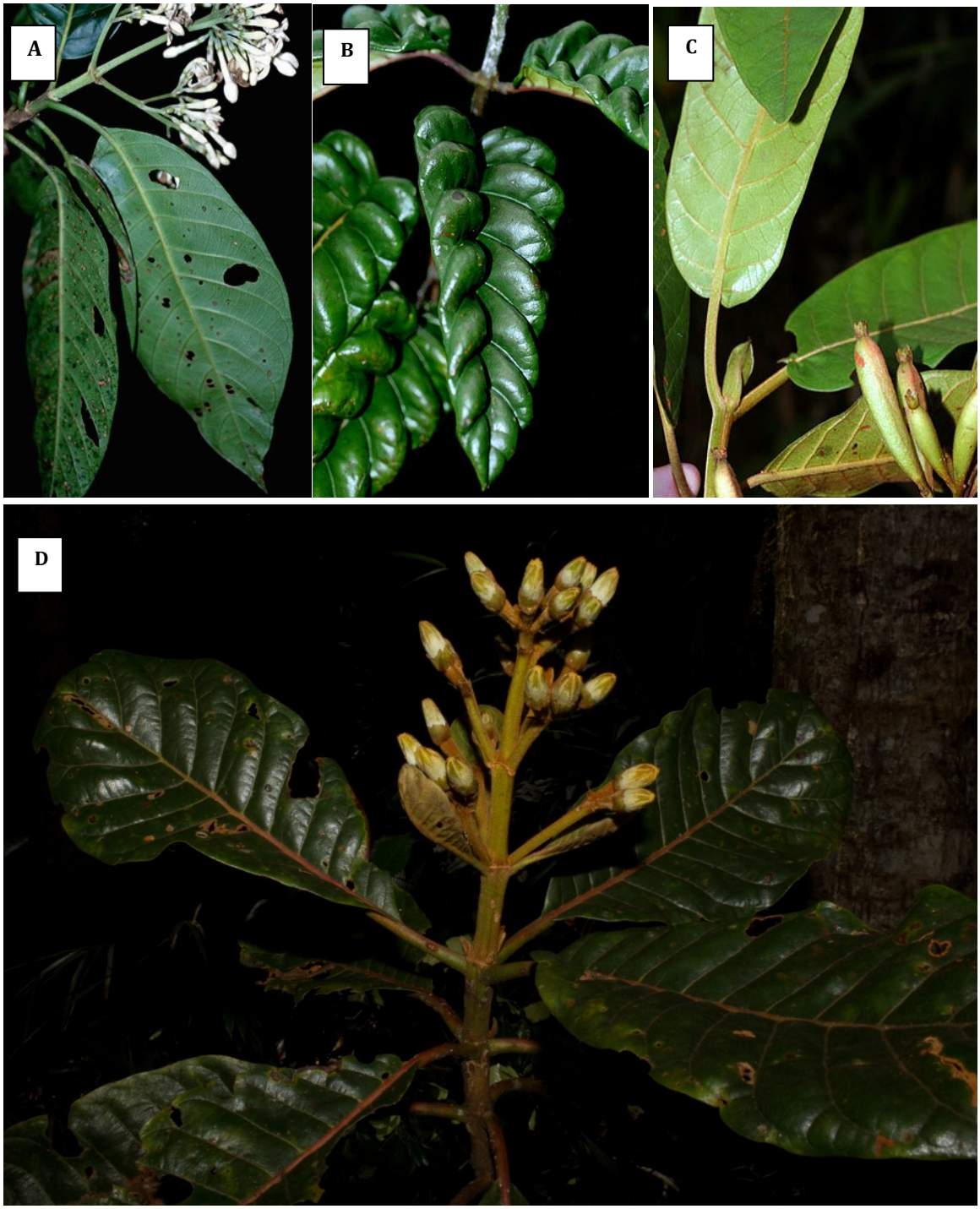

Fig 2. Leaf blades detail in *Ladenbergia*. A. Elliptic leaves and plane margin in *Ladenbergia stenocarpa*. B. O ovate leaves and bullate blade in *Ladenbergia bullata.* C. Oblong leaves and cordate at base in *Ladenbergia carua*. D. Ternate arrangements of the leaves in *Ladenbergia macrocarpa* (Photos: Robin Foster and Paola Pedraza).

Inflorescences. The inflorescence is terminal, cymose and determinate. They may be positioned at the end of axillary shoots and give the impression of being

axillary. The branches are predominantly dichasial (Fig 3).

The inflorescence varies greatly in size and number of lateral order (1-5 orders). The largest inflorescences are found in the Andean species *L. oblongifolia*, *L. riveroana, L. pittieri* and *L. stenocarpa*. The number of flowers per inflorescence varies between 3-45 (pauciflora) and 50-200 (multiflora). In *L. fosteri* and *L. pauciflora*, the inflorescence is few-flowered and highly congested, looking like subumbellate and usually covering by involucral bract.

We can establish three inflorescence forms in *Ladenbergia*: pyramidal (primary axes well developed and equal to or longer than other axes); corymbiform or radiate (primary axes not better development than secondary axes) and racemiform or spiciform (primary axes well developed and secondary axes very short).

The main axes of the inflorescence may be articulate or not and it is usually green. Some species may present ferrugineous indument (*L. carua, L. macrocarpa, L. crassifolia*).

The inflorescence may be short or long pedunculate. The length of the peduncle is very variable and it may reach the 3-5 cm (*L. fosteri* and *L. pauciflora*) to the 10-20 cm (*L. oblongifolia*, *L. heterophylla*, *L. pavonii*).

Flowers. The flowers are predominantly pentamerous (5-7 merous) and heterostylous. Nocturnal anthesis occurs and exhibits strong fragancy, like “azucena”. The texture of the corolla is membranaceous or fleshy, salver-shaped (Fig 4). Except for the part covered by the calyx, it is always +/- densely pubescent outer surface. All species are white colored. The tube is distinctly longer than lobes and mostly glabrous inside; sometimes it has a sparse indument, +/- wavy hairs. An indumentum usually appears only close to filament bases, but it may be continuous up to tube aperture. The diameter of the corolla tube can be slender or coarse. The lobes are valvate in bud, with a distal part ridge-shaped densely puberulent outside and densely papillose-tomentose inside the ridged part.

The stamens are inserted in the corolla tube, usually somewhere between one-

third and two-thirds of tube length. There may be a slight tendency to have the stamens inserted somewhat higher up in short-styled than in long-styled flowers. The anthers are elongated; dorsifixed near base, and the thecae open +/- introrsely by longitudinal slits.

The hypanthium (include ovary, tube calyx and calyx lobes) is persistent, glabrous, densely puberulous or villosulous outside. The ovary is consistently bilocular and each locule has many ovules. The size and indumentum inside of the calyx's tube are diagnostic characters in *Ladenbergia*. The depth of calyx lobes is difficult to use with this purpose because of large intraspecific variation.

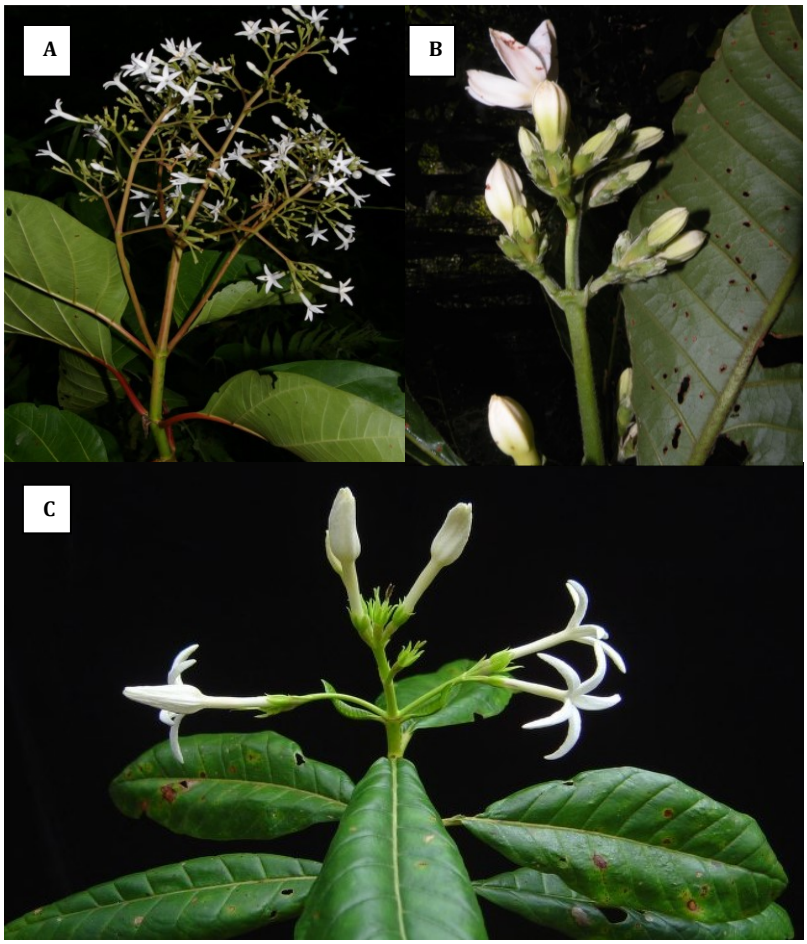

Fig 3. Inflorescence in *Ladenbergia*. A. Multiflora and pyramidal inflorescence in *L. oblongifolia.* B. Pauciflora and spicate inflorescence in *L. muzonensis*. C. Pauciflora Inflorescence with lateral axes dichasial in *L. bullata* (Photos: Rodolfo Vasquez, Robin Foster and Alfredo Fuentes).

Fig 4. Flowers in *Ladenbergia*. A. Corolle tube membranaceous and slender in *L. riveroana.* B. Corolle tube fleshy and coarse in *L. muzonensis*. (Photos: Missouri Botanical Garden and Robin Foster).

Colleters are present inside the calyx tube in some species (*L. macrocarpa*, *L. dwyeri*, *L. carua*). These are grouped in pairs located in the sinus or in small groups at base or distributed along all calyx tube.

The styles of longystylous flowers are slightly shorter than the corolla tube and they are just below the tube aperture. In brevystylous flowers, style length is roughly half of long-styled ones. Styles can be glabrous or hirsute.

Fruit. The fruit is a septicidal capsule, usually ovoid to ellipsoid, and it is generally between 2 to 10 cm long. The dehiscence is usually basipetal but in some species it is acropetal (*L. cujabensis* and *L. muzonensis*). *Ladenbergia discolor* and *L.. acutifolia* are characterized by very short capsules and species as *L. heterophylla* are characterized by very long ones. *Ladenbergia bullata*, *L. moritziana*, *L. undata*, *L. macrocarpa* are characterized by having a thick, +/- woody endocarp.

Seed. The seed are lenticular with a central hilum on flattened side and with an elongate exotesta wing. They are generally larger than species of related genera, mainly 10-20 cm long, including wing.

DISTRIBUTION AND ECOLOGY

Ladenbergia is distributed from Central America to Bolivia. Its distribution is essentially Andean with a half the species occur here and the others occur in the Amazon, Cerrado, Atlantic Forest, Magdalena and Choco region (Fig 5).

In the tropical Andes, the species of *Ladenbergia* show three areas of endemism (Andersson, 1997): five species are endemic to the northern Andes (*L. lehmanniana*, *L. undata*, *L. moritziana*, *L. pittieri*, L. obovate and *L. buntingii*); three species are endemic the northern central Andes (L. *crassifolia*, *L. franciscana* and *L. stenocarpa*), and only *L. oblongifolia* is widespread throughout the tropical Andes. Two species are common in the northern and central Andes (*L. macrocarpa* and *L. pavonii*). Of those, *L. pavonii* occurs mainly in the northern Andes, whereas *L. macrocarpa* is widespread in both areas. *L. heterophylla*, *L. epiphytica* and *L. dwyeri* are common to the northern and central Andes, and southern Central America. Four species are endemic the south central Andes (*L. acutifolia*, *L. discolor*, *L. muzonensis* and *L. fosteri*). One species, *L. riveroana,* is common to the north and south central Andes and two species are endemic to the southern tropical Andes (*L. bullata* and *L. carua*). One species, *L. klugii,* is distributed the north central Andes to the southern tropical Andes.

Most species of *Ladenbergia* ocurrs mainly in the pre-montane zone but some few species are reported in the montane zone (*L. macrocarpa*, *L. crassifolia* and *L. bullata*). One species, *L. pittieri,* occurs between 1200 -1500 m altitudes in the Andes and Guiana Highlands.

Some species of the genus seems to be adapted to areas in higher elevations with sandy soils in the younger Andes (*L. crassifolia*, *L. riveroana*, *L. stenocarpa*, *L. discolor*). The reasons why these species have restricted ranges are poorly understood. The majority of *Ladenbergia*'s species occurs in secondary forests. In our field experience with *Ladenbergia*, we have seen some species occupying these areas: *L. oblongifolia*, *L. heterophylla, L. riveroana, L. carua*, *L. klugii* and *L. crassifolia*.

Fig 5. Distributions of *Ladenbergia* species. White circles represent point of occurrence of the species.

SYSTEMATIC TREATMENT

Ladenbergia Klotzsch

Getr. Darst. Gew. 14: ad tab. 15 (1846).- Type: *Ladenbergia undata* Klotzsch in Hayne; Moritz 963, Venezuela, Mérida, vecinity of Mérida (B Holotype, destroyed (Fragment type in F - 0069664); K ex herb. Bentham (lectotype designated in Andersson, 1997); BM, BR, G, HBG, K ex herb. Hooker isotypes; NY probable isotype without number, S posible isotype ascribed to "Dr. Sonder").

Cinchona [sect.] *Cascarilla* Endl., Gen. 556 (1838).- *Cascarilla* (Endl.) Wedd., Ann. Sci. Nat., Sér. 3, 10: 10 (1848).- Type: *Cinchona macrocarpa* Vahl = *Ladenbergia macrocarpa* (Vahl) Klotzsch in Hayne; Ortega s.n.; Colombia, "in regno Santa Fé", 1785 (BM lectotype designated in Andersson, 1994; cf. also under *L. macrocarpa* below).

Cascarilla [sect.] *Pseudoquina* Wedd., Hist. Nat. Quinquinas 79 (1849). – Type: *Cascarilla magnifolia* [var.] vulgaris Wedd. = *Cinchona oblongifolia* Mutis= *Ladenbergia oblongifolia* (Mutis) L. Andersson; Mutis 2908; Colombia (MA lectotype designated in here; US isolectotype)

Cascarilla [sect.] *Carua* Wedd., op. Cit. 83. – Type: *Cascarilla carua* Wedd. = *Ladenbergia carua* (Wedd.) Standley: Weddell s.n.; Perú, Puno, " Vallée de Tambopata, Prov. de Carabaya" (P lectotype designated in Andersson, 1994).

Cascarilla [sect.] *Calyptria* Wedd., op. Cit. 89. – Tipo: *Cascarilla macrocarpa* (Vahl) Weddell = *Cinchona macrocarpa* Vahl = *Ladenbergia macrocarpa* (Vahl) Klotzch; Ortega s.n.; Colombia, " in regno Santa Fé" (BM lectotype designated in Andersson, 1994).

Cascarilla (sect.) *Muzonia* Wedd., op. Cit. 90. – *Muzonia* (Wedd.) N. Osorio, Estudio Quinas Est. Unid. Colombia, ed. 2. 24 (1874). – Type: *Cascarilla muzonensis* (Goudot) Standley; Goudot s.n.; Colombia, Santander, Muzo (P lectotype designated in Andersson, 1994).

Etymology: *Ladenbergia* was named in honor of this Excellency Phillipp von Ladenberg (1769-1847). Prussian civil servant and "geheime Staatsminister"

Trees or rarely shrubs. Leaves decussate, occasionally ternate, stipules interpetiolar, usually large, caducous, fused shortly in the base or across petiole to form a basal sheath, or sometimes fused throughout to form a calyptra, free part, when presented, triangular to lingulate or obovate, held flat back to back in bud. Inflorescence terminal, subumbellate, cymose or in axes dichasial. Flowers fragant, heterostylous, normally 5-7 merous; hypanthium obtuse, calyx lymb campanulate to tubular, with or whitout distinct lobes; corolla thick-textured, salver-shaped, white generally or with pink corolla tube, tube distinctly longer than lobes, densely puberulent outside, densely papillose-tomentose inside on ridged part, stamens attached to corolla tube ¼-4/5 above base (usually somewhat higher in brevistylous than in longistylous flowers), filaments shorter than anthers, glabrous, anthers linear, dorsifixed near base, semi-exserted in brevistylous flowers, included in longistylous ones. Capsules septicidal with basipetal or acropetal dehiscence, crowned by the persistent calyx, valves not split at apex. Seeds irregularly elliptic to narrowly oblong in outline (wing included), wing margin nearly entire to dentate or fimbriate, often deeply cleft in basiscopic end, hilum located centrally on the seed body.

Ladenbergia comprises 34 species in this treatment (31 species well defined and 03 dubious species), that occurrs in southern Central America and South America. In the tropical Andes are recognized 18 species. These species differ with those proposed in the circumscription made by Andersson (1997) due to a nomenclatural changes such as: synonym, re-establishment and descriotion of the new species (Appendix I).

IDENTIFICATION KEY TO SPECIES OF *LADENBERGIA* KLOTZSCH

1. Inflorescence unbranched, umbel or subumbel with peduncles up to 0.5 cm and involucral bracts
   2. Corolla tube >50 mm, 6-10 flowers per inflorescence, leaf blades roundish…….. ***L. pauciflora***

2’. Corolla tube < 50 mm, 3 flowers per inflorescence, leaf blades elliptic ……..***L. fosteri***

1’. Inflorescence branched with lateral dichasial axes with peduncles longer than 0.5 cm without involucral bracts

3. Stipules fused throughtout, “caliptrate”

4. Leaf blade suborbiculate to roundish with abaxial side pubescent throughout, corolla tube 32-45mm long ……..***L. macrocarpa***

4. Leaf blade elliptic to ovate with abaxial side glabrous or puberulous only in midrib, corolla tube 15-25 mm long…….***L. crassifolia***

3’. Stipules fused in the base or forming sheath, never caliptrate

5. Fruit with acropetal dehiscence

6. Leaf blades elliptic or obovate, stipules with revolute margin, flowers fleshy, 25-45 mm long…..***L. muzonensis***

6’. Leaf blades ovate or rounded, stipules with plane margin, flowers membranaceous, 15-25 mm long....***L. cujabensis***

5’. Fruit with basipetal dehiscence

7. Corolla tube > 30 mm, fruit > 60 mm width

8. Calyx tube with lobes > 10 mm……..***L. buntingii***

8’. Calyx tube with lobes < 10 mm

8. Inflorescence lax, 2-4 lateral order, multiflore……..***L. pavonii***

8’. Inflorescence congested, 1-2 lateral order, pauciflora……***L. heterophylla***

7’. Corolle tube < 30 mm, fruit < 60 mm width

9. Calyx tube with lobes > 10 mm long……..***L. rubiginosa***

9’. Calyx tube with lobes < 10 mm long

10. Surface of the leaf blade bullate

11. Leaf blades elliptic, glabrous, acuminate in the base and in the apex…….. ***L. bullata***

11’. Leaf blades rounded, puberulous, cordate in the base and obtuse in the apex……..***L. undata***

10’. Surface of the leaf blade plane

12. Inflorescence pauciflore with lateral branches up to order 1-2.

13. Endocarp thick (≥ 0.6 mm thick)

14. Leaf blades oblong with patent hirsute indumentum in all over surface……***L. carua***

14’. Leaf blades elliptic glabrous or puberulous in the midvein ……***L. mortiziana***

13’. Endocarp membranaceous (≤ 0.4 mm thick)

15. Texture of the leaf blades coriaceous when dry, fruit with thick endocarp …..***L. nubigena***

15’. Texture of the leaf blades membranceous or chartaceous when dry, fruit with thin endocarp

16. Flower pedicellate (5-12mm), fruit 35-60 mm long…….***L. lehmanniana***

16’. Flower subsessile or pedicellate (3-4 mm), fruit ≤ 30 mm…….***L. discolor***

12’. Inflorescence multiflore with branches lateral up to order 2-4.

17. Inflorescence with superior axes contracted

18. Lateral axes dichasial, sessile or subsessile flowers

19. Calyx tube truncate, fruit fleshy……***L. hexandra***

19’. Calyx tube irregularly dentate, fruit membranaceous

20. Indument on underside of leaf blades ferrogineus, calyx lobes reptade, tube / lobe radio (1:1).....***L. klugii***

20. Indument on underside of leaf blades brown-golden, calyx lobes acute, tube / lobe radio (2:1).....***L. riveroana***

18’. Lateral axes corymbiform, pedicellate flowers

20. Flowers up to 35 mm length with calyx lobes at ½ calyx lymb

21. Fruit the form pyriform and coarse, leaf blade rounded…….***L. amazonensis***

21’. Fruit the form linear and slender, leaf blade elliptic to ovate……..***L. lambertiana***

20’. Larger Flowers (≥ 35 mm length) with calyx deeply lobed

22. Basal diameter of the corolla tube 3-4 mm; occurs in SE of Brazil, Pará……***L. paraensis***

22’. Basal diameter of the corolla ca 2 mm; Western South America/ Colombia, Ecuador, Peru, Bolivia and Brasil.

23. Flowers sessile and subsessile, Amazon basin……***L. graciliflora***

23’. Flowers pedicellate, Andes and Guiana Shield……***L. pittieri***

17’. Inflorescence with superior axes not contracted

24. Leaf blades oblong to roundish, stipules roundish and forming sheath

25. Corolla tube ≥ 25 mm length, fruit with thick endocarp; Central America…***L. brenesii***

25’. Corolle tube ≤ 25 mm length, fruit with thin endocarp; South America

26. Corolla tube 13-15 mm long with outside hirtellous……***L. magdalenae***

26’. Corolla tube 7-14 mm long with outside glabrous or puberulous……***L. oblongifolia***

24’. Leaf blades elliptic, acuminate or slightly ovate, stipules ovate and fused basally only

27’. Leaf blades lanceolate to oblong with base cuneate, fruit pyriform of 15-55 mm length …….***L. acutifólia***

27. Leaf blades elliptic, with base acute, fruit slender and narrowly 30-80 mm lenght

28’. Venation terciary of the leaf blades evident, fruit slender narrollwly, distribution in the northern of the Andes.....***L. stenocarpa***

28’. Venation terciary of the leaf blades obscure, fruit cilindrical to pyriform, distribution in the central America.....***L. laurifolia***

1. *Ladenbergia acutifolia* (Ruiz & Pav.) Klotzsch. Getr. Darst. Gew. 14: ad tab. 15 (1846). *Cinchona acutifolia* Ruiz & Pav., Fl. Peruv. 3: 1 (1802). *Cascarilla acutifolia* (Ruiz & Pav.) Wedd., Ann. Sci. Nat. Sér. 3., 10: 11 (1848). *Buena acutifolia* (Ruiz & Pav.) Wedd., Linn. Soc. 11: 186 (1869). Type: Ruiz & Pavón; Peru, Huánuco, Chicoplaya (MA image! lectotype designate here; B possible isotype, destroyed, photo F-136; BM image!, G ex herb. Ventenat image!).

Note nomenclatural: Ruiz & Pavon not appointed a holotype for the species. Andersson (1997) mentions that the holotype should be in MA herbarium, but he was unable to find the material so not make a formal lecotypification. There are two collections: one deposited in BM and another in G ex herb. Ventenat Herbarium that are labeled for Ruiz & Pavon, however the information is limited and it cannot establish whether the collections correspond to the type collection. With new information I find the collection in MA, which is labeled by Ruiz & Pavon, with locality collection information, collection date and iconography that matches with the protologue. Due to this reason the MA collection is chosen as lectotype of the species.

Shrub or small tree 5 (-10) m tall. Young branches glabrous to puberulous. Stipules fused at ¼ forming sheath, ovate to oblong in the basal portion with upper part acuminate, generally glabrous to puberulous, 0.8-1.2 x 0.3-0.45 cm long; petioles 1-3.5 cm long, glabrous to sparcely puberulent; leaf blades plane, +/- thick in texture, chartaceous when dry, 12-18 x 3.5-7 cm, ovate to lanceolate (length/width 2.5-3.3), cuneate to rounded at base, acute to acuminate at apex, midvein above deeply sulcate, secondary veins prominulous above and slightly sulcate, prominent beneath, 6-8 pairs with arrangement brochidodromous, tertiary venation obscure to slightly impressed above, slightly distinct below with pattern alternate percurrent, adaxial surface matte to nitid, glabrous, abaxial surface with midrib and veins sparsely puberulous, intervenous surface glabrous or minutely strigulose, margin plane, tuft domatia present. Inflorescence terminal, branched in one to three lateral order, multi-flowered (30-75 flowers), broadly triangular in outline, axes puberulous or slightly villosulous, not contracted, peduncles 4-6 cm, rachis 7-10 cm long composed by 2-3 nodes with axes articulated, dichasial, bracts lanceolate, acuminate, generally

deciduous. Flowers 5-merous, strongly fragant, nocturnal, distylous, sessile to subsessile or on short axes in dichasial congested groups of 3-6; hypanthium obconical, puberulous to villosulous, ca. 2-3.2 x 1.8-2 mm, calyx limb 1.8-2.5 mm long, lobes deeply generally acute to triangular, 1.2-2.1 mm long, glabrous to sparsely puberulous outside, glabrous inside, colleters evident in the sinus; corolla salverform, white, tube in brevistylous flowers 10-13.5 mm, in diameter 1.5-2.5 mm, tube in longistylous flowers 10-12.5 mm, in diameter 1.5-2.7 mm, lobes in brevistylous flowers 6-6.5 mm and in longistylous flowers 8.5-9.5 mm, filaments attached ca 4.5-5.5 mm above base of corolla tube (ca. 50 % of tube length) in longistylous flowers and ca 9 mm above base of corolla tube (ca. 65 % of tube length) in brevistylous flowers, anthers 4.5-5.5 x 1-1.5 mm; style glabrous, ca. 3.5-4.5 mm long in brevistyls flowers and 9.5-11.5 mm long in longistyls flowers, stigmatic lobes ca 2.5-3.1 mm. Capsules woody, narrowly ellipsoid to cylindrical, pyriform, externally glabrous to slightly puberulous, 15-55 x 4.5-6.5 mm, endocarp 0.2-0.3 mm thin. Seeds oblong-fusiform (17-30 x 1.8-3.5 mm long.) with wings marginally fimbriate.

Distribution, habitat and phenology. *Ladenbergia acutifolia* is found on eastern slopes of the Andes in northeaster and central of Peru and southern of Ecuador; it grows at altitudes between 750 and 1400 msnm in sandy rocky soils (Fig 6). This species is little collected because it occurs in areas of difficult access. It has been collected in flower and fruit in March-April and December.

Diagnostic Characters and Discussion. *Ladenbergia acutifolia* is characterizaded by its proportionally narrow (length/ width 2.5-3.3), lanceolate leaf blades wich are +/- narrowly cuneate at base and acute to acuminate at apex with tuft domatia in the abaxial side, a multiflora inflorescence with one to three lateral ordens, its small flowers with short calyx limb with narrowly triangular to acute lobes and small, pyriform capsules.

Three morphotypes are identificated within of *L. acutifolia*, the first restrict at Ecuatorian Andes and the second the Central Andes in Peru, both morphotypes are distinguished by form of the leaf blades (ovate-elliptic in Ecuadorian morphotype vs

narrowly lanceolate in the Peruavian morphotype), inflorescence patterns (multiflora in Ecuadorian morphotype vs pauciflora in the Peruvian morphotype).

Examined material.

Ecuador. Morona Santiago: Limon Indaza. Cordillera del Condor, 1130 m, 20 Dec 2005, Kajekai et al 257 (MO), Katan et al 312 (MO), Morales & Tupiza 1266 (MO), Wisum et al 321 (MO), Kajekai et al 346 (MO), Morales 1577 (MO), Neill et al 14809 (MO). Taisha, Cordillera de Cutucu, 1390 m, 14 Jul 1997, Kajekai & Wisum 1359 (MO), Neill et al 15656. Napo, Parque Nacional Sumaco Galera, 1590 m, 02 Apr 2008 (MO).

Peru. Huánuco: Prov. Leoncio Prado, distr. Rupa Rupa, Ynti, road to Río Rondos, 750 m, 24 mar 1972, Schunke 5310 (F, G, NY), San Martín: prov. Lamas, Distr. Lamas, trail from Lamas to San Antonio near Río Chipiseña, 23-30 Sep 1937, Belshaw 3464 (MO, NY); ca. 16 km NE of Tarapoto on road to Yurimaguas, 800 m, 22 Jul 1982, Gentry et al. 37910 (MO).

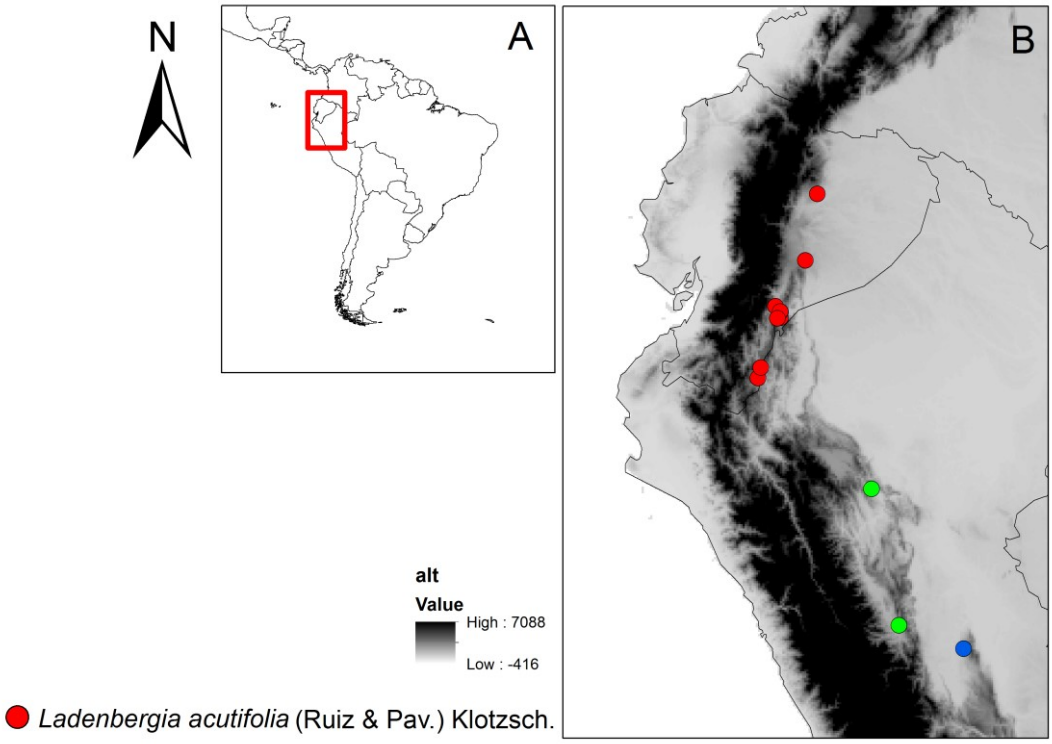

Fig 6. A. Northern of Peru, Ecuador, South America. B. Enlarged map showing the distribution the *L. acutifolia* K. Schum. Circles red, green and blue show morphotypes of *L. acutifolia* K. Schum.

2. *Ladenbergia bullata* (Wedd.) Standl. Trop. Woods 34. 41 (1933). *Cascarilla bullata* Wedd., Ann. Sci. Nat., Ser. 3, 10: 11 (1848).- *Buena bullata* (Wedd.) Wedd., J. Linn. Soc. 11: 187 (1869).-Type: Weddell 4358; Peru, Puno, prov. de Carabaya, 1846 (G, lectotype designated here; isolectotypes, possibly BR image!, possibly P image!).

Nomenclatural Note: The identification of the type locality was very minimal ("hab. In Peruvia") in the protologue. Weddell in his taxonomic treatment (1849) added information about the locality, “in sylvis provinciae Carabaya Peruvianorum ad altitudinem 2000-2500 metr., Junio et Julio fructiferam legi”. He further added that “apud incolas […] valium Tambopata et San Juan del Oro, ubi frequentius occurrit, Cargua-Cargua chica dicitur”. Andersson (1997) mentioned the locality is differently phrased on the three cited specimens, but all are annotated *Cascarilla bullata* in Weddell’s handwriting but it should be considered, that at the time of Weddell, the premise of having a single type did not exist. The three duplicates of the type specimens seen by Andersson were: one deposited in the G herbarium, which has a type locality, a collection number that matches the protologue, and a collection date in 1846 and is identified as belonging originally to the Delessert Herbarium; a second specimen deposited in BR, which has type locality, a collection number that matches the protologue, and a collection date in 1847; and a third specimen that comprises four sheets in P. Three of these sheets have the type locality but no number or date. The fourth sheet has a collection number and type locality that matches the protologue but no date. I here chose the specimen deposited at G as lectotype for *Cascarilla bullata*, because it has complete collection data and was considered by Standley (1936) to be authentic material that he used to determine the identity of this name.

Shrub or small tree 2 (-8) m tall. Young branches glabrous or sparsely puberulous. Stipules shortly fused at the base, oblong in the basal portion with upper part acuminate, glabrous to puberulous, 0.8-2.8 cm x 0.3-0.6 cm; petioles 1-2 cm long, glabrous to sparsely puberulent; leaf blades bullate, thick in texture, +/- chartaceous when dry, 15-25 x 3.3-6.4 cm, narrowly oblanceolate-oblong (length/width 3.8-4.5), acute at base, attenuate to acuminate at apex, secondary veins 8-13 pairs with

arrangement cladodromous, slightly to strongly sulcate above, prominent beneath, tertiary venation +/- obscure above, distinct below with an opposite-percurrent arrangement, adaxial surface matte to subnitid and glabrous, abaxial surface with midrib and veins glabrous or sparcely puberulous and intervenous surface glabrous or puberulent, margins revolute, tuft domatia present. Inflorescence terminal, branched in one to two orders, few-flowered (generally 9-25 flowers), broadly triangular in outline, axis hirsute with trichomes ferruginous, peduncle 1.5-1.8 cm long, rachis 1.5-2.5 cm long composed for 2-3 nodes with axes articulated and dichasial, bracts generally deciduous. Flowers 5-merous, strongly fragant, nocturnal, distylous, subsessile to separated on pedicels 6-8 mm long or axes in dichasial groups of 3-6; hypanthium obconical densely pilosulose to tomentulose, ca. 4.5-5 x 3 mm, calyx limb 6.2-7 mm long with lobes generally acute and irregular 4-5.5 mm long, glabrous to sparsely puberulous outside, glabrous inside, with colleters 0.7-1.3 mm long evident in sinuses between lobes; corolla salverform, fleshy, tube in brevistylous flowers 18-26 x 5-6 mm long in diameter, lobes 14-20 mm long, longistylous flowers not seen,; filaments in brevistylous flowers attached ca. 12-15 mm above base of corolla tube (i.e., ca. 45 % of tube length above base), anthers 4.7-6 x 1-1.5 mm; style glabrous to slightly puberulous, ca 5-8 mm long, stigmatic lobes ca 2-2.5 mm. Capsules woody, oblong- cylindrical, externally puberulous, 40-80 x 5.5-7.5 mm, endocarp 0.6-0.7 mm thick. Seeds oblong-fusiform, 12-15 x 3-3.75 mm, with wings marginally fimbriate (Fig 7 A-H).

Vernacular names: This species is called **"**cargua cargua" or **"**cargua-cargua chica" by people in southern Peru (Weddell, 1849). "unganangi" by tribes in Ecuador (Alban 2013).

Distribution, habitat and phenology. *Ladenbergia bullata* is found in montane wet forest in southern Peru, in Pasco departament, Cusco (probably) and Puno, and northern Bolivia in La Paz department (Figure 8). It has been collected between 1800 and 2400 msnm. This species was reported by Weddell (1849) to be frequent in the Tambopata valley, but though today is hardly reported. It has been collected in flower and fruit in April and September.

Diagnostic Characters and Discussion. *Ladenbergia bullata* is a shrub or small tree characterized by its glabrous stipules that are apparently interpetiolar but shortly fused at base; with bullate, narrowly oblanceolate leaf blades; few-flowered inflorescences with comparatively large flowers; fleshy large corollas; and its calyx with the inside glabrous and the lobes irregular and generally obtuse. Presumably the name refers to the bullate leaves. Standley (1936) in the Rubiaceae treatment for Peru distinguished *Ladenbergia bullata* from similar species, *L. crassifolia,* based on the bullate leaf blade (vs not bullate in *L. crassifolia*) with short-hispid indument on veins at abaxial blade (vs glabrous in *L. crassifolia*).

Andersson (1997) included *L. crassifolia* within the circumscription of *L. macrocarpa*, and distinguished *L. bullata* from *L. macrocarpa* by its stipules shortly fused at base (vs calyptrate in *L. macrocarpa*), its narrower leaf blades that are generally acuminate (vs. broader blades that are usually rounded to obtuse in *L. macrocarpa*), its calyx with colleters arranged in distinct groups (vs +/- evenly spread all around the calyx base in *L. macrocarpa*), and its glabrous style (vs nearly always hirsute in *L. macrocarpa*).

Andersson (1997) mentioned that the calyx lobes of *Ladenbergia bullata* are very short (for *Ladenbergia*). However with more material available now it is possible to notice that the calyx lobes sizes are unequall in the same flower and it is variable in length too.

These may be irregular on the same individual plant (*Fuentes et al 11693*; *Perea & Mateo 4347*). Similar calyx limb variation is found in several other related *Ladenbergia* species, for example *L. macrocarpa*, *L. discolor*, *L. klugii*, *L. riveroana*. Andersson (1997) also mentioned the presence of colleters arranged in distinct groups in *L. bullata*; more precisely, the colleters are arranged in pairs and located in the sinus between the calyx lobes.

Fig 7. *Ladenbergia bullata* (Wedd.) Standl. (A-H). A. Terminal shoot with inflorescence B. Stipule. C. Hypanthium. D. Inside Calyx Limb. E. Inside the corolla tube. F. Stile. G. Fruit. H. Seed. *Ladenbergia undata* Klotzsch (I-P). I. Habit. J. Stipule. K. Hypanthium. L. Inside Calyx Limb M. Inside the corolla tube. N. Stile. O Fruit. P. Seed.

Examined material.

Peru. Pasco: Oxapampa, Dist. Villa Rica, Camino de Bocaz al Abra San Lorenzo-PNYCH, 1850 m, May 2005, Ortiz et al 669 (MO); Camino de Bocaz al Purus, 1870 m, May 2010, Perea & Mateo 4347. **Puno:** Carabaya, Distr. Sandia, Between Yuncacoya and Ramospata, Raimondi 10068 (F, USM).

Bolivia. La Paz: Prov. La Paz, Cotapata, Estacion Biologica de Tunquini, 1710 m, 26 Sep 2001, Maldonado et al 159 (LPB, MO); 24 May 2003, Apaza 237 (LPB, MO); Prov. Franz Tamayo. Area natural de manejo integrado Madidi, Entre Pata y Santa Cruz, 10 Jul 2005, Fuentes et al 9704 (MO); Campamento Fuertecillo, 2090 m, 05 May 2007, Fuentes el al 11693 (MO); distr. Bautista Saavedra. Madidi, 23 Apr 2005, Fuentes et al 7222 (MO); 06 Nov 2003, Araujo et al 691 (MO).

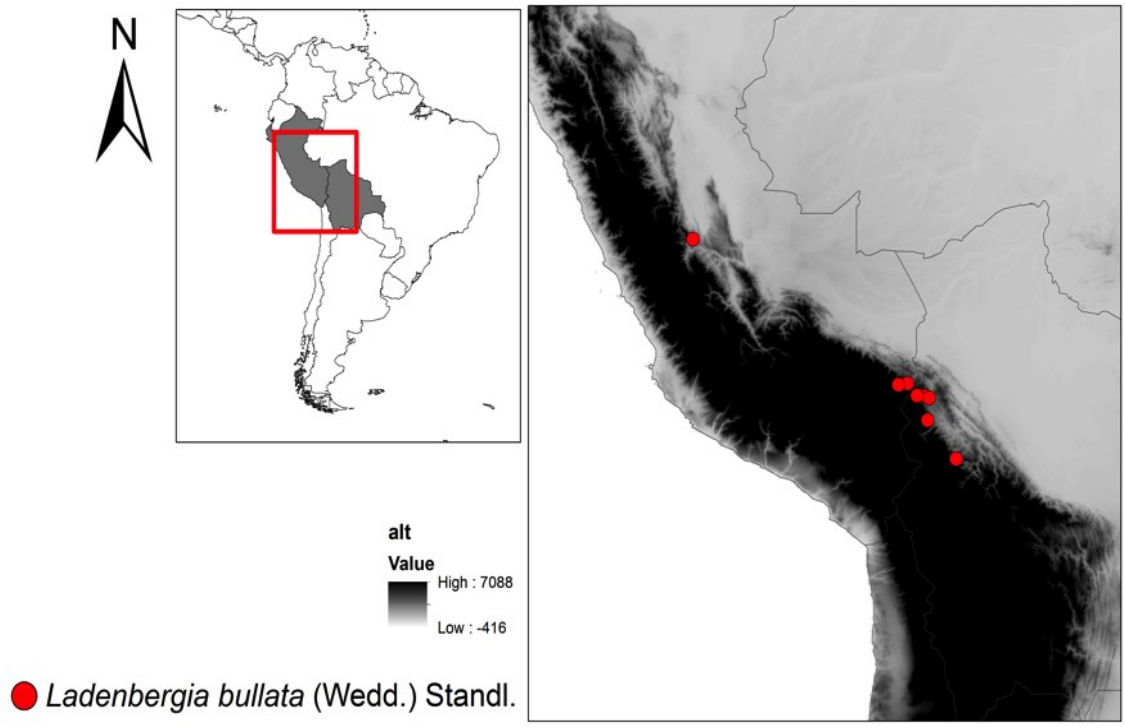

Fig 8. Distribution map the *L. bullata* (Wedd.) Standl.

3. *Ladenbergia carua* (Wedd.) Standl. Publ. Field Mus. Nat. Hist., Bot. Ser. 7: 274. 1931. *Cascarilla carua* Wedd., Ann. Sci. Nat., Bot. Ser. 3, 10: 12 (1848).- *Cinchona carua* (Wedd.) Miq., Ann. Mus. Bot. Lugduno-Batavi. 4: 275 (1868) -*Buena carua* (Wedd.) Wedd., J. Linn. Soc., Bot. 11: 187 (1869).-Type: Weddell s.n.; Peru, Vallée de

Tambopata, prov. de Carabaya. (P (N 01900414), lectotype designated here; isolectotype P (N 01900415)).

Nomenclatural Note: The information about the type locality is incomplete in the protologue ("hab. In Peruvia"). Weddell (1849) added information about the locality, “Hab. Peruvia et Bolivia”, and mentioned that the species was reported in “Prov. Cuzco et Carabaya” in Peru. Andersson (1997) mentioned two syntypes based in Weddell’s collections made in the Tambopata Valley, Prov. Carabaya, Peru, at herbarium P, but he did not choose a lectotype. I did not find any collection of this species from Cusco. The only collection made by Weddell in Peru are two syntypes mentioned by Andersson, so I choose the syntype with voucher P01900414 deposited in Herbarium P as the lectotype because it is the most complete and best preserved specimen.

Shrub to tree 2-25 m tall. Young branches puberulous or hirtellous, with bark ferrugineous. Stipules shortly fused at the base, oblong in the basal portion with upper part acuminate, hirtellous externally and internally, 2.5-4.5 cm x 0.45-0.6 cm, with colleteres arranged in one row on the base; petioles 2.7-3.5 cm long, hirtellous; leaf blades plane, thick in texture, chartaceous when dry, 30-40 x 18-21 cm, elliptic-oblanceolate to ovate-oblong (length/width 1.6-2.1), obtuse or cordate at base, attenuate to acuminate at apex, secondary veins 8-12 pairs with arrangement weak brochidodromous, slightly sulcate above, prominent beneath, tertiary venation +/- obscure above, distinct below with an alternate-percurrent arrangement, adaxial surface matte to subnitid and glabrous to puberulous, abaxial surface with midrib and veins hirtellous ferrugineous and intervenous surface puberulous to hirtellous, margins revolute, tuft domatia absent. Inflorescence terminal, branched in one to two orders, few-flowered (generally 9-39 flowers), broadly triangular in outline, axes densely hirtellous with trichomes ferruginous, peduncle 3-4.8 cm long, rachis 4-6.4 cm long with all axes articulated, higher order axes two pairs, contracted and dichasial, bracts ovate to lanceolate. Flowers 5-merous, strongly fragant, nocturnal, distylous, subsessile to separated on pedicels 2-3.5 mm long or on axes in dichasial groups; hypanthium obconical, densely hirtellous, 3.5-4 x 2.5-3 mm, calyx limb 3.5-4 mm long lobes generally obtuse and irregular 2-2.5 mm long, hirtellous outside, glabrous inside,

colleters not seen; corolla salverform, pilose externally and glabrous inside, white, tube in brevistylous flowers 22-26 mm, in diameter 2-2.5 mm, tube in longistylous flowers 21-23 mm, in diameter 2 mm, lobes in brevistylous flowers 10-12 mm long and in longistylous flowers 9-10 mm; filaments attached ca 20 mm above base of corolla tube (ca. 70 % of tube length) in brevistylous flowers and ca 15-16 mm above base of corolla tube (ca. 60 % of tube length) in longistylous flowers, anthers 5.2-6.2 x 1-1.5 mm; style glabrous, ca. 4.5-5.2 mm long in brevistylous flowers and 22-24 mm long in longistylous flowers, stigmatic lobes ca 4.2-4.5 mm. Capsules woody with dehiscence basipetal, oblong-cylindrical to subglobose-pyriform, externally hirtellous, with the wall ferrugineous, 31.5-60 x 8-12 mm, endocarp 0.6-0.7 mm thick. Seeds oblong-fusiform, 12.2-13.5 x 4.8-5.2 mm, with wings marginally fimbriate (Fig 9A-I).

Vernacular names: This species is called **"**cargua cargua" or **"**cargua-cargua grande" by people in southern Peru (Weddell, 1849). Information additional find in exsiccatea report names "mula morada" (Hodge 6161) or "oso oso" (Hodge 6009) in the South of Peru.

Distribution, habitat and phenology. *Ladenbergia carua* is found in montane wet forest in southern Peru, in Cusco and Puno departaments, and in northern Bolivia in La Paz department (Figure 10), at 900 and 2400 msnm, in where its occurrence is well reported. It has been collected in flower and fruit in April and September.

Diagnostic Characters and Discussion. *Ladenbergia carua* is a shrub or tree characterized by its hirtellous indumentum, oblong stipules that are apparently interpetiolar but actually shortly fused at the base; ovate-oblong leaf blades with the base generally cordate and that are matte above and densely hirtellous beneath; few-flowered inflorescences with the branches ferrugineous; large slender corollas that are pilose externally and glabrous inside; externaly densely hirtellous hypanthium; calyx limb hirtellous externally with the inside glabrous and the lobes irregular and generally obtuse. Fruits woody and thick.

Fig 9. *Ladenbergia carua* (Wedd.) Standl (A-I). A. Habit. B. Abaxial indumentum of the leaf blade. C. Stipule. D. Hypanthium. E. Adaxial face of calyx. F. Inside the corolla tube. G. Stile. H. Fruit. I. Seed. *Ladenbergia riveroana* (Wedd.) Standl. (J-Q). J. Habit. K. Stipule. L. Hypanthium. M. Adaxial face of calyx. N. Inside the corolla tube. O. Brevistylous flowers. P. Longystilous flowers. Q. Fruit. R. Seed.

In his treatment of Rubiaceae from Peru, Standley (1936) distinguished *Ladenbergia carua* from the similar species *L. malacophylla* based on the size of the corolla tube (4.5-5 cm long in *L. carua* vs. 3.5 cm in *L. malacophylla*) and on the size of the inflorescence (few flowered in *L. carua* vs. many flowered in *L. malacophylla*). Andersson (1997) included *L. malacophylla* within the circumscription of *L. carua*, based on its similar inflorescence and similarly long flowers. He mentioned that the difference between the lectotype of *L. malacophylla* and *L. carua* is the inside of the calyx limb, totally glabrous in *L. malacophylla* vs. puberulous in *L. carua*. A continuous variation of the internal pubescence of the calyx limb, which is located only on the upper edges of the calyx lobes, is evident in the material examined, and thus is not a good character to differentiate two groups of plants.

Examined material.

Peru. Cusco: La Convencion, Echarati, 1650 m, 14 Apri 1998, Baldeon et al 2982 (USM), 3156 (USM); Katarompanaki, 1500 m, 05-08 May 2004, Salinas et al 7020 (USM); R.C. Machiguenga, 1446 m, 19-29 March 2007, Tello PM10UR2-3/17 (MOL), PM10UR1/11 (MOL). Paucartambo, Cosnipata, 800-900 m, 04 Dec 1985, Foster et al (F, MO, NY). **Puno:** Carabaya, Cabeceras del Rio Candamo, 800-850 m, 16 Nov 1996, Cornejo & Balarezo 2733 (MO); 29 May 1944, Hodge 6161 (USM). Sandia, Bella Vista, Tambopata Valley, 1360 m, 7 Apri 1943, Hodge 6009 (F, MO, USM), 6072 (USM), 6162 (F); 1000-1300, 26 May 1942, Metcalf 30611 (F, G).

Bolivia. La Paz: Prov. Franz Tamayo, Santo Domingo, Tintaya, 1459 m, 10 Oct 2006, Cornejo et al, 46 (MO); Cornejo et al, 118 (MO). Parque Nacional Madidi, 1367 m, 06 Oct 2009, Arellano et al, 910 (MO); 400-1000 m, Fuentes et al 4208 (MO); 1876 m, 10 Jul 2005, Fuentes et al 9713 (MO); 1616 m, 01 Sep 2010, Fuentes et al 17273 (MO). Prov. Murillo, camino al valle Zongo, 1200 m, 30 Oct 1988, Beck & Foster 13962 (GB). Prov. Larecaja, Mapiri, 1140 m, 08 Ago 2004, Beck et al 29508 (LPB, MO); Beck 17209 (GB); Buchtien 1403(F fragments), 1404 (F), 1405 (F fragments), 1406 (NY); Krukoff, 11021 (F, G, K, MO, NY); 10921 (F, K, MO, NY); Rea 269 (GB, MO); Rusby G1 (F fragments, G, MO, NY, P); Weddell 4359 (P). Prov. Pararani, 1900 m, Ago 1933, Cardenas 1214 (F, G); 1000-1600 m, 24 Jul 2002, Clark & Barrientos (MO). Prov. Nor

Yungas, road Incahuara-Mejillones, 1500 m, 15-16 Jan 1983, Solomon 9291 (MO), 9510 (GB, MO), 14873 (GB). Prov. Sud. Yungas, Rio Bopi, 690-730 m, Jul 27-31. 1939, Krukoff 10618 (F, MO, S); Cotapata, Santa Barbara, 2260 m, 25 Jul 2001, Navarro et al 1609 (MO). Prov. Caravani, road Bella Vista-Carasco, Km 6., 1250 m, 14 Sep 1996, Persson & Gusstafsson, 247 (MO).

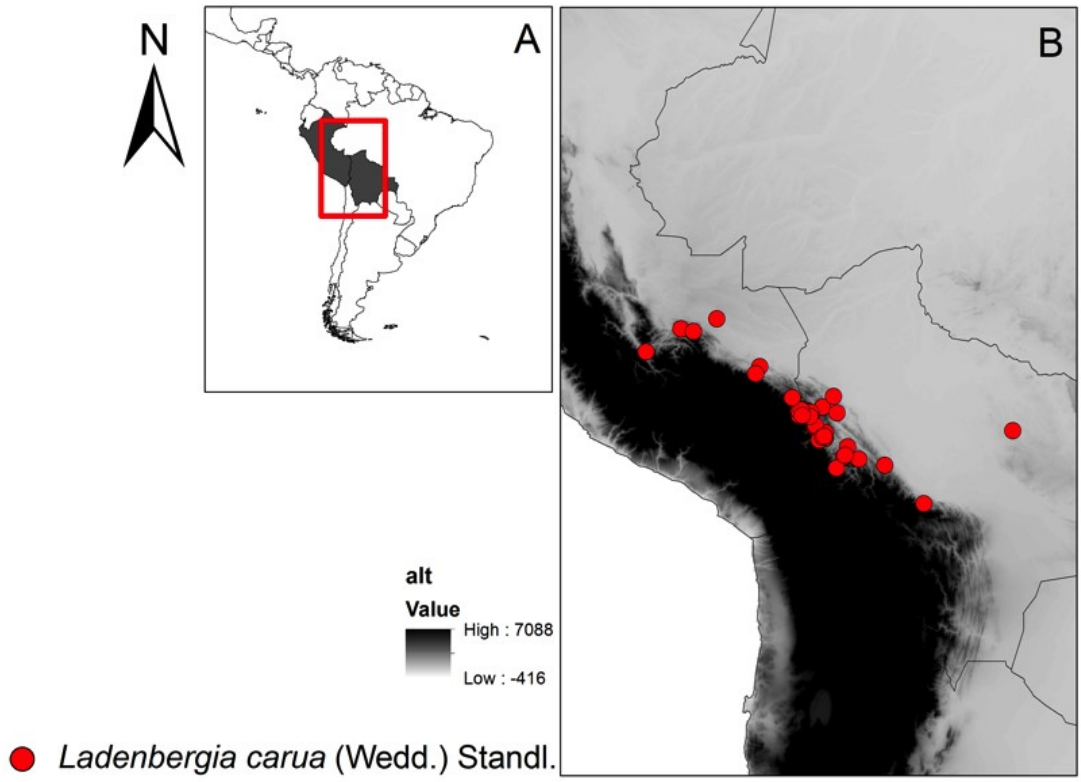

Fig 10. A. Southern of Peru, Bolivia and South America. B. Enlarged map showing the distribution the *L. carua* (Wedd.) Standl.

4. *Ladenbergia crassifolia* (DC.) Standley. Publ. Field Mus. Bot. Ser., 7: 200 (1931). *Cinchona crassifolia* Pavon ex DC., Bibl. Univ. 41: 151 (1829).- *Buena crassifolia* (DC.) Weddell, J. Linn. Soc. 11: 187 (1869).- Type: [Tafalla in] Pavon ; Ecuador, "Quito and Loja" (G ex Herb. Moricand, lectotype designated here, photo F-25716; P isolectotype).

Cascarilla calyptrate Weddell, Ann. Sci. Nat., Ser. 3, 10: 13 (1848).- Type: Based on *Cinchona crassifolia* Pavon ex DC.

Ladenbergia franciscana C.M. Taylor, Novon 20(4): 476–477 (2010).- Type J. Homeier & I. Kottke 1406. Ecuador, Zamora-Chinchipe, area of Estación Científica San Francisco, rd. Loja-Zamora, ca. 35 kmfrom Loja, 3°58'S, 79°04'W, 2250 m, 16 Oct 2004 (LOJA holotype; GOET image!, MO, QCNE image! isotype).

Shrub or small tree 5 (-8) m tall. Young branches glabrous or sparcely puberulous. Stipules fused throughout forming a conical calytra, densely puberulous external and internal glabrous to puberulous, 0.9-2.5 cm x 2-2.5 cm; petioles 0.5-3.2 cm long, glabrous to sparcely puberulent; leaf blades plane, thick in texture, chartaceous when dry, 4-15 x 2.4-7.5 cm, elliptic to ovate (length/width 1.7-2.6), cuneate in the base, acuminate at apex, secondary veins 6-10 pairs with arrangement brochidodromous, prominolous above, prominent beneath, tertiary venation +/- evidente distinct above with an alternate-percurrent, adaxial surface nitid and glabrous, abaxial surface with midrib and veins sparcely puberulous, intervenous surface glabrous or minutely strigose, tuft domatia present. Inflorescence terminal branched in one to two orders, few-flowered (generally 9-30 flowers), broadly triangular in outline, axis glabrous to puberulous, peduncles 1.5-3.5 cm long, rachis 5-10 cm long, bracts lanceolate, caducous. Flowers 5-merous, fleshy, fragant, nocturnal, distylous, sessil to subsessile or axes in dichasial groups 3-6 flowers; hypanthium obconical, puberulous to villosulous, ca. 3.2-4 mm x 2-3 mm, calyx limb 3-3.2 mm long with lobes generally truncate to undulate 0.2-0.7 mm long, moderadely villosulous outside, usually glabrous to puberulos inside, colleters in group towards base; corolla salverform, white, tube in brevistylous flowers 20-24 mm, in diameter 3-4.1 mm, tube in longistylous flowers 21-25 mm, in diameter 3-3.6 mm, lobes in brevistylous flowers 13-16 mm and in longistylous flowers 12-13.5 mm, filaments attached ca 15-16.5 mm

above base of corolla tube (ca. 65 % of tube length) in longistylous flowers and ca 17-21 mm above base of corolla tube (ca. 80 % of tube length) in brevistylous flowers, anthers 6-8 mm x 1-1.5 mm; style glabrous to moderadely hirtellous, ca. 5-7 mm long in brevistyls flowers and 19-21 mm long in longistyls flowers, stigmatic lobes ca 5-6.5 mm. Capsules woody, cylindrical to obovoid, externally glabrous to puberulous, 15-47 x 11-12 mm, endocarp 0.4-0.6 mm thick. Seeds oblong-fusiform 12-16 mm x 4-6 mm with marginally fimbriate wings .

Distribution, habitat and phenology. *Ladenbergia crassifolia* is found on montane wet forest from Central Andes and Southern tropical Andes. It has been collected in flower and fruit in October-December to March-May.

Diagnostic Characters and Discussion.

Ladenbergia crassifolia is characterized by its stipules calyptrate, comparatively small (4-15 x 2.4-7.5 cm), thick leaves, wich are usually +/- matte above, sparingly hairy beneath, have distict tuft domatia, flowers fleshy with corolla tube fleshy (20-24 mm x 3-4 mm) and fruit with endocarp thick.

Ladenbergia crassifolia is morphologically similar to *L. macrocarpa* (see *L. macrocarpa* for differences). Some populations of *L. crassifolia* are restricted to areas of sandstone in Ecuador and northern Peru. Recently it was described *L. franciscana* for this place, which resembles to *L. crassifolia*. Taylor & Gereau (2010) in the *L. franciscana* protologue do not discuss the relationship of this species with *L. crassifolia* and *L. macrocarpa.* Analysis of now available material shows that both species share characteristics such as shape and indumentum of leaves, longitude and width of corolla tube, pattern shape of the inflorescence, longitude and width of the corolla tube length and texture fruits, because this is *L. franciscana*, synonymized within *L. crassifolia*.

One collection the sandstone in the northern of Peru (Rodriguez et al 2947) showed a very small leaf (3.5 cm x 3 cm) and pyriform fruits with endocarp thick, separated material within the exsicatae showed flowers resembles a *L. crassifolia* so this feature

in the leaves represents the limit of the species and this could be an adaptation to cold environments and poor soils.

Collections of *L. crassifolia* that come from the Central Andes of Peru show a slight variation in leaf size and style pubescence, which is related to the growth stage and habitat where they occur. These characteristics could lead to misinterpretation of the species, but the pattern of the inflorescence and fruit are maintained.

Examined material.

Ecuador. Morona-Santiago: Limon Indaza, Cordillera de Huaracayo, 1950 m, 20 March 2001, Neill et al 13076. Zamora Chinchipe, Reserva San Francisco, 2070 m, 15 Feb 2013, Homeier (MO), Homeier 1005 (MO), Homeier & Kocke 1406 (MO), Neill et al 12644 (MO). El Pangui, Cordillera del Condor, 1800 m, 15 dec 2000, Miranda et al 153 (MO).

Peru. San Martin: Rioja, Buenos Aires, 2000 m, 21 March 1998, Van der Werff et al 15382 (MO). Pasco: Oxampa, Dist. Huancabamba, Parque Nacional Yanachaga Chemillen, Sector Tunqui, 1895 m, 18 Oct 2008, Cueva 235 (MO). Cusco: Paucartambo, trocha Union Km 11, 18 Sep 2001, Farfan et al 1167.

Bolivia. La Paz: Franz Tamayo, Parque Nacional Madidi, 2000 m, 08 Jul 2005, Fuentes et al 9571 (MO), Fuentes et al 11680 (MO).

5. *Ladenbergia discolor* K. Schum., Fl. Bras., 6(6): 146 (1889).**-** Type: Spruce 4247. Peru. San Martin, near Tarapoto, Nov. 1855. (B destroyed (F–negative N°140); K, lectotype designated here, Isolectotypes BM image!, BR image!, C image!, E image!, G image!, LD image!, NY, RB).

Nomenclatural Note: Schumann (1889) does not mention a holotype in the protologue for this species. Andersson (1997) based on the negative picture at Herbarium F mentions that the holotype material was destroyed in the Herbarium of Berlin (1943). Considering that today there are several syntypes, which are well preserved and represent a complete material, I chose the material deposited in the Herbarium K as lectotype, because the main collections made by Spruce are deposited here.

Shrubs or small trees 2 (-8) m tall. Young branches rather densely villosulous. Stipules shortly fused at the base, oblong in the basal portion with upper part acuminate, generally glabrous to puberulous, 0.8-2 x 0.5-0.65 cm long; petioles 1.3-1.8 cm long, glabrous to sparcely puberulent; leaf blades plane, thick in texture, +/- chartaceous when dry, 4.5-12 x 1.5-6.5 cm, elliptic to ovate (length/width 1.8-3), obtuse to cuneate at base, attenuate to acuminate at apex, midvein above deeply sulcate, secondary veins prominulous above and slightly sulcate, prominent beneath, 7-9 pairs with arrangement brochidodromous, tertiary venation +/- obscure above, slightly distinct below with pattern alternate percurrent, adaxial surface matte to subnitid, glabrous, abaxial surface with midrib and veins sparsely puberulous, sometimes also with bristly hairs along margin of midrib, intervenous surface glabrous or minutely strigose, margin slightly revolute, tuft domatia absent. Inflorescence terminal, branched in one to two orders, few-flowered (generally 9-30 flowers), broadly triangular in outline, axes puberulous to +/- hirsute, with trichomes ferruginous, peduncles 2-4 cm, rachis 0.8-2 cm long composed by 2-3 nodes with axes articulated, dichasial, bracts lanceolate, acuminate, generally deciduous. Flowers 5-merous, strongly fragant, nocturnal, distylous, sessile to subsessile or short axes in dichasial congested groups of 3-6; hypanthium obconical, densely tomentulose with ferrugineous trichomes, ca. 2-3 x 2 mm, calyx limb 1.8-5.5 mm long, lobes generally repand to irregular, 0.5-1.8 mm long, sparsely puberulous outside, glabrous inside, without colleters evident; corolla salverform, white, tube in brevistylous flowers 15-17 mm, in diameter 1.2-1.8 mm, tube in longistylous flowers 8.5-9.5 mm, in diameter 2-2.5 mm, lobes in brevistylous flowers 7-9.5 mm and in longistylous flowers 6.2-7.5 mm, filaments attached ca 14 mm above base of corolla tube (ca. 70 % of tube length) in longistylous flowers and ca 4.5-5 mm above base of corolla tube (ca. 50 % of tube length) in brevistylous flowers, anthers 4.7-6 x 1-1.5 mm; style glabrous, ca. 4-7 mm long in brevistyls flowers and 8.5-9.5 mm long in longistyls flowers, stigmatic lobes ca 2-2.5 mm. Capsules woody, cylindrical to obovoid, externally puberulous, 12.5-30 x 4-5.5 mm, endocarp 0.2-0.4 mm thick. Seeds oblong-fusiform (5-11 x 1.5-3 mm long.) with marginally fimbriate wings.

Distribution, habitat and phenology. *Ladenbergia discolor* is found on upper slopes from northeastern to central Peru in Loreto, Amazonas and San Martin departament (Figure 11). It grows in sandy rocky soils at 260 and 1200 msnm. The specimen *Ule* 6767 is reported for Loreto department but It is possible that is a mistake, and actually it was collected in the area of mountains that borders with of San Martin department, in sandstone areas (Neill et al, 2014). This species is poorly collected because it occurs in areas of difficult access. It has been collected in flower and fruit in February-March and July-October.

Diagnostic Characters and Discussion. *Ladenbergia discolor* is a shrub or small tree characterized by its glabrous to puberulous stipules that are shortly fused at base, small, coriaceus, ovate leaf blades, which often dry contrastingly blackish and light grayish beneath (reference for the epithet), the midvein above deeply sulcate and the intervenous abaxial surface glabrous; few-flowered inflorescences with axes shortly dichasial; small sessile or subsessile flowers; short calyx limbs with lobes generally repand (at ½ calyx limb) and small capsules with thin endocarp.

In the Flora brasiliensis treatment (Schumann 1889), *Ladenbergia discolor* is distinguished from *L. lambertiana* based on its discolored leaves (vs concolor in *L. lambertiana*) and basifixed anthers (vs versatile in *L. lambertiana*). The variation in color between the above and beneath surface of leaves occurs in several species of the genus, apparently it is a variation by for habitat condition, therefore it is not a good character to differentiate species. The attachment position of filament to the anther is variable in this species and it will be necessary to review a larger number of specimens to generalize this pattern. *Ladenbergia discolor* differ from *L. lambertiana* in length of the corolla tube (8.5-18 mm in L. discolor vs 20-25 mm in L. lambertiana), form and length of calyx lobes (generally repand, 0.5-1.8 mm in *L. discolor* vs acute 1-2 mm in *L. lambertiana*) and fruit length (1.2-3 cm in L. discolor vs 4-6 cm).

Standley (1936), in the Rubiaceae treatment for Peru, distinguished *Ladenbergia discolor* from *L. ferruginea* based on small leaf blades (7-10 x 2-4.5 cm) with abaxial surface glabrous in *L. discolor* vs. large leaf blades (14-25 x 5.5-9 cm) with abaxial

surface pubescent in *L. ferruginea*. Pubescence on abaxial surface of leaf is highly variable in the genus and it depends of habitat conditions, so this is not a good character to differentiate species.

Ladenbergia discolor is morphologically related to *Ladenbergia klugii* because both have stipules generally glabrous to puberulous and shortly fused at base; small flowers clustered in congested dichasial grouds; the calyx lobes generally reptaded; and the same geographic distribution. However these can be differentiated by coriaceous smaller leaves in *L. discolor* (vs papyraceus-subcoriaceus larger leaves in *L. klugii*), with the leaf undersurface glabrous or puberulous in *L. discolor* (vs puberulous to densely hirtellous or villosulous in *L. klugii*), the midrib above deeply sulcate in *L. discolor* (vs slightly sulcate in *L. klugii*), the inflorescence few-flowered with 1-2 orders of ramification in *L. discolor* (vs inflorescence few- to multi-floweed with 2-3 (-4) orders of ramification in *L. klugii*) and fruit size smaller (1.2-3 cm) in *L. discolor* (vs larger fruits 4.5-6 cm, in *L. discolor*).

Two morphotypes can be seen recognized within *L. discolor*, both of them restricted to sandstone areas. The first is found on slopes of the eastern Andes (Tarapoto-Yurimaguas road), where Spruce's type collection was found, which has sub-coriaceous leaves, flowers with calyx lobes repand and fruits smaller (12.5-22 x 4-4.5 mm). The second morpho-type is restricted to northeastern slopes further north in Amazonas (Cerro Tayu) and has coriaceous leaves, long calyx tubes, calyx lobes that vary in depth (lobes at 1/2 the limb of the calyx), and the corolla tube (13-17 mm long) and fruit slightly larger (15-25 mm long). A detailed analysis of flowers shows that collections with smaller flowers belonging to the first morpho-type longistylous flowers; and its sub-coriaceous leaves may be associated with open areas and lower altitude. The slightly larger flowers belong to the second morpho-type represent brevistyls flowers; and its coriaceous leaves would be associated with higher altitude places. One collection (Rodriguez 2694) shows a gradual variation in leaves texture. The slight variation in the depth of the calyx lobes has also been reported in other morphologically related species (*L. klugii*, *L. bullata*, *L. riveroana,* etc).

Examined material.

Peru. Loreto: Canela Ucsha, 1000 m, Mar 1903, Ule 6767 (G, K; locality possibly in San Martin). **Amazonas:** distr. Imaza, Tayu Mujaji. Comunidad de Wawas, 21 Oct 1997, Rojas et al 358 (MO, USM); 25 Oct 1997, Vasquez et al 24674 (MO); 22 Mar 2001, Van der Werff 16320 (MO, USM); 20 Jul 2004, Rojas et al 3162 (MO). Soldado Oliva. Carretera entre Bagua - Imaza, 07 Feb 1999, Diaz et al 10656 (MO). **San Martin:** distr. Tarapoto. Carretera Tarapoto-Yurimaguas, Km 12 to 16, 23 Aug 1978, Rimachi 3821 (F, MO, NY, USM); 14 Jun 1980, Rimachi 5161 (MO, USM); 19 Jul 1982, Gentry et al 37785 (MO); 25 Feb 2004, Rodriguez 2694 (MO); distr. La Banda de Shilcayo, 13 km from Tarapoto on road to Yurimaguas, 10 Apr 1972, Schunke 5367 (F, G, K, MO, NY, P). Prov. Lamas. On old trail drom Yumbatos to San Antonio de Cumbasa, S of Shapajilla, upper slopes of Cerro Isco, 05 Oct 1986, Knapp et al 8523 (USM).

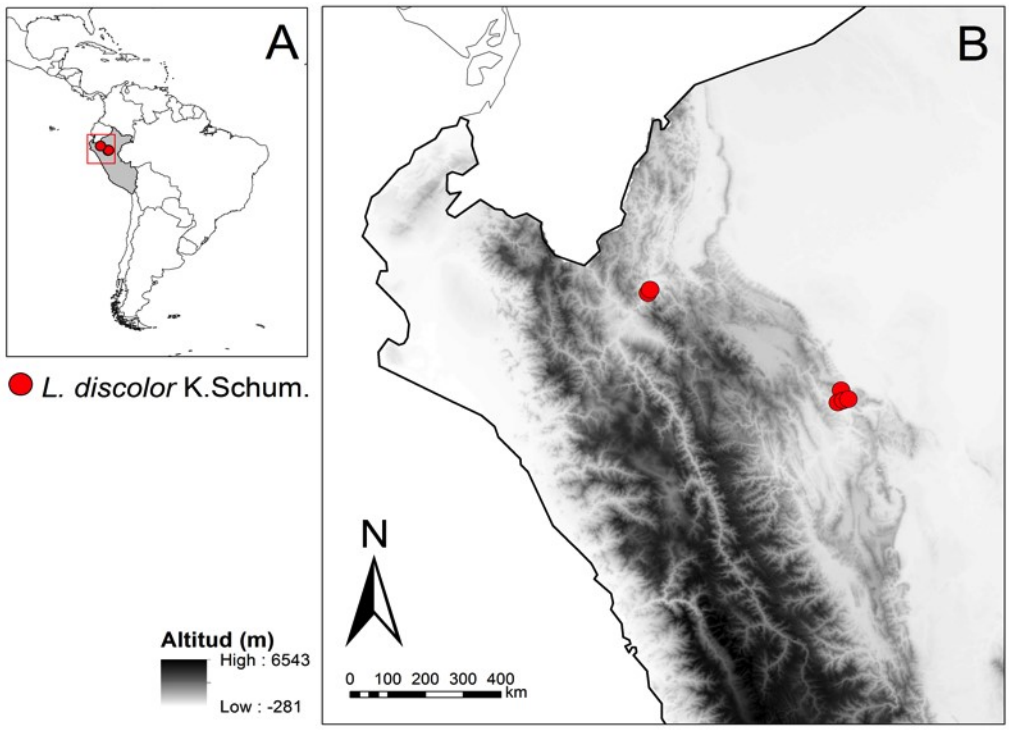

Fig 11. A. Amazonas province, Peru and South America. B. Enlarged map showing the distribution the *L. discolor* K. Schum.

6. *Ladenbergia fosteri* E. Chilquillo- TYPE: PERU. Loreto. Cordillera Escalera, Provincia Datem del Marañon. Distrito Cahuapanas; Field Museum Inventario Rapido # 26, Campanento Alto Cahuapanas. 76°50'20.4" W, 5°39'51.8" S, 1028 m.s.n.m. 29 Sep

2013, M. Rios, T. Mori, D. Neill, L. Torres and C. Vriesendorp 3531 (holotype: F; isotypes: USM; AMAZ; ECUAMZ).

Shrub, 5 m tall. Young branches glabrous or sparsely puberulous, ferrugineous. Stipules shortly fused at the base, oblong to deeply cuneate in the basal portion with upper part acuminate, glabrous to puberulous, 1-1.2 cm x 0.45-0.5 cm; petioles 0.3-0.45 cm long, glabrous to sparsely puberulent; leaf blades not bullate, thick in texture, chartaceous when dry, 1.3-6.4 x 0.9-2.1 cm, narrowly elliptic to obovate (length/width 2.1-2.9), acute at base, attenuate to acuminate at apex, secondary veins 5-7 pairs with arrangement weak brochidodromous, slightly to strongly sulcate above, prominent beneath, tertiary venation obscure above, slightly distinct below with an opposite-percurrent arrangement, adaxial surface matte to subnitid and glabrous, abaxial surface with midrib and veins glabrous and intervenous surface glabrous, margins revolute, tuft domatia absent. Inflorescence terminal, strongly congested, umbelliform cyme, few-flowered (3 flowers) with bract 0.6-0.75 cm long, peduncles 0.4-0.45 cm long. Flowers 6-merous, strongly fragant, nocturnal, distylous, sesile to subsessile; bracteole 0.18-0.21 cm long, hypanthium obconical pilosulose – tomentulose, ca. 3-3.5 x 2.7-3 mm, calyx limb 4-4.5 mm long with lobes deeply generally obtuse and irregular 3.9-4.3 mm long, glabrous to sparsely puberulous outside, glabrous inside, colleters not seen; corolla salverform, fleshy, white, tube ca. 16-18 mm long, hirtellous outside and villous inside in upper half, lobes ca. 10-13 mm, ridged part ca. 8.5-10.5 mm, center-field hirtellous; filaments attached ca. 10-12 mm above base of corolla tube (ca. 70 % of tube lenght) in macrostylous flower (brevistylous not seen), ca. 0.8-1.2 mm long, anthers 3-3.5 mm; style ca. 16 mm long in macrostylous flower, rather sparcely hirsute in lower half, stigmatic lobes ca. 3.2 mm. Capsules woody, oblong- cylindrical, externally puberulous, 25-28 x 4.5-5.5 mm, endocarp 0.5-0.6 mm thick. Seeds oblong-fusiform, 11-13 x 4-5 mm, with wings marginally fimbriate.

Distribution, Habitat and Phenology - *Ladenbergia fosteri* is a species only know from the type collection, located in South West of Loreto, Peru (Fig 12). The species occurs within a system of small mountains of the formation Cushabatay called "Cahuapanas" located at the northern margins of the Alto Mayo Valley, between the neighboring

departments of San Martin and Loreto. The area is uninhabited and without traces of human activities. Altitude ranges from 1000 m a.s.l. to the highest peak at 1500 m. The vegetation pertains to the lower montane forests. It has been collected in flower and fruit in November.

Diagnostic Characters and Discussion. *Ladenbergia fosteri* is characterized by the presence of stipules shortly fused at the base, leaf blades narrowly elliptic, thick in texture, inflorescence terminal strongly congested, umbelliform cyme with three flowers sessile to subsessile and covered by the bracts, corolla with tube villous inside in upper half, and style sparcely hirsute.

Ladenbergia fosteri is similar to *L. pauciflora* L. Andersson of the premontane forest of the Colombian Andes but is distinguished by the number the flowers in the inflorescence (3 flowers in *L. fosteri* vs ca. 10 flowers in *L. pauciflora*), length the tube corolle (16-18 mm in *L. fosteri* vs 55-60 mm in L. pauciflora) and size of the fruit (25-28 mm in *L. fosteri* vs 60-80 mm in *L. pauciflora*). Characteres vegetative in *L. fosteri* resembles a *L. moritziana* of the montane forest of northern Venezuela, but can be distinguished for the inflorescence form (subumbella in *L. fosteri* vs dichasial in *L. moritziana*), length of the tube corolla (16-18 mm in *L. fosteri* vs 30-40 mm in *L. moritziana*) and length the pedicels of the flowers (sessile to subsessile in *L. fosteri* vs conspicuous pedicellate in *L. moritziana*).

Examined material.

Peru. Dpto. Loreto. Prov. Datem del Marañon, Cahuapanas, Cordillera Escalera, 1028 m.s.n.m. 29 Sep 2013, M. Rios et al 3531 (F, USM, AMAZ, ECUAMZ).

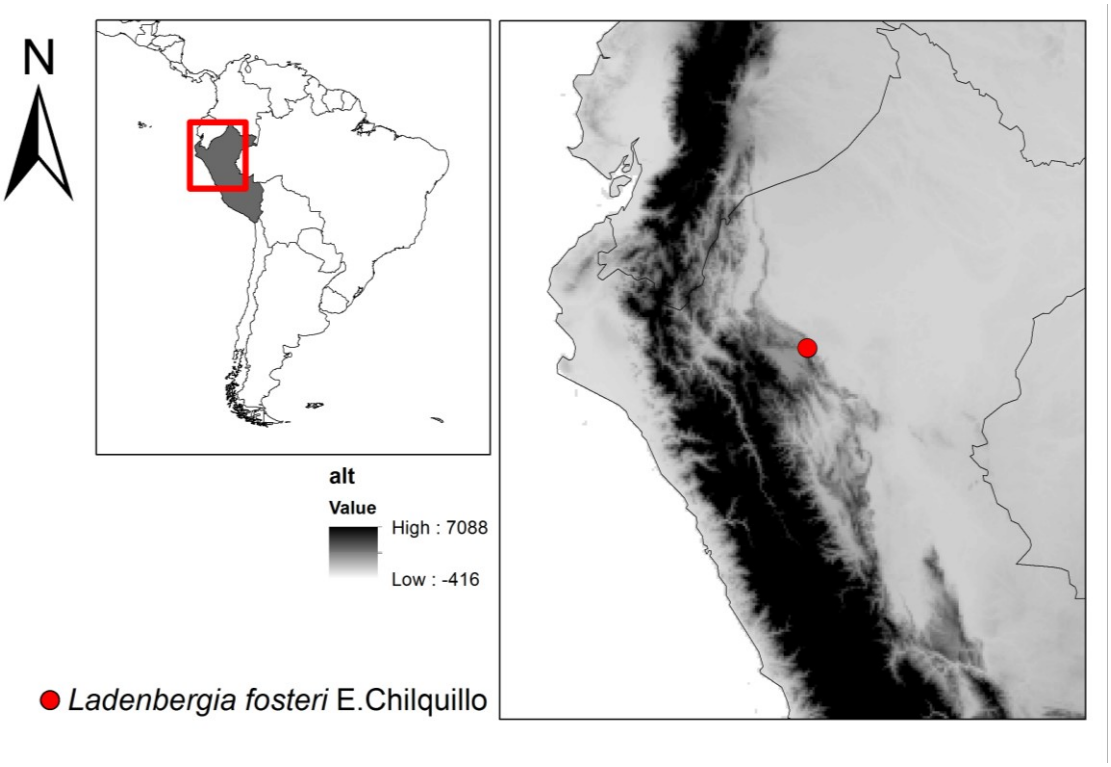

Fig 12. Distribution map the *Ladenbergia fosteri* E. Chilquillo

7. *Ladenbergia heterophylla* (Wedd.) Standl. Publ. Field Mus., Bot. Ser., 7: 18 (1930). *Cascarilla heterophylla* Wedd., Ann. Sci. Nat., Sér. 3, 10: 10 (1848). *Buena heterophylla* (Wedd.) Wedd., J. Linn. Soc. 11: 186 (1869). Type: Purdie s. n. ("seed 362"); Colombia, Norte de Santander, "mountains of Ocaña (…) June 1845 "(K lectotype (With original label), designated in Andersson 1997, K isolectotype).

Cinchona bogotensis Karsten, Fl. Columb. 1: 83, tab. 41 (1860). *Ladenbergia bogotensis* (Karsten) Standl., Publ. Field Mus., Bot. Ser., 7: 18 (1830). Type: Karsten s. n.; Colombia, Cundinamarca, Susumuco (W, the lower brach is lectotype, designated in Andersson 1997).

Ladenbergia sericophylla Standl., Publ. Field Mus., Bot. Ser., 18: 1324 (1938). Type: Danforth 32; Costa Rica, San José, 3.2 Km SE of San Isidro del General, Aug 1936 (F holotype).

Shrubs or small trees 4 (-15) m tall. Young branches glabrous or +/- pubescent. Stipules fused at 1/3 the base forming sheath, free part with margens revolute, rounded in the basal portion with upper part obtuse, generally glabrous to puberulous, 2.5-3.8 x 2—2.8 cm long; petioles 2-7 cm long, glabrous to sparcely puberulent; leaf blades plane, thinnish in texture, papyraceous to +/- chartaceous when dry, 12-45 cm x 6.5-33 cm, broadly elliptic to suborbiculate (length/width 1.3-2.2), broadly cuneate to rounded at base, obtuse at apex, midvein above deeply sulcate, secondary veins prominulous above and slightly sulcate, prominent beneath, 8-9 pairs with arrangement brochidodromous, tertiary venation distinctly on both sides with pattern alternate percurrent, adaxial surface matte, glabrous, abaxial surface puberulous with midrib and veins strigose, intervenous surface glabrous or minutely strigose, margin slightly revolute, tuft domatia present. Inflorescence terminal, branched in one to two orders, few-flowered (generally 9-35 flowers), broadly triangular in outline, axes glabrous to puberulous, peduncles 2-5 cm, rachis 4-8.5 cm long composed by 2-3 nodes with axes articulated, dichasial, bracts lanceolate, acuminate, generally deciduous. Flowers 5-merous, strongly fragant, nocturnal, distylous, sessile to subsessile or short axes in dichasial congested groups of 3-6; hypanthium obconical, puberulent or villosulous in outside, 4-6.5 mm x 3-3.5 mm, calyx limb 4-6 mm long, lobes generally undulate to rounded irregular, 1-2mm long, glabrous both in outside and inside, without colleters evident; corolla salverform, white, tube in brevistylous flowers 37-50 mm, in diameter 5-7.8 mm, longistylous flowers not seem, lobes of the flowers 19-25 mm, filaments attached 27-34 mm above base of corolla tube (ca. 75 % of tube length), anthers 7-8 mm x 1.4-1.7 mm; style glabrous, ca. 14 mm long, stigmatic lobes ca 9-10 mm. Capsules woody, narrowly ellipsoid or fusiform to cylindrical, externally glabrous to puberulous, 50-140 x 10-15 mm, endocarp 0.35-0.45 mm thick. Seeds oblong-fusiform (16-21 x 3.5-3.7 mm long.) with marginally fimbriate wings.

Distribution, habitat and phenology. *Ladenbergia heterophylla* is found the rainforest in Costa Rica to montane rainforest in the Central South Andes to northern Peru (Fig 13). It has been collected in flower and fruit in September-November to February-May.

Diagnostic Characters and Discussion.

Ladenbergia heterophylla is characterized by its often thinnish leaf blades, wich are puberulous on midrib and veins beneath and strigulose on the actual surface, having small but usually distinct tuft domatia. It is further characterized by its basally fused stipules with margens revolute, by its inflorescence with one –three lateral orders, distinctly lobed calyx (usually undulate) with lobes shorter than lymb, long tube (31-56 mm) corolla and large (30-170 mm x 10-17 mm) fruits.

Andersson (1994) put *L.heterophylla* in *L. sericophylla*, which differed from *L. epiphytica* by papyraceous to subchartaceous leaves (vs firmly chartaceous to coriaceous in *L. epiphytica*), adaxial surface matte (glossy in *L. epiphytica*), presence of tuft domatia (vs absent in *L. epiphytica*) and corolla tube of 37-47 mm (vs 65-75 mm in *L. epiphytica*). Andersson (1997) synonymized *L. sericophylla* in *L. heterophylla*, but he not given an explanation about his decision. In this treatment, the synonymy proposed by Andersson is maintained, because material examined of both species differs only in the abaxial indumentum of the leaves and the presence of domatia, characters that are highly variable and depend on the stage of growth and habitats where they occur.

Examined material.

Costa Rica. Alajuela: Herrera 1262 (MO), Chavarria 1189 (INB). Cartago: Barbour 1017 (F, MO). Guanacaste: Herrera & Rivera 836 (F, Mo), Rivera 848 (K). Heredia: Hammel 10970 (CR), Carvallo 156 (INB), Acevedo et al. 155 (K), Herrera 4083 (F, K), Shank 13961 (F), Skutch 5324 (F, US), Williams & Molina 13961 (F). San José: Jiménez 3730 (F, MO), Lems 5005 (NY), Lems 5166 (F, NY), Molina et al. 18097 (F, NY), Skutch 2539 (CR, MO, NY), Utley & Utley 4929 (CR, F, MO). Limon: Pococi, Acosta et al 3651 (INB). Puntarenas: Reserva Forestal Golfo Dulce, Aguilar 591 (INB), Aguilar 6779 (GB), Estrada et al 2607 (CR).

Panama. Darién: Folsom et al. 6344 (MO), Herrera et al. 882 (MO), McPherson 9800 (MO). San Blas: de Nevers et al 5391 (MO).

Colombia. Caquetá: Cuatrecasas 9138 (F). Chocó: Silverstone-Sopkin 1395 (COL). Cundinamarca: Triana 1808, 1814 (P). Norte de Santander: Fosberg 21422 (K, NY).

Valle: Cuatrecasas 14868 (F), 17464 (F), 23840 (F). Prov. Unknown: Triana s. num. (BM). Antioquia: Municipio de San Luis, Betancour et al 712 (MO)

Ecuador. Chimborazo: Camp E-4044 (MO ster.). El Oro: Steyermark 54168 (F ster.). Napo: Jaramillo et al. 12340 (QCA), 13083 (QCA), Palacios 4171 (GB), Alvarez et al 1706 (GB, MO), Alvarez et al 2042 (MO). Pastaza: Asplund 18914 (S), Mexia 6910 (F ster.). Tungurahua: Fosberg 22474 (F ster.), 54550 (F), 54554 (F, NY, both ster.) Zamora Chinchipe: Cordillera del Condor, Quizhpe 973 (MO).

Peru. Cajamarca: San Ignacio, Campos & Garcia 3956 (MO), Diaz & Fernandez 10156 (MO)

Doubius and Excluded Species

In Anderson (1997), *L*. *obovata* L. Andersson was described from the Andes of Ecuador, this species is quite similar to *L*. *heterophylla* because of the inflorescence patterns, the sizes of the tubes of the corolla and fruits. The only difference is the shape of the leaves (which are elliptical and oblong in *L*. *heterophylla* and obovate in *L. obovata*). *L*. *obovata* is known only from very few collections, so the available material not helps to establish whether this is true species or if it is a gradual variation of *L*. *heterophylla*.

Material from Panama derteminate as *L. macrocarpa*, *L. heterophylla* and *L. hamiltonii* (nom. inv) shows a similar morphology of *L*. *heterophylla* with chartaceous leaves, revolute stipules, longer flowers and fruits. These characteristics resemble *L. epiphytica* L. Andersson species described by Andersson (1994) only known the Ecuadorian Andes. However these materials along their distribution show that leaf texture is very variable, so from the material examined (main in fructification) can not be established if both species represent separate species or just a variation of *L. heterophylla*. In conclusion, collections of *L. epiphytica* are insufficient to establish whether this corresponds to a different species of *L. heterophylla*.

Collections made after of Andersson (1997) in areas surrounding the National Park Las Orquideas (Antioquia, Colombia) show an morphotype entirely pubescent with papyraceous to chartaceous leaves, cylindric fruits and flowers indument villous that resemble inflorescence indument and lenght flowers in *L. sericophylla* (*L. heterohylla* considered here). These collections also resemble *L. dwyeri* L. Andersson, known only from Panama, which is characterized by bullata leaves and inflorescences patterns and flowers similar a *L. heterophylla*. While collections in Panama show that bullate leaf blades feature is a varying character in its distribution. However to date it has only a collection of flower buds of this morphotyphe the Antioquia (Callejas et al 8945), so it can not establish whether it represents a new species or if it is a variation of *L. heterophylla* or *L. dwyeri*.

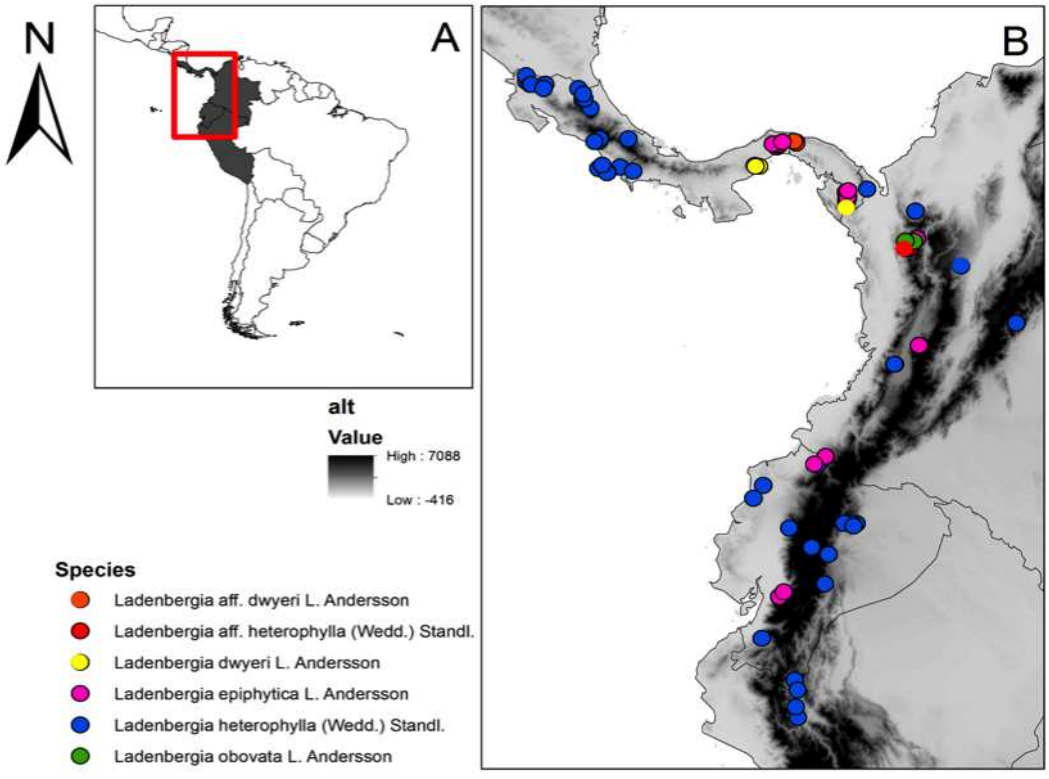

Fig 13. Northern of Peru, Ecuador, Colombia and South America. B. Enlarged map showing the distribution the *Ladenbergia heterophylla* (Wedd.) Standl. Doubius and excluded species are showed in circles red, yellow, green, pink and orange.

8. *Ladenbergia klugii* L. Andersson. Nordic Journal of Botany 17 (3): 295. (1997). Type: G. Klug 3515; San Martin, Zepelacio [Jepelacio] near Moyobamba, 1200-1600 m, forest, Jan 1934 (F holotype, G image!, K image!, NY image! GH image! A image! isotypes).

Ladenbergia ferruginea Standl. Publ. Field Mus., Bot. Ser., 8: 336 (1931).- Type: Wueberbauer 1175; Peru, Chunchusmayo, in forest near the river, 900 m, 13 Jun 1902 (B holotype, destroyed, photo F-49904; fragmente ex B).

Shrub or tree 3 (-20) m tall. Young branches rather densely villosulous. Stipules shortly fused at the base, ovate in the basal portion with upper part acuminate, generally densely puberulous, 1.2-2.5 x 0.8-1.8 cm long; petioles 1.5-3.5 cm long, +/- densely villosulous outside; leaf blades plane, thin to thick in texture, +/- chartaceous when dry, 10-35 x 6-13.5 cm, elliptic-ovate to oblong (length/width 1.7-2.6), acute to obtuse-cuneate at base, attenuate to acuminate at apex, midvein above slightly sulcate, secondary veins prominulous above and slightly sulcate, prominent beneath, 10-17 pairs with arrangement brochidodromous, tertiary venation +/- obscure above, distinct below with pattern alternate percurrent, adaxial surface subnitid, glabrous, abaxial surface +/- densely hirtellous or villosulous all over, margin plane, tuft domatia absent. Inflorescence terminal, branched in two to three orders, multi-flowered (ca. 65-90 flowers), broadly triangular in outline, axes villosulous, with trichomes ferruginous, peduncles 2-5 cm, rachis 7-12.5 cm long composed by 2-3 (-4) nodes with axes articulated, dichasial, bracts lanceolate, acuminate, generally deciduous. Flowers 5-merous, strongly fragant, nocturnal, distylous, sessile to subsessile or on short axes in dichasial congested groups of 3-6; hypanthium obconical, densely puberulous to villosulous with trichomes ferrugineous, ca. 2-3.5 x 2 mm, calyx limb 2.7-4 mm long, lobes generally repand to irregular, 0.5-1.5 mm long, sparsely puberulous outside, glabrous inside, colleters absent; corolla salverform, pilose externally and glabrous inside, white, long with tube in longistylous flowers 10-15 mm (Fig 24), in diameter 1.5-2.2 mm, brevistylous flowers not seen, lobes of the flowers 10-12.5 mm; filaments attached ca 5.5-7.5 mm above base of corolla tube (ca. 55 % of tube length), anthers 4-5.5 x 0.8-1.2 mm; style glabrous, 15-19 mm long, stigmatic lobes ca 2.5-3.5 mm.

Capsules woody, narrowly ellipsoid to cylindrical, externally puberulous to villosulous, 35-55 mm x 4-5.5 mm, endocarp 0.3-0.4 mm thin. Seeds oblong-fusiform, 10-13.5 x 2-3 mm, with wings marginally fimbriate.

Distribution, habitat and phenology. *Ladenbergia klugii* is a widely distributed species in the Andes of Peru and Ecuador. It is found in secondary forests and sandstone soil areas, occuring from 500 m - 2200 m (Fig 14). It has been collected in flower and fruit in November and December.

Diagnostic Characters and Discussion. *Ladenbergia klugii* is characterized by indumentum ferrugineous on the leaf blades, inflorescences multiflora with 2-3 (-4) orders lateral, small flowers with lobes proporcionally at corolla tube, calyx with lobes repand and glabrous inside and small capsules (35-55 mm lenght).
Andersson (1997) in the protologue of *L. klugii* compared this species with *L. carua* and L. *riveroana*. But he not compares *L. klugii* vs *L. discolor*, as wich are similar based in flower size and form the calyx lobes. L. Klugii is distinguished L. discolor by pattern of the inflorescence (multiflora with 2-3 (4) lateral orders in *L. klugii* vs pauciflora with 1-2 orders in *L. discolor*), shape and indumentum beneath of the leaf blades (ovate to oblong and villosulous ferrugineous in *L. Klugii* vs elliptic-ovate and glabrous in *L. discolor*) and size of the fruit (35-55 mm in *L. klugii* vs 15- 30 mm in *L. discolor*).

Ladenbergia ferruginea known only the type is synomizated within of *L. klugii*. Andersson (1997) not compares this species. Observations of the fragment of the type (leaf blades elliptic with side abaxial puberulous ferrugineous and part of the inflorescences with small flowers with lobes calyx repand) deposited in Herbarium F matches with morphotypes of *L. klugii* that ocurrs in the southern of Peru.

Morphotypes the *L. klugii* ocurrs in the northern of Peru (Amazonas) at 1000-2200 m showed a form oblong and texture chartaceous of the leaf blades and larges fruits. It resembles a *L. riveroana* that ocurrs in these areas. *L. klugii* is distinguished *L. riveroana* by having flowers with calyx lobes repand (vs calyx lobes acute in *L.*

riveroana) and flowers with the lobes proporcionally corolla tube (vs flowers with corolla tube larger than lobes 2:1).

Examined material.

Ecuador. Zamora Chinchipe, Cordillera del Condor, Canton El Pangui, 1330 m, 07 Oct 2006, Morales & Reyes 1958 (GB, MO), Neill et al 15506 (MO), Neill et al 15122 (MO), Quizhpe & Luisier 2003 (MO), Quizhpe & Luisier 2065 (MO), Quizhpe & Luisier 2086 (MO), Quizhpe et al 1811 (MO), Homeier et al 1500 (MO).

Peru. Amazonas: Condorcanqui, El Cenepa, 1010 m, Vasquez et al 22533 (F, MO); Imaza, 320 m, 09 Sep 1994, Jaramillo et al 434 (GB, MO), Vasquez et al 22533 (MO), Vasquez et al 22548 (GB, MO), Vasquez et al 24131 (GB, MO); Quebrada El Almendro, 430 m, 08 Mar 1998, Van der Warff et al 14510 (MO), Van der Warff et al 16149 (GB, MO), Van der Warff et al 13046 (GB, MO). Cajamarca: San Ignacio, La Union, 2200 m, Diaz & Torres 7659A (AMAZ, GB, MO). Oxapampa: Palcazu, Parque Nacional Yanachaga Chemillen, Estacion Paujil, 780 m, 25 Oct 2002, Monteagudo et al 4258 (AMAZ, GB, MO), Vasquez et al 32298 (GB, MO), Vilca & Ciriaco 349 (GB, MO); Bosque de Proteccion San Matias San Carlos, 1350 m, 28 Jun 2003, Monteagudo & Ortiz 5546 (GB, MO), Vasquez et al 27927 (MO), Monteagudo & Ortiz 5546 (MO), Monteagudo & Ortiz 5486; Pozuzo, 1500 m, 29 Jun 2008, Rojas & Ortiz 5790 (MO); Reserva Comunal Yanesha, Pampa Hermosa, 675 m, 07 Sep 2008, Valenzuela et al 11912 (MO). Ucayali: Coronel Portillo, 1200 m, Graham 4872 (MO), Graham 6604 (MO). San Martin: Moyobamba, Distrito de Calzada, 1050-1380 m, 11 Nov 1996, Sanchez Veja & Dillon 8620 (GB); Rioja, Distrito de Pardo Miguel, 1060-1200 m, 28 Jun 1999, Sanchez Veja et al 9911 (GB). Huanuco: Pachitea, Cordillera del Sira, 750 m, 28 Jan 1988, Morawetz & Wallnofer 12-28188 (GB), Wallnofer 11-2488 (GB), Wallnofer 11-29588 (GB), Wallnofer 11-9688 (GB). Cusco: Paucartambo, Kosnipata, 1020 m, 24 Dec 2007, Huamantupa 10595 (MO); Quispicanchis, Camanti, 1103 m, 13 May 2010, Clark et al 11402 (MO).

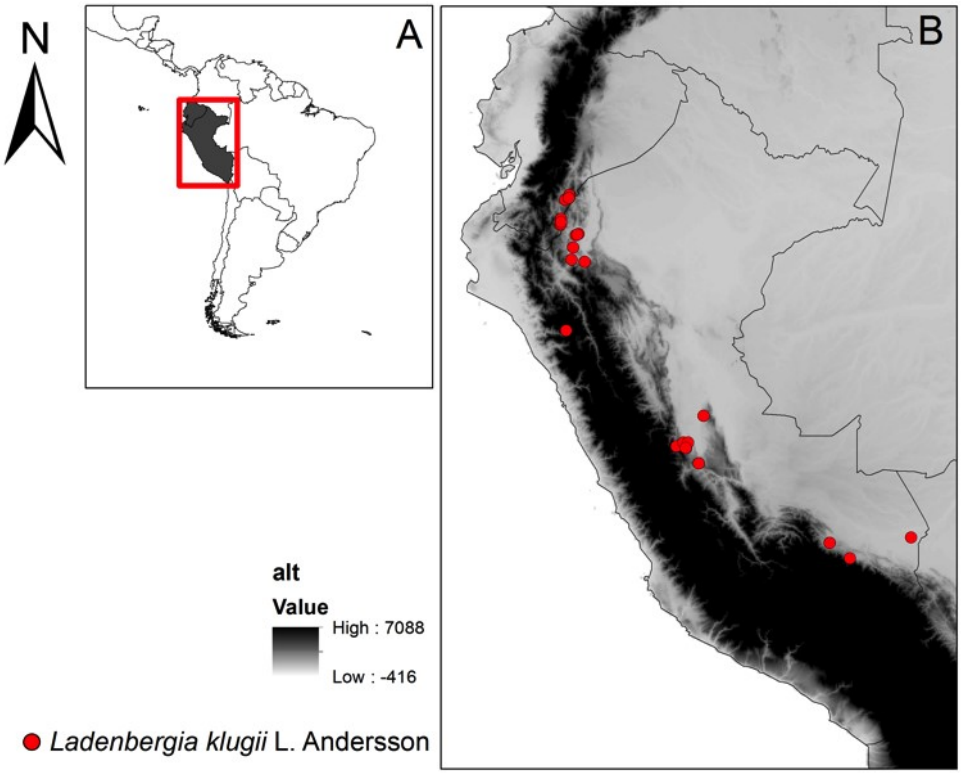

Fig 14. A. Peru and South America. B. Enlarged map showing the distribution the *Ladenbergia klugii* L. Andersson

9. *Ladenbergia lehmanniana* L. Andersson. Nordic Journal of Botany 17 (3): 295. (1997). Type: Lehmann 8627; Colombia, Cauca, "Las Estrellas, west Andes of Popayan", May [1854] (F holotype, K image! two isotypes).

Tree 8 (-20) m tall. Young branches rather sparcely puberulous. Stipules shortly fused at the base, ovate in the basal portion with upper part acuminate, generally sparcely puberulous, 2.2-4 x 0.5-0.65 cm long; petioles 0.8-2.5 cm long, glabrous to sparcely puberulent; leaf blades plane, thinly in texture, +/- chartaceous when dry, 10-23 x 4.6-8.5 cm, elliptic to ovate (length/width 2.1-2.5), obtuse to cuneate at base, attenuate to acuminate at apex, midvein above slightly sulcate, secondary veins prominulous above and slightly sulcate, prominent beneath, 7-12 pairs with arrangement brochidodromous, tertiary venation obscure above and below with pattern alternate percurrent, adaxial surface +/- matte, glabrous, abaxial surface with midrib and veins puberulous, intervenous surface glabrous or minutely strigose at least when young,

margin plane, tuft domatia present. Inflorescence terminal, branched in one to two orders, many-flowered (generally 30 - 60 flowers), broadly triangular in outline, axes densely pubescent, with trichomes ferruginous, peduncles 3-4.5 cm, rachis 3.5-6.5 cm long composed by 2-3 nodes with axes articulated, dichasial, bracts lanceolate, acuminate, generally deciduous. Flowers 5-6 merous, strongly fragant, nocturnal, distylous, pedicellate or on short axes in dichasial congested groups of 3-6; hypanthium obconical, puberulous or densely hirtellous, ca. 4-6.5 x 2-3.2 mm, calyx limb 5-8.5 mm long, lobes irregular generally undulate to truncate, 2.5-5.5 mm long, glabrous or puberulous outside, glabrous inside, without colleters evident; corolla salverform, white, tube in brevistylous flowers 14-16 mm, in diameter 2.5-3 mm, tube in longistylous flowers 15-17 mm, in diameter 2-2.5 mm, lobes in brevistylous flowers 7-8.5 mm and in longistylous flowers 7.6-8.1 mm, filaments attached ca 6.7 mm above base of corolla tube (ca. 40 % of tube length) in longistylous flowers and ca 9-10.5 mm above base of corolla tube (ca. 70 % of tube length) in brevistylous flowers, anthers 4.7-5.2 x 1-1.5 mm; style glabrous, ca. 3.5-4.5 mm long in brevistyls flowers and 12-15 mm long in longistyls flowers, stigmatic lobes ca 2.5-3.5 mm. Capsules woody, narrowly cylindrical, externally glabrous or slightly puberulous, 32-65 x 7-8 mm, endocarp ca. 0.2 mm thick. Seeds not seen.

Distribution, habitat and phenology. *Ladenbergia lehmanniana* is found in the western slopes of Andes from central Colombia to north of Ecuador (Fig 15). This species is known from few specimens because it occurs in areas of difficult access. It has been collected in flower and fruit in February-March and August.

Diagnostic Characters and Discussion. *Ladenbergia lehmanniana* is characterized by its comparatively narrow leaf blades, its large calyx with undulate to truncate lobes somewhat shorter than the tube, and by its comparatively small corolla and short, thin walled fruits.

Andersson (1997) compare *L. lehmanniana* with *L. heterophylla and L. obovata*, which present similar indumentum in leaf blades and large calyx with lobes undulate. These species can be separated by the length of the corolle tube (15-20 mm in *L.*

lehmanniana vs 50-70 in *L. heterophylla* and *L. obovata*), and texture and size of the fruit (thin and 32-65 mm in *L. lehmanniana* vs thick and 85-150 mm in *L. heterophylla* and *L. obovata*).

Examined material.

Colombia. Valle. Mpio. Buenaventura, córrego Chanco, shore of Rio Calima, 17 Feb 1989, Devia & Prado 2466 (MO). Antioquia: Urrao Municipio, Zona limítrofe del Parque Nacional Natural Las Orquideas, 30 Nov 1993, 1400-1500 m, Pipoly et al 17387 (GB, MO), Pipoly et al, 17411 (GB, MO). Choco: Cerro Mecana, 8 Jan 1984, Juncosa 1780 (MO).

Ecuador. Carchi. Canton Tulcan, Parroquia Tobar Donoso, Reserva Indigena Awa, Centro El Baboso, 17-27 Aug 1992, Tipaz et al, 2001.

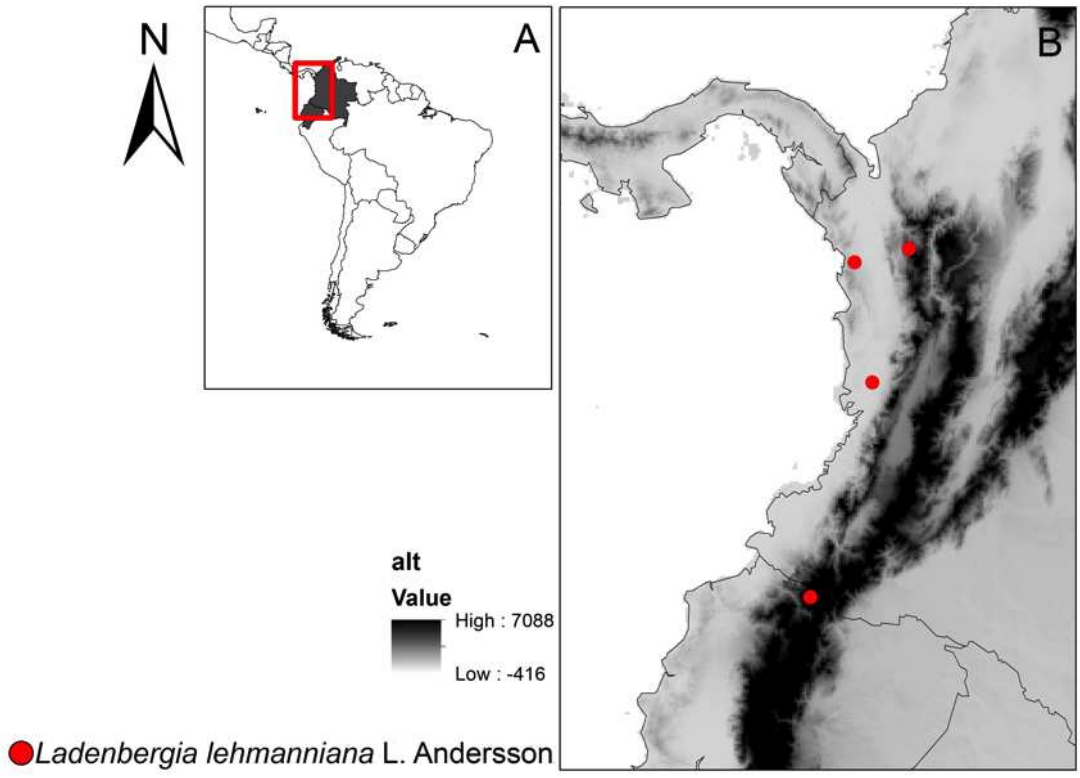

Fig 15. A. Northern Ecuador, Colombia and South America. B. Enlarged map showing the distribution the *Ladenbergia lehmanniana* L. Andersson

10. *Ladenbergia macrocarpa* (Vahl) Klotzsch. Getr. Darst. Gew. 14: ad tab. 15 (1846). *Cinchona macrocarpa* Vahl, Skrivt. Naturhist. Selsk. (Kioben- havn) 1: 20 (1790). *Cascarilla macrocarpa* (Vahl) Wedd., Ann. Sci. Nat., Sér. 3, 10: 12 (1848)**.** Type: Ortega; Colombia, ïn regno Santa Fé 1785 (BM lectotype, designated by Andersson 1994: 28). *Cinchona ovalifolia* Mutis, Papel Periódico de Santa Fé 111: 465 (1793). Type: Mutis 620; Colombia, without further notes (MA lectotype designated by Andersson 1997, US ster. Isolectotype).

Cinchona magniflora Pav. Ex DC., Prodr. 4: 354 (1830), pro syn. *Cinchona macrocarpa*

Cinchona prismatostylis Karsten, Fl. Columb. 1: 12, tab. 7 (1858). *Remijia primatostylis* (Karsten) Benth. & Hook. F. ex Flueck., Chinarinden 16 (1883). *Cascarilla primatostylis* (Karsten) Tiana, Rev. Acad Colom. 2: 412 (1938). Type: Karsten s. N; Colombia, Cundinamarca, “Pipiral prope Bogotam” (W lectotype designated in Andersson 1997).

Tree to 25 m tall. Young branches densely villosulous. Stipules fused throughout forming a conical calytra, densely villosulous to hirtellous external and internal puberulous to villosulous, 1.7-5.2 cm x 2-3.2 cm; petioles 1.8-5.2 cm long, moderadely to densely villosulous; leaf blades plane or slightly bullate, thick in texture, chartaceous when dry, 11-35 x 5-25 cm, ovate to suborbicular (length/width 1.4-2.2), broadly cuneate or rounded at base, obtuse to rounded at apex, secondary veins 8-11 pairs with arrangement brochidodromous, slightly sulcate above, prominent beneath, tertiary venation +/- evidente distinct above with an alternate-percurrent or opposite-percurrent arrangement, adaxial surface nitid and glabrous to hirtellous, abaxial surface adpresse to +/- hirtellous throughout, tuft domatia absent or indistinct. Inflorescence terminal branched in one to three orders, few-flowered (generally 12-35 flowers), broadly triangular in outline, axis densely reddish pubescent, peduncles 2.5-5 cm long, rachis 8-12 cm long, bracts lanceolate, caducous. Flowers 5-merous, fleshy, fragant, nocturnal, distylous, sessil to subsessile or axes in dichasial groups; hypanthium obconical, puberulous to villosulous, ca. 3.5-5.5 x 2-3.5 mm, calyx limb 3.8-6.5 mm long with lobes generally truncate to undulate 1.2-2 mm long, moderadely to densely villosulous outside, densely sericeous to puberulos inside, colleters in group towards base; corolla salverform, pilose externally and glabrous inside, white, long

with tube in longistylous flowers 32-44 mm, in diameter 3-7.5 mm, brevistylous flowers not seen, lobes of the flowers 15-18 mm; filaments attached ca 15-20 mm above base of corolla tube (ca. 60 % of tube length), anthers 11-13 x 1.8-2.5 mm; style hirtellous, 24-33 mm long, stigmatic lobes ca 4.9-11 mm. Capsules woody, cylindrical to obovoid, externally glabrous to puberulous, 70-130 x 9-15 mm, endocarp thick 0.5-0.6 mm. Seeds oblong-fusiform, 12-15 x 3-5.5 mm, with wings marginally fimbriate.

Distribution, habitat and phenology. *Ladenbergia macrocarpa* is found on montane wet forest from northern Colombia and northwesternmost Venezuela, southern Ecuador to north of Peru (Fig 16). It has been collected in flower and fruit in November to March.

Diagnostic Characters and Discussion. *Ladenbergia macrocarpa* is characterized by its calyptrate stipules, large flowers with a truncate to subtruncate calyx wich is +/- extensively velutinous inside with colleters in the base, a coarse tubed corolla, and by its large, thick-walled capsules.

Standley (1931) in his treatment of Rubiaceae from Colombia establishes the differences between *L. macrocarpa* of *L. crassifolia* based on the length of fruit (50-80 mm vs 30-50 mm in *L. crassifolia*) and the abaxial indument of leaf blades (hirtellous in *L. macrocarpa* vs. glabrous in *L. crassifolia*).

Andersson (1994) with material from Ecuador found differences between *L. macrocarpa* and *L. crassifolia*, based on the indument and form of the leaves (rounded and hirtellous in *L. macrocarpa* vs. elliptic, glabrous to strigose in *L. crassifolia*), the presence of domatios (absent in *L. macrocarpa* vs present in *L. crassifolia*), and pubescence of internal calix limb (*puberulous* in L. macrocarpa vs. glabrous in *L. crassifolia*).

Andersson (1997) based on material from Ecuador, Colombia and Venezuela, synonymize *L. crassifolia* within *L. macrocarpa*, he point out the characters using to separate species are a combination of features from leaves, internal calix tube, and all

these characters present a gradual variation. Furthermore, he mention that morphotypes of *L. crassifolia* seems to have a continuous distribution until to the south and north boundaries of *L. macrocarpa*. During my studies, I have observed two morphotypes inside of *L. macrocarpa*, one of them with glabrous leaves, adpressed indument and slightly small fruit (collected in low altitud from Venezuela, Colombia y Ecuador); and a second morphotype with pubescent, long fruit (collected in high altitudes from Colombia, Ecuador y Perú).

One part of the material from Colombia examined by Andersson (1994) as *L. crassifolia* correspond to glabrous morphotype of *L. macrocarpa*, which had small fruit due to the early growth stage. Materials from Ecuador examined by Andersson (1994) as *L. crassifolia* correspond with the type material described for the specie. Both species coexist within the same area in the south of Ecuador and the northern boundaries of Perú, therefore It could be possible the presence of hybrids between the two species.

In conclusion *L. macrocarpa* can be differenciated of *L. crassifolia* based on the form of the leaves (ovate-oblong to rounded in *L. macrocarpa* vs elliptic in *L. crassifolia*), abaxial leaf indument (villosulous to hirtellous in all abaxial leaf blades in *L. macrocarpa* vs glabrous or puberulous only in the vein on abaxial leaf blades in *L. crassifolia*), length and width of the corolla tube (32-60 mm x 4.5-5.5 mm in *L. macrocarpa* vs 20-25 mm x 2.5-3.5 in *L. crassifolia*), and width of the capsules (70-110 mm in *L. macrocarpa* vs 15-45 mm in *L. crassifolia*).

Examined material.

Colombia. Antioquia: Camargo et al 7074 (COL), Escobar et al 6123 (COL, NY), Escobar & Velásquez 7374 (GB, MO), MacDouglas & Roldán 3665 (MO), Palacios et al 86 (COL), Zarucchi & Cárdenas 4304(MO). Boyacá: Espinal & Montenegro 1711 (COL) Rangel et al. 2283 (COL), Uribe 6486 (NY), Valencia 3 (COL). Cauca: Andesson et al. 2103 (COL, GB, S), Cuatrecasas 23504 (F, US), Lehmann 866, 2112 (G), 2122 (BM, G), von Sneidern 2659 (G), Chocó: Gentry & Rentería 24212 (COL), Silverstone-Sopkin et al, 1769 (COL), 1811 (COL, NY). Cundinamarca: Barclay & Juajibyoy 3780 (COL, US), Díaz 3148 (COL), Idrobo 5350 (COL), Linares & Morales 2533 (COL), Triana 1812 (BM, P). Huila: Croat

51927 (MO), Lozano et al. 4130 (MO), Murcia 14 (MO), Pérez Arbeláex & Cuatrecasas 8386 (F), Stein 3723 (COL, G, B) . Meta: Camargo & Huertas 7960 (COL). Nariño: Mexia 7575 (F), Mexia 7642 (F). Norte de Santander: Cuatrecasas et al. 12742, 12815 (F), Lozano et al. 5522 (COL), Wilde 2703 (COL). Santander: Castro & Rodríguez 1030 (COL), Díaz & Lozano 405 (COL). Tolima: Lehmann 2332a (BM, G). Valle: Silverstone- Sopkin et al. 2765 (MO).

Venezuela. Táchira: Steyermark 57350 (F, NY), Steyermark et al. 98776 (K, MO, NY), 100792 (G, NY).

Ecuador. Azuay: Camp E-4322 (COL, K, MO, NY, S, US), (Tafalla in) Pavón 602 (MA; G without locality or number). Carchi: Mexia 7459 (F, MO), Palacios & Rubio 7276 (MO). Loja: Fosberg & Giler 23089 (NY), Prieto AP-26B (F, NY), Steyermark 54756 (F), Steyermark 54757 (F), Tafalla 565 (G, MA, P). Morona- Santiago: Camp E-1618 (NY, US), Jorgensen CuJ-51 (US), Steyermark 54306 (F, MO ster., NY). Sucumbios: Boom et al, 1406 (F, K, NY, QCA, U, US), Harling 4090 (S), Jaramillo 9313 (NY, QCA), 9352 (F, NY, QCA), Steere 8004 (NY ster.). Zamora Chinchipe: Fosberg & Giler 23139 (NY).

Peru. Cajamarca: San Ignacio. Diaz et al 10018 (MO); Rodriguez et al 2947 (MO).

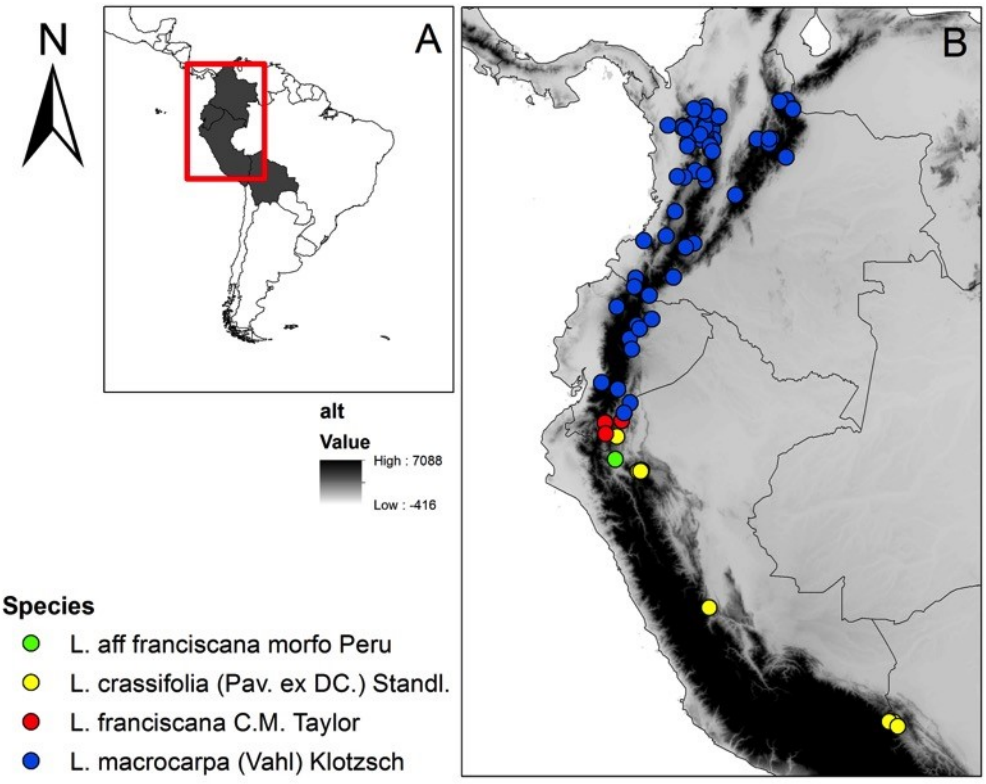

Fig 16. A. Peru, Ecuador, Colombia, Venezuela and South America. B. Enlarged map showing the distribution the *Ladenbergia macrocarpa* (Vahl) Klotzsch and *Ladenbergia crassifolia* (DC.). Morphotypes considered as *L. franciscana* (*L. crassifolia* considered here) and *L. aff. franciscana* (Rodriguez et al 2947) (*L. crassifolia* considered here) are showed in circles red and green respectively.

11. *Ladenbergia moritziana* Klotzsch. Gentr Darst. Gew. 14: ad tab 15 (1846). *Cinchona moritziana* (Klotzsch) Karsten, Fl. Colum.1: 133 (1861). *Cascarilla moritziana* (Karsten) Triana, Rv. Acad Colomb. 2: 414 (1938). Type: Moritz 962; Venezuela, Distrito Federal, Picacho Galipan in the Cordillera del Avila (BM lectotype designated by Andersson 1994, F fragment, HBG image! P image!)

Cascarilla calycina Wedd. Amm. Sci. Nat., Sér 3, 10: 12 (1848). *Ladenbergia calycina* (Wedd.) Standl., Publ. Field Mus., Bot. Ser., 7: 18 (1930). Type: Linden 1630; Colombia, Magdalena, 'prov. de Río Hacha", Feb 1844 (P lectotype designated in Andersson 1997, BM, G, isolectotypes)

Cascarilla citrifolia Wedd., Ann. Sci. Nat., Sér. 3, 10: 11 (1848). *Buena citrifolia* (Wedd.) Wedd., J. Linn. Soc. 11: 187 (1871). Type: Funck & Schlim 104; Venezuela, Distrito Federal, "prov. de Caracas, Galipan", Jan 1846 (P lectotype designated in Andersson, 1997, photo F- 37214; BM, F fragment, G, isolectotypes)

Cinchona tovaroensis Karsten, Fl. Columb. 1: 134 (1861). *Ladenbergia tovaroensis* (Karsten) Standl., Publ. Field Mus., Bot. Ser., 7; 364 (1931). Type: Karsten; Venezuela, Aragua, Colonia Tovar (W Lectotype designated here; NY possible isotype).

Shrub or small tree 2 (-12) m tall. Young branches glabrous. Stipules shortly fused at the base, ovate or oblong in the basal portion with upper part rounded or obtuse, generally glabrous to puberulous, 2.1-3 x 0.8-1.5 cm long; petioles 1.3-5 cm long, glabrous; leaf blades plane, thick in texture, +/- chartaceous when dry, 6-15 cm x 2.5-11 cm, elliptic to oblong (length/width 1.4-2.4), obtuse to cuneate at base, obtuse at apex, midvein above deeply sulcate, secondary veins prominulous above and slightly sulcate, prominent beneath, 6-10 pairs with arrangement brochidodromous, tertiary venation +/- obscure above, slightly distinct below with pattern alternate percurrent,

adaxial surface matte to subnitid, glabrous, abaxial surface with midrib and veins glabrous to sparsely puberulous, margin slightly revolute, tuft domatia present. Inflorescence terminal, branched in one to two orders, few-flowered (generally 9-36) flowers), broadly triangular in outline, axes glabrous to puberulous, peduncles 2-5 cm, rachis 1.5-8 cm long composed by 2-3 nodes with axes articulated, dichasial, bracts lanceolate, acuminate, generally deciduous. Flowers 5-merous, coarse, strongly fragant, nocturnal, distylous, sessile to subsessile or on short axes in dichasial congested groups of 3-6; hypanthium obconical, tomentulose with trichomes ferrugineous, ca. 3-4 mm x 2.5-3.5 mm long, calyx limb 1-2.5 mm long, lobes generally rounded-obtuse to irregular, 1-3.5 mm long, glabrous outside, glabrous inside, with colleters in the sinus; corolla salverform, white, tube in brevistylous flowers 25-35 mm, in diameter 3-5.5 mm, longistylous flowers not seen, lobes flowers 10-20 mm, filaments attached ca 14 mm above base of corolla tube (ca. 50 % of tube length), anthers 5-6.5 x 1-1.5 mm; style glabrous, ca. 20-22 mm long, stigmatic lobes ca 2-3 mm. Capsules woody, elliptic to oblanceolate, glabrous, 25-40 x 5-8 mm, endocarp 0.2-0.4 mm thick. Seeds oblong-fusiform (9-10 x 1.5-2.5 mm long.) with wings marginally fimbriate.

Distribution, habitat and phenology. *Ladenbergia moritziana* is found in the Sierra Nevada de Santa Marta in the NE Colombia and the Cordillera Costa and Distrito Federal of Venezuela (Fig 17). Is few reported in material of herbarium and floristic list, habit in cloud forest at altitudes between 1300-2000 m. It has been collected in flower and fruit in May and October.

Diagnostic Characters and Discussion.

Ladenbergia moritziana is characterized by its chartaceous leaf blades, wich are glabrous beneath except for conspicous tuft domatia, its calyx with reounded to obtuse lobes wich are much longer than the tube, its coarse but not particular long corolla (tube 25-35 x 5 mm) and thick walled, comparatively short capsules (25-40 mm x 5-8 mm).

Andersson (1997) compare *L. moritziana* and *L. brenesii*, which present similar indumentum and leaf shape. These two species can be separated by branching of the inflorescence (1-2 orders in *L. moritziana* vs. 2-3 orders in *L. brenesii*), the lenght and form the calyx lobes flowers (1.3-5 mm and rounded in *L. moritziana vs.* 1-2.5 mm and acute in *L. brenesii*).

Some glabrous and firmly chartaceous morphs of *L. macrocarpa* from Colombia resemble *L. moritziana*, but they may be distingued by the stipular fusion (caliptrate in *L. macrocarpa* vs. fusion at ½ forming sheath in *L. moritziana*), lenght of the corolla tube (25-35 mm in *L moritziana* vs 35-45 mm in *L. macrocarpa*), and lenght of the fruit (25-40 mm in *L. moritziana* vs. 70-110 mm in *L. macrocarpa*).

Examined material.

Colombia. Magdalena: Dawe 706 (K), Kirkbride 2343 (NY, US), Romero Castaneda 948 (Col, F), 7012 (COL).

Venezuela. Aragua: Edwards et al, 183, 198 (MO), Fendler 579 (F, G, K, NY), Steyermark 91525 (NY). Distrito Federal: Steyermark 56944 (F), 92014 (NY). Falcón: Steyermark 99315 (NY).

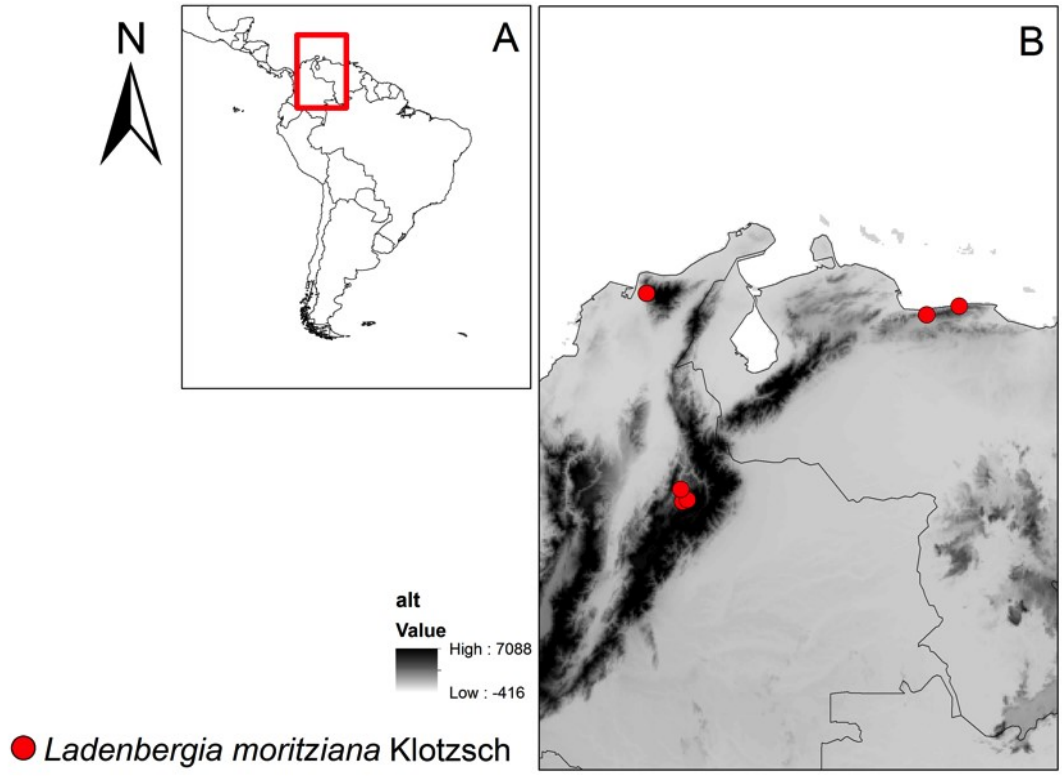

Fig 17. A. Colombia, Venezuela and South America. B. Enlarged map showing the distribution the *Ladenbergia moritziana* Klotzsch

12. *Ladenbergia muzonensis* (Goudot) Standl. Publ. Field Mus., Bot. Ser. 7: 20. 1931. *Cinchona muzonensis* Goudot, Phil. Mag., New Ser., 3: 132 (1828).- *Cascarilla muzonensis* (Goudot) Ann. Sci. Nat., Ser. 3, 10: 11 (1848) .- *Henlea muzonensis* (Goudot) Klotzsch & Karsten ex Walp., Ann. Bot. 2: 788 (1851-1852) .- Buena muzonensis (Goudot) Wedd., J. Linn. Soc. 11: 187 (1869).- *Muzonia muzonensis* (Goudot) N. Osorio, Estudio Quinas Estad. Unid. Colomb., ed. 2, 24 (1874). Type: Goudot s.n.; Colombia, Santander, near Muzo, 1845 (P lectotype designated by Andersson 1997; B destroyed (F–negative N°129); G, fragment in F, photo F-25717; K, photo NY-NS3169, G isolectotype).

Cascarilla hookeriana Wedd., Hist. Nat. Quinquinas 91 (1849).- *Buena hookeriana* (Wedd.) Wedd., J. Linn. Soc. 11: 187 (1869).- *Muzonia hookeriana* (Wedd.) N. Osorio, Estudio Quinas Est. Unid. Colomb. ed. 2, 24 (1874).- *Ladenbergia hookeriana* (Wedd.) Standl., Publ. Field. Mus., Bot. Ser. 7: 18. 1930.- Type: Purdie s.n.; Colombia, Norte de

Santander, Ocaña, June 1845 (P ex herb. Hooker, lectotype designated for Andersson, 1997; K ex herb. Hooker, isotype, photo NY-NS3167).

Cinchona henleana Karsten, Fl. Columb. 1: 55 (1860).- Type: Karsten s. n.; Venezuela, Aragua, Colonia Tovar (W lectotype designated for Andersson, 1997).

Ladenbergia ulei Standl., Publ. Field. Mus., Bot. Ser. 11: 220 (1936).- Type: Ule 6765; Peru, Loreto, Pampas de Ponasa, Mar 1903 (G, lectotype designated in here; B destroyed; F Fragments).

Cinchona henleana var. *trichophylla* Steyerm., Acta Bot. Venez. 8: 247 (1973).- Type: Steyermark & Steyermark 95374; Venezuela, Carabobo, S of Borburata, 750-1100 m, 31 Mar 1966 (VEN holotype, B, F, K, NY, P, U isotypes)

Note nomenclatural. Andersson (1997) considered *Henlea rosea* Klotzsch & Karsten ex Walp as a synonym of *L. muzonensis*, but that is an invalid name, as this name appears as synonym of *Cascarilla muzonensis* Wedd [Ann. Bot. 2: 788 (1851-1852)] without a formal description validly published (nom. nud).

Shrub to Tree 4-20 m tall. Young branches puberulous or hirtellous. Stipules interpetiolar shortly fused at base, oblong in the basal portion with upper part acuminate ending generally at apex, margins conspicuously revolute, glabrous-puberulous to hirtellous externally and internally, 2-2.5 cm x 0.85-1.2 cm, colleters in one row at base, 1-1.2 mm; petioles 2-4.5 cm long, glabro-purberulo to hirtellous; leaf blades not bullate, thin in texture, membranaceous when dry, 17.5-55 x 5.8-25 cm, elliptic-oblanceolate to obovoid (length/width 2.2-3.1), cuneate or attenuate at base, acuminate at apex, secondary veins 11-17 pairs with brochidodromous arrangement, slightly sulcate above, prominent beneath, tertiary venation +/- evident above, distinct below with an alternate-percurrent or opposite-percurrent arrangement, adaxial surface glossy and glabrous to puberulous, abaxial surface with midrib and veins glabrous-puberulous to hirtellous-hirtello and intervenous surface glabrous-puberulous to hirtellous, margins revolute, tuft domatia absent. Inflorescence terminal

decussate, branched in one to two orders, few-flowered (generally 27-48 flowers), broadly triangular in outline, axis glabrous to densely hirtellous, peduncles 2.5-4 cm long, rachis 11-18 cm long with all axes continuos, higher order (1-2) eixes contracted and dichasial, bracts cupuliform to cuneiform apiculate. Flowers 5-merous, fleshy, fragant, nocturnal, distylous, sessil to subsessile or axes in dichasial groups; hypanthium narrowly obconical, corrugated texture in dry material, glabrous to densely hirtellous, ca. 4-6.5 x 3.3-4 mm, calyx limb 4.5-6.2 mm long with lobes generally laciniate and irregular 2.8-3.5 mm long, glabrous to hirtellous outside, densely hirtellous inside, colleters arranged in 2-3 rows; corolla salverform, pilose externally and glabrous inside, white, long with tube in brevistylous flowers 32-37 mm, in diameter 3.5-4.1 mm, with longistylous flowers 19.5-22.5 mm, in diameter 4.2-4.5 mm, lobes in brevistylous flowers 19.5-30 mm long and in longistylous flowers 16-18.5 mm; filaments attached ca. 26 mm above base of corolla tube (ca. 70 % of tube length) in brevistylous flowers and ca 8-10 mm above base of corolla tube (ca. 40 % of tube length) in longistylous flowers, anthers 6.5-11 x 1-1.3 mm; style glabrous, ca. 4.5-5 mm long in brevistyls flowers and 12-14 mm long in longistyls flowers, stigmatic lobes ca. 4-6mm. Capsules woody with dehiscence acropetal, narrowly oblong to cylindrical, externally hirtellous, 3.2-60 x 6-12 mm, endocarp 0.3-0.4 mm thin. Seeds oblong-fusiform, 13-14.5 x 2.5-3.2 mm, with wings marginally fimbriate (Fig 18 A-J).

Vernacular names: This species is called **"**quina morada" in the Cordillera Oriental of Colombia (voucher: Fosberg, 21413); "tsánnum (aguaruna name)" "nugkam" in the northwestern of Peru. "unt tsachik" by huambisa tribe in Peru (Alban, 2013).

Distribution, habitat and phenology. *Ladenbergia muzonensis* is found in Cordillera Costa and lowlands of the Andes in Venezuela, northern Choco region and northern of Magdalena Valley, Cordillera Condor in Ecuador and north lowlands of central western Andes in Peru, at 200 and 1800 msnm (Fig 19). It has been collected in flower and fruit in February-March and November-December.

Diagnostic Characters and Discussion. *Ladenbergia muzonensis* is a shrub or tree characterized by its long persistent stipules, with oblong base and acuminate apex,

with conspicuously revolute margins, its pauciflora inflorescences with 1-2 orders with lateral axes contracted, flowers fleshy, sessile to subsessile or dichasial clustered, it's usually large calyx limb with lobes truncate to fimbriates and by acropetal dehiscent capsules.

Besides the names mentioned above to *L. muzonensis*, there are labels of Sullivan (1984) with names for species included in the genus *Muzonia* that were not properly published and can lead to misunderstood. The only document published by Sullivan, his treatment about new *Muzonia*'s species, is a memoir of one of his conferences (Amer. Journal Botany, 1970). There, the author considers the genus with a total of six species, among those he describes three are new species based on the bracts' shape and pubescence.

Analyzing the same specimens that Sullivan (1984) observed, I can understand his idea of the different flower clustering, the length of corolla's tubes and the length of lateral inflorescence axis to distinguish their species. Certainly, based on vouchers available now, we can find that the last order dichasium can cluster 3-6 (7) sessile and subsessile flowers, the length of corolla tubes varies accordingly to heterostily and also the flower ontogeny and length of lateral axis varies from contracted to elongated ones. Finally, we considerer that names cited by Sullivan: *M. alopekia* G.A Sullivan & Steyerm., *M. soejartiana* G.A Sullivan & Steyerm, and the combinations of *M. henleana* (Karst.) G.A Sullivan & Steyerm., are not valid because these were not validly published.

Fig 18. *Ladenbergia muzonensis* (Goudot) Standl. (A-I). A. Habit. B. Stipule. C. Abaxial indumentum of the leaf blade. D. Hypanthium. E. Inside Calyx Limb. F. Inside the corolla tube. G. Stile. H. Fruit. I. Seed. *Ladenbergia pavonii* (Lamb.) Standl. (J-P). J. Habit. K. Stipule. L. Hypanthium. M. Inside Calyx Limb N. Inside the corolla tube O. Stile. P Fruit.

Examined material.

Colombia. Amazonas: Fernández-Perez 20001 (MO). Antioquia: Denslow 2610 (MO), Soejarto et al, 4115 (MO, NY). Bolívar: Pennell 4506 (NY). Boyacá: Lawrance 426 (F, G, K, NY). Caquetá: Cuatrecasas 9126 (COL, US), Juzepczuk 6548 (F). Chocó: Forero 4091 (COL), Forero et al 4300 (COL), Forero & Jaramillo 4493 (COL), Forero et al 8811 (COL, MO), Forero 9488 (COL, MO), Forero et al 9623 (COL), García-Barriga 11196 (COL, US), Gentry & Rentería 24026, 24297 (COL), Juncosa 1261 (MO). Norte de Santander: Fosberg 21405 (K), Hermann 10920 (F), Kalbreyer 1002 (K). Santander: Fosberg & Fassett 21805 (B, G, P), 21806 (NY, P), 21812 (C. K, S), Steeere 7063 (COL, F, NY, US). Vaupés: Schultes 5549 (COL) Departament unKnown: Lehmann B. T. -1225 (G, NY), B. T. -1226 (K).

Ecuador. Napo: Archidona, Parque Nacional Napo-Galera, Freire & Cerda 508 (GB, MO). Zamora-Chinchipe: Nangaritza, Cordillera del Condor, Qhizhpe et al 1810 (MO), Qhizhpe et al 699 (MO), Croat et al 91392 (MO), Neill & Qhizhpe 14935 (MO)

Perú. Amazonas: Bagua, Imaza. Berlin 967 (NY), Chavez 05 (MO), Diaz et al 7735A (MO, GB), Diaz et al 7949 (MO), Diaz et al 8480 (AMAZ, MO), Diaz et al 8654 (GB, MO, USM), Jaramillo et al 1168 (GB, MO, USM), Rodriguez et al 999 (MO), Van der Werff et al 14491 (GB, MO), Vasquez et al 21213 (MO, USM), Vasquez et al 21175 (MO), Vasquez et al 26107 (GB, MO). Loreto: Prov. Requena, Sierra del Divisor, Davila et al 1529 (AMAZ, F), Davila et al 1916 (AMAZ, MO). Cerro Pomasa, 1200 m, Ule 6765 (G). San Martin: Prov. Rioja, Dist. San Miguel, 1220 m, Sanchez Veja et al, 9455 (GB). Huanuco: Prov. Pachitea, Pucallpa, Sira Mountains, 800 m, Morawetz & Wallnofer (GB).

Bolivia. La Paz: Prov. Franz Tamayo, Santo Domingo, Tintaya, 1459 m, 10 Oct 2006, Cornejo et al, 46 (MO); Cornejo et al, 118 (MO). Parque Nacional Madidi, 1367 m, 06 Oct 2009, Arellano et al, 910 (MO); 400-1000 m, Fuentes et al 4208 (MO); 1876 m, 10 Jul 2005, Fuentes et al 9713 (MO); 1616 m, 01 Sep 2010, Fuentes et al 17273 (MO). Prov. Murillo, camino al valle Zongo, 1200 m, 30 Oct 1988, Beck & Foster 13962 (GB). Prov. Larecaja, Mapiri, 1140 m, 08 Ago 2004, Beck et al 29508 (LPB, MO); Beck 17209 (GB); Buchtien 1403(F fragments), 1404 (F), 1405 (F fragments), 1406 (NY); Krukoff,

11021 (F, G, K, MO, NY); 10921 (F, K, MO, NY); Rea 269 (GB, MO); Rusby G1 (F fragments, G, MO, NY, P); Weddell 4359 (P). Prov. Pararani, 1900 m, Ago 1933, Cardenas 1214 (F, G); 1000-1600 m, 24 Jul 2002, Clark & Barrientos (MO). Prov. Nor Yungas, road Incahuara-Mejillones, 1500 m, 15-16 Jan 1983, Solomon 9291 (MO), 9510 (GB, MO), 14873 (GB). Prov. Sud. Yungas, Rio Bopi, 690-730 m, Jul 27-31. 1939, Krukoff 10618 (F, MO, S); Cotapata, Santa Barbara, 2260 m, 25 Jul 2001, Navarro et al 1609 (MO). Prov. Caravani, road Bella Vista-Carasco, Km 6., 1250 m, 14 Sep 1996, Persson & Gusstafsson, 247 (MO).

Venezuela. Aragua: Croat 60563 (MO, NY), Fenfler 580 (G, K), Luteyn et al, 8205 (NY), Median 538 (NY), Pittier & Nakichonovich 15373 (US), Poelt & Oberwinkler14742 (M), Steyermark 86325 (NY), Wood 220 (NY). Distrito Federal. Delgado 66 (F), 341 (G, US), Liesner & Medina 13606 (MO), Pittier 8053 (US), Pittier s.n. (G), Steyermark & Aristiguietia 111 (NY), Steyermark 55096 (F, NY). Falcón: Steyermark 99207 (NY). Lara: Steyermark et al. 111712 (F). Yaracuy: Aristiguieta & Pannier 1913 (NY), Davise et al. 20826 (MO), Diedrichs 135 (NY), Fernández 3975 (NY), Rutkis 455 (MO), Styermark 105389 (NY, US) Steyermark et al, 106733 (US).

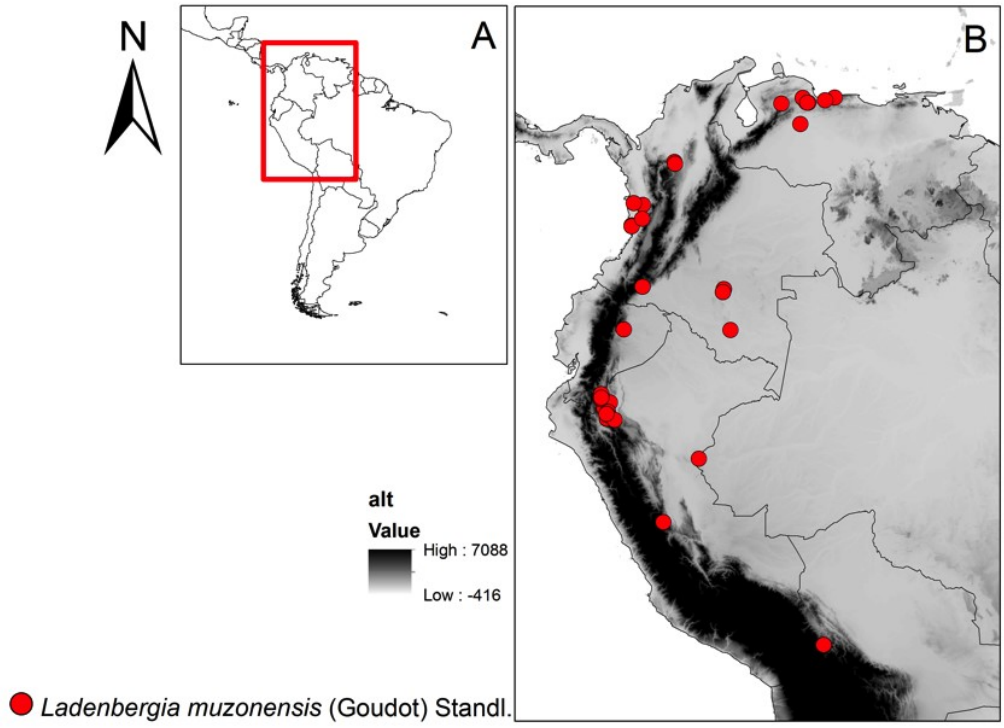

Fig 19. A. Peru, Ecuador, Colombia, Venezuela and South America. B. Enlarged map showing the distribution the *Ladenbergia muzonensis* (Goudot) Standl.

13. *Ladenbergia oblongifolia* (Mutis) L. Andersson. Fl. Ecuad. 50:19 (1994). *Cinchona oblongifolia* Mutis, Papel Periódico de Santa Fé 111: 465 (1793). *Cascarilla oblongifolia* (Mutis) Wedd., Ann, Sci. Nat., Sér. 3, 10:12 (1848). Type: Mutis 2908; Colombia, without notes (MA, lectotype designated here; US isolectotype).

Cinchona magnifolia Ruiz & Pav., Fl. Peruv. Chil. 2:53 (1799). *Ladenbergia magnifolia* (Ruíz & Pav.) Klotzsch in Hayne, Getr. Darst. Gew. 14: ad tab. 15 (1846). *Cascarilla magnifolia* (Ruiz & Pav.) Wedd., Ann. Sci, Nat., Sér. 3. 10:10 (1848). *Cascarilla magnifolia* (var.) *vulgaris* Wedd., Ann. Sci. Nat., Sér. 3, 11: 271 (1849). *Buena magnifolia* (Ruiz & Pav.) Weed., J. Linn. Soc. 11: 186 (1869). Type: Ruíz & Pavón; Peru, Dept. Huánuco, Cuchero (MA lectotype designated here; BM, G, G-DC isolectotypes).

Cinchona lutescens Ruiz & Pavón ex Vitman, Summa Pl. Suppl. 1: 262 (1802). Type: not traced; cf. Andersson 1994: 19-20.

Cinchona grandifolia ruiz & pav. ex Poir., Encycl. Metg. 6: 38 (1804), sphalm. pro *C. magnifolia.*

Cinchona caduciflora Hum. & Bonpl., Pl. Aequin. 1: 168 (1806). *Cascarilla caduciflora* (Hm. & Bonpl.) Wedd., Ann. Sci. Nat., Sér. 3, 10:10 (1848). *Cascarilla magniflora* (var) *caduciflora* (Hum. & Bonpl.) Wedd., Ann. Sci. Nat., Sér. 3, 11: 271 (1849). Type: Humbolt & Bonpland s. n.; Peru, Cajamarca, Jaén (B-W 4039:1 isolectotype designated by Andersson 1994: 19, G possible isotype).

Cinchona nitida Benth., Pl. Hartw. 190 (1845), non Ruiz & Pav. *Ladenbergia nitida* (Benth.) Klotzsch in Hayne, Getr. Darst. Gew. 14: ad tab. 15 (1846). *Cascarilla nitida* (Benth.) Wedd., Ann. Sci. Nat., Sér. 3, 10: 11 (1848). Type: Hartweg 1048; Colombia, Cundinamarca, between Fusagasugá and Pandi (K ex herb. Benth., lectotype designated by Andersson 1994: 19, photo NY- NS3168; B destroyed isolectotype, photo F- 137; BM, G, P isolectotypes).

Cascarilla rostrata Wedd., Ann. Sci. Nat., Sér. 3, 10: 10 (1848). *Cascarilla magnifolia* (var) rostrata (Wedd.) Wedd., Ann, Sci. Nat., Sér. 3, 11: 271 (1849). Type: Weddel 4112; Bolivia, La Paz, "prov. de Yungas", Dec. 1846 (P lectotype designated by Andersson 1994: 19; P, P-JU 9920, probable isolectotypes without numbers).

Cascarilla gavanensis Schltdl., Linnaea 26: 730 (1854). *Ladenbergia gavanensis* (Schltdl.) Standl., Punl. Field Mus., Bot. Ser., 13 (6): 42 (1936). Type: Lechler in Hohenacker 2349; Peru, Puno, "in montibus pr. San Govan (San Gavan), inl. M. 1854"(G lectotype designated here; BR, K, O, P, S isolectotypes).

Cinchona heterocarpa Karsten, Fl. Columb. 1: tab. 6 (1859). Type: Karsten s.n.; Colombia, Cauca, "Venta Quemada Popayán"(W lectotype designated by Andersson 1997; LE possible isotype, not seen).

Cinchona cuatrecasasii Standl. Ex Steyerm., Acta Biol. Venez. 4: 21 (1964). Type: Cuatrecasas 15546; Colombia, Valle, W slope of the Cordillera occidental, basin of Río Sanquininí, La Laguna 1250-1400m, 10-20 Dec 1943 (US holotype).

Tree to 25 (-35) m tall. Young branches glabrous to puberulous. Stipules fused at 1/2-forming sheath, ovate to rounded in the basal portion with upper part rounded, free part slightly revolute, generally glabrous to puberulous, 0.1-3.2 cm x 0.2-2 cm long; petioles 2.2-7.5 cm long, glabrous to sparcely puberulent; leaf blades plane, thin to rather tick in texture, papyraceous to chartaceous when dry, 12-35 x 5.5-27 cm, elliptic to suborbiculate (length/width 1-1.9), broadly cuneate to rounded at base, obtuse to rounded at apex, midvein above slightly sulcate, secondary veins prominulous above and slightly sulcate, prominent beneath, 6-10 pairs with arrangement brochidodromous, tertiary venation obscure to distinct above, slightly distinct below with pattern alternate percurrent, adaxial surface matte to subnitid, glabrous, abaxial surface with midrib and veins sparsely puberulous to hirtellous, intervenous surface glabrous or minutely strigulose to puberulous, margin plane, tuft domatia present. Inflorescence terminal, branched in one to four lateral orders, multi-flowered (45-135 flowers), broadly pyramidal in outline, axes glabrous to puberulous, peduncles 3.5-8

cm, rachis 7-13 cm long composed by 2-4 nodes with axes not articulated, dichasial, bracts lanceolate, acuminate, generally deciduous. Flowers 5-merous, strongly fragant, nocturnal, distylous, sessile to subsessile or on short axes in dichasial congested groups of 3-6; hypanthium obconical, glabrous to puberulous, ca. 2-3.2 x 1.8-2 mm, calyx limb 1.8-2.5 mm long, lobes deeply generally acute to triangular, 0.5-2.3 mm long, glabrous to sparsely puberulous outside, glabrous inside, colleters evident in the sinus; corolla salverform, white, tube in brevistylous flowers 10-13 mm, in diameter 1.5-2.5 mm, tube in longistylous flowers 10-12.5 mm, in diameter 1.5-2.7 mm, lobes in brevistylous flowers 6-6.5 mm and in longistylous flowers 8.5-11.5 mm, filaments attached ca 1.5-2.5 mm above base of corolla tube (ca. 20 % of tube length) in longistylous flowers and ca 4-7 mm above base of corolla tube (ca. 55 % of tube length) in brevistylous flowers, anthers 4.5-6.5 x 0.5-1.5 mm; style glabrous to rarely with bristes in the base, ca. 1.5-2.5 mm long in brevistyls flowers and 8.1-11.5 mm long in longistyls flowers, stigmatic lobes ca 2.5-4 mm. Capsules woody, narrowly ellipsoid to cylindrical, externally glabrous to slightly puberulous, 25-85 x 4.5-7 mm, endocarp 0.2-0.3 mm thin. Seeds oblong-fusiform (11-21 x 2.3-5.5 mm long.) with wings marginally fimbriate.

Vernacular names: “cascarilla macho”, “cascarillon” (Andersson 1994).

Distribution, habitat and phenology. *Ladenbergia oblongifolia* is found along the Andes from northern Colombia, Venezuela to central Bolivia (Fig 20). This species is commom and occurs in secondary forest at altitudes from 150-2300 m. It has been collected in flower and fruit in February-April and December.

Diagnostic Characters and Discussion. *Ladenbergia oblongifolia* is characterizaded by its stipules fused, thin or rather thick leaf blades with rounded to broadly acute apex, usually with distinct tuft domatia beneath, by its inflorescence pyramidal, its small flowers (corolla tube 7 -14 mm) and by thin walled fruit.

Andersson (1994) circumscribed *L. oblongifolia* and showed several morphotypes within the species. With more material from new collections I can confirm that the appreciation of Andersson was correct but that some of these morphotypes could also

correspond to hybrids between different related species that occurring in sympatry (*L. acutifolia* and *L. heterophylla*)

Morphotypes of *L. oblongifolia* ocurrs in the Colombia Andes are characterized by usually having firmer leaf blades, petiole with tuft hair in the base and diameter of the corolla tube coarse (2.5-3 mm), these characters resembles a *L. brenesii* that ocurrs in Costa Rica but are distinguished by size the corolla tube (10-15 mm in *L. oblongifolia* and in 15-35 mm *L. brenesii*) and calyx limb (1.8-2.5 mm in *L. oblongifolia* and in 2.3-3.2 mm *L. brenesii*).

Morphotyphes hairy of *L. oblongifolia* ocurrs in Central Andes in Peru and northern of Bolivia resembles a *L. magdalenae*, reported in Colombia. These species are distinguished by fusion of stipule (fused at ½ in *L. oblongifolia* vs used only in the base in L. magdalenae), shape of the leaf blades (suborbiculate to rounded in *L. oblongifolia* vs elliptic to oblong in *L. magdalenae*), number of lateral orders in the inflorescence (3-4 orders in *L. oblongifolia* vs 1-2 (-3) orders in *L. magdalenae*).

Examined material.

Colombia. Antioquia: Espinal & Montenegro 159 (COL), Fonnegra et al. 3132 (GB, MO), Ramírez & Cárdenas López 1819 (COL), Roldán & Marulanda 242 (GB), Toro 1316 (NY). Bolivar: Cuadros 1633 (US). Boyacá: Lawrance 740 (F, G, K, MO). Caquetá: Gentry et al. 9184 (MO). Cauca: Dawe 817 (K), Lehmann 3448 (BM, F, G, K), Mejía 97 (COL), Pérez Arbeláez & Cuatrecasas 6065, 6327 (F), Sneidern 500 (F, NY). Cundinamarca: García-Barriga 20026 (COL, NY), 21202 (COL, MA), Lehmann 7514 (F, K, NY), Triana 1810 (BM, K, P), Uribe 4747 (COL). Huila: Rusby & Pennell 1053 (NY). Nariño: Benavides 2839 (MO), Gentry et al. 34928 (MO). Quindio: Arbalaez et al. 1904 (NY), 2190 (COL, NY), 2382 (NY), Vélez et al. 1904 (NY), 2190 (NY), 2382 (NY), Vélez et al. 1054 (COL). Risaralda: Idrobo et al. 9952 (COL), Wolf 1091, 1261(MO). Tolima: Cuatrecasas 5726 (F), García- Barriga 8299, 12024 (US), Idrobo et al. 10495, 10613 (COL). Valle del Cauca: Cuatrecasas 18306, 19564 (F, US), Devia & Prado 2107 (COL, GB, MO, US), García-Barriga 18832 (F, US), Murphy & Madrid 669 (MO, NY), Stahl et al. 668 (GB).

Venezuela. Amazonas: Steyermark 106107 (NY).

Ecuador. Morona-Santiago: Gentry 30949 (Mo, NY), Jorgensen OHJ-4 (F, NY), Palacios 571 (MO, NY), 1446 (GB, MO), Schwabe 68233 (B), Zaruma 303 (GB, MO). Napo: Neill et al. 6482 (GB, MO), Pennington et al. 122210 (K, MO). Pastaza: Steere & Camp 8299 (F). Zamora-Chinchipe: Camp E-43 (NY, S, US), E-55 (NY, S), Little et al. 288 (Us), Neill 9580 (Gb, MO), Palacios et al. 8735 (GB).

Peru. Amazonas: Woytkowski 8067 (MO). Cuzco: Dudley 10208 (F, MO, NY), Gentry et al. 23650 (F, MO, NY), 23663 (F, MO), Núñez & Alanya 13327 (GB). Huánuco: Asplund 13345 (G), Gentry & Daly 18771 (F,MO,US), Gutiérrez Ruíz 112, 133 (F), Mexia 8170 (F, MO, NY), Schunke 10204 (MO, NY, F,US). Junín: Isern 2321, 2379, 2399, 2400, 2403 (F), Stein & Todzia 2393 (MO, NY), Weberbauer 1843 (F fragm., G). Loreto: Klug 3142 (F, G, K, K, MO, NY). Madre de Dios: Foster et al. 10914 (F). Pasco: Hartshorn et al. 2612 (MO), Smith 5190 (F, MO, NY). Puno: Dillon et al. 1179 (F), Hodge 6006 (F). San Martín: Belshaw 3475 (F, K, MO, NY), Knapp & Mallet 6491 (F, K, US), Schunke 5920 (NY, U), 9771 (F, G, MO, NY), Spruce 4843 (B, C, F fragment, G, K, NY, P), Woytkowski 6142 (US), 35319 (F, G, MO). Ucayali: Sullivan & Young 1190 (C, F, MO, NY).

Brazil. Roraima: Prance et al. 9727 (F, K, NY).

Bolivia. Beni: Killeen et al. 3092 (GB), Smith et al. 13306 (G), 13961 (MO), Smith & García 14151 (MO). Cochabamba: Cárdenas 2165 (F). La Paz: Bang 1661 (BM, F, G, K, MO, NY), Beck 9189 (GB, NY), Buchtien 1408 (HDG, NY), Krukoff 10293, 11222 (F, G, K, MO, NY), Rea et al. 38 (GB), Seidel & Vargas 1102 (GB), Solomon 9361 (MO, NY, U), 17628 (GB). Santa Cruz: Cárdenas 4010 (F, US).

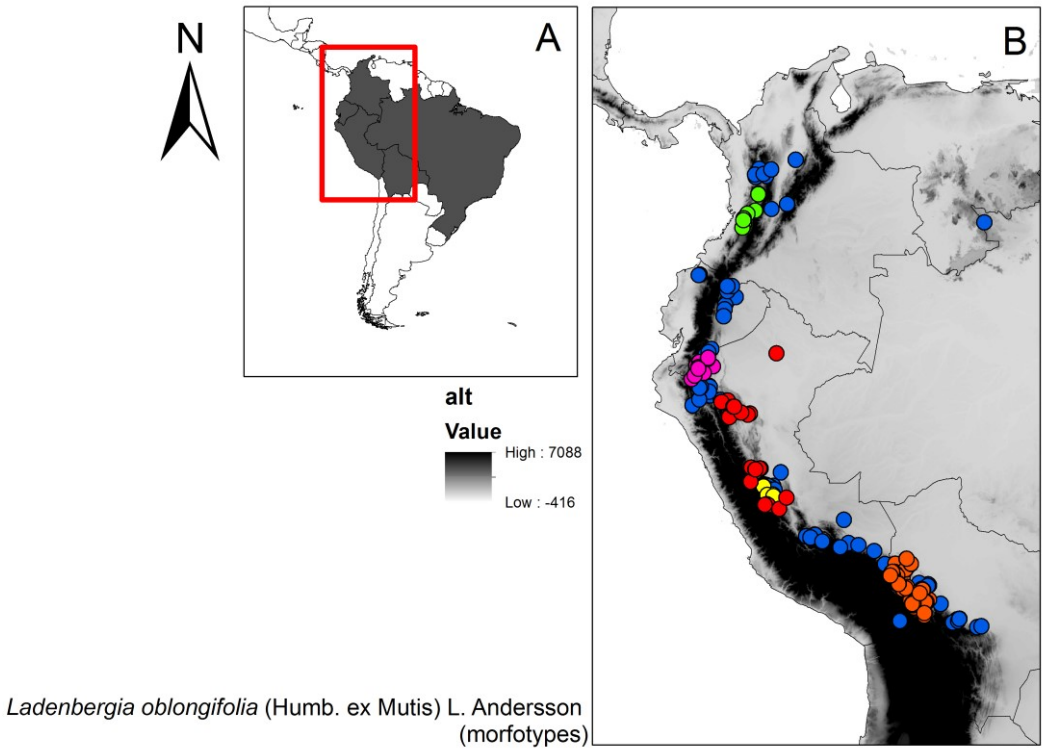

Fig 20. A. Bolivia, Peru, Ecuador, Colombia, Venezuela, Brasil and South America. B. Enlarged map showing the distribution the *Ladenbergia oblongifolia* (Mutis) L. Andersson. Morphotypes are showed in circles orange, red, yellow and green.

14. *Ladenbergia pavonii* (Lamb.) Standl. Publ. Field Mus., Bot. Ser., 7: 201 (1931). *Cinchona pavonii* Lamb., III Cinch. 8 (1821). *Cinchona cava* Pav. Ex Lamb., III Cinch. 8 (1821), pro syn. *Ladenbergia cava* (Lamb.) Klotzsch in Hayne, Gentr. Darst. Gew. 14: ad tab. 15 (1846). *Cascarilla pavonii* (Lamb.) Wedd., Ann. Sci. Nat., Sér. 3, 10:11 (1848). *Buena pavonii* (Lamb.) Wedd., J. Linn. Soc. 11: 186 (1869). Type: Pavón, Ecuador, "mountains of Loja" (BM lectotype designated by Andersson 1994; B destroyed, photo F-134; BM image!, MA image!, P image! possible isolectotypes).

Tree to 20 m tall. Young branches moderately to densely ferrugineous-pubescent. Stipules interpetiolar fused at 1/3-1/2 forming a sheath, rounded in the basal portion with upper part obtuse ending generally rounded, margins slightly revolute, densely puberulous or hirtellous externally and puberulous internally, 2.3-4.5 cm x 2-3.5 cm, colleters in one row at base, 1-1.2 mm; petioles 3.8-5.5 cm long, +/- densely hirtellous when young, eventually glabrescent; leaf blades plane, thin in texture,

membranaceous when dry, 17.5-45 x 18-31 cm, rounded-ovate to suborbicular (length/width 1.2-1.6), broadly cuneate or subcordate at base, rounded at apex, secondary veins 7-13 pairs with arrangement brochidodromous, slightly sulcate above, prominent beneath, tertiary venation evident in both sides with an alternate-percurrent or opposite-percurrent arrangement, adaxial surface matte and glabrous to puberulous, abaxial surface +/- hirtellous throughout, tuft domatia absent. Inflorescence terminal branched in two to three orders, multi-flowered (generally 30-80 flowers), broadly triangular in outline, axis densely reddish pubescent, peduncles 2.5-4 cm long, rachis 8-15 cm long, bracts lanceolate, caducous. Flowers 5-merous, fragant, nocturnal, distylous, sessil to subsessile or axes in dichasial groups; hypanthium narrowly obconical, glabrous to puberulous, ca. 3.5-6 x 2-3.2 mm, calyx limb 3-3.2 mm long with lobes generally irregular and undulate to round 2.8-3.5 mm long, glabrous to puberulous outside, glabrous inside, colleters absent; corolla salverform, pilose externally and glabrous inside, white, tube in longistylous flowers 35-75 mm, in diameter 3-4.1 mm, brevistylous flowers not seen, corolla lobes 12-20 mm; filaments attached ca. 31-41 mm above base of corolla tube (ca. 70 % of tube length), anthers 7-9 x 1-1.5 mm; style glabrous, 41-53 mm long, stigmatic lobes ca. 5-9mm. Capsules woody, narrowly ellipsoid to cylindrical, externally glabrous to puberulous, 52-150 x 9-11 mm, endocarp 0.5-0.6 mm thick. Seeds oblong-fusiform, 18-22 x 3-5 mm, with wings marginally fimbriate (Fig 18J-P).

Vernacular names: “cascarilla amarilla”, “cascarilla macho”, “huhuaco” (Andersson, 1994).

Distribution, habitat and phenology. *Ladenbergia pavonii* is found in the Ecuadorian Andes, mainly in western slopes, in wet forest at altitudes between 150 – 1600 m (Fig 21). It has been collected in flower and fruit in March and November.

Diagnostic Characters and Discussion. *Ladenbergia pavonii* is characterized by its large, rounded, thinnish leaf blades, which are matte above and densely hirtellous beneath, and its large flowers with calyx obscurely lobed and glabrous inside and often very long capsules (150 x 10 mm).

Ladenbergia pavonii is morphologically related to *L. heterophylla* due to the lenght of corolla tube, calyx undulate to rounded and long capsules, it differs by having different patterns of inflorescence (2-3 lateral order and laxa in *L. pavonii* vs 1-2 lateral order and slightly congested in *L. heterophylla*), indumentum of leaf blades (pubescente and ferugineous in *L. pavonii* vs glabrous to puberulous in *L. heterophylla*) and shape of leaf blades (suborbicular to rounded in *L. pavonii* vs elliptic-oblong in *L. heterophylla*).

Examined material.

Ecuador. Azuay: Ortiz 168 (QCA image!), (Tallafa in) Pavón 602 (G). Bolívar: Acosta Solís 6003, 6382 (F), Palacios & Neill 2155 (GB, MO), Rimbach 862 (F). Carchi: Madison et al. 4864 (F), Madison & Besse 7240 (QCA image!). Chimborazo: Acosta Solís 5221 (F). Cotapaxi: Mexia 6681 (F), Onore s. N. (QCA image!). El Oro: Steyermark 54234 (F, NY). Esmerada: Bonifaz & Cornejo 3496 (MO), Clark 2106 (GB). Imababura: Ownbey 2630 (F, MO). Los Ríos: Dodson & McMahon 5102 (F, QCA), Gentry et al. 54751 (GB, MO). Manabi: Cornejo & Bonifaz 7125 (GB), Raponen & Lindstrom 164 (GB). Pichincha: Dodson & Gentry 9716 (F), Little 6141 (F, K image!), Neil & Castro 9774 (MO), Webster & Urtecho 27631 (QCA image!), Delprete & Onore 6483 (NY). Sucumbios: Ownbey 2654 (F, MO).

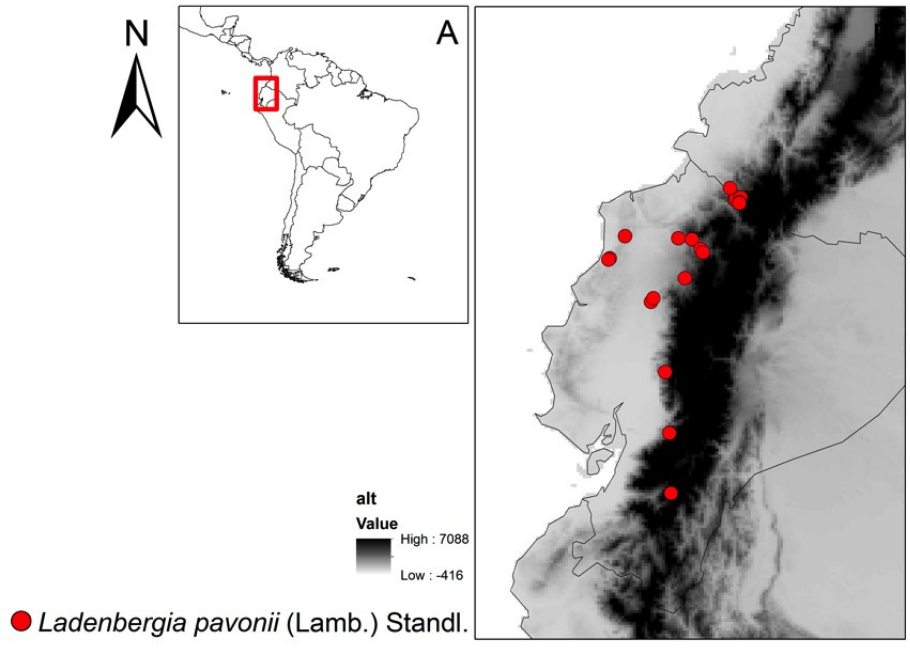

Fig 21. A. Ecuador and South America. B. Enlarged map showing the distribution the the *Ladenbergia pavonii* (Lamb.) Standl.

15. *Ladenbergia pittieri* Standl. Publ. Field Mus., Bot. Ser., 8:51 (1930). Type Pittier 12943; Venezuela, Trujillo, road Valera-Carora near La Cuchilla, 10 Feb 1928 (F holotype, G image! fragmets; G image! MO, NY isotypes).

Shrub or tree 3 (-7) m tall. Young branches glabrous. Stipules fused in the base, ovate to oblong in the basal portion with upper part acuminate, generally glabrous to puberulous, 2.5-3.5 x 1.1-1.5 cm long; petioles 2.5-5 cm long, glabrous to sparcely puberulent; leaf blades plane, thick in texture, chartaceous when dry, 10-26 x 6.5-15 cm, ovate to suborbiculate (length/width 1.5-1.7), cordate to rounded at base, acuminate at apex, midvein above slightly sulcate, secondary veins prominulous above and slightly sulcate, prominent beneath, 5-12 pairs with arrangement brochidodromous, tertiary venation obscure to impressed above, slightly distinct below with pattern alternate percurrent, adaxial surface matte to nitid, glabrous, abaxial surface with midrib and veins sparsely puberulous to +/- hirsute, intervenous surface glabrous, margin plane, tuft domatia present. Inflorescence terminal, branched in three to four orders, multi-flowered (70-110 flowers), broadly triangular in outline, axes glabrous to slightly strigose, peduncles 6-10 cm, rachis 5-10 cm long composed by 2-3 (-4) nodes with axes not articulated, dichasial, bracts lanceolate to subobtuse, acuminate, generally deciduous. Flowers 5-merous, strongly fragant, nocturnal, distylous, sessile to subsessile or on short axes in dichasial congested groups of 3-6; hypanthium obconical, puberulous to villosulous, ca. 2.5-3.1 x 1.8-2 mm, calyx limb 1.8-2.2 mm long, lobes deeply generally acute, 0.8-1.5 mm long, sparsely puberulous outside, glabrous inside, colleters evident in the sinus; corolla salverform, white, tube in longistylous flowers 25-40 mm, in diameter 1.2-2 mm, brevistylous flowers not seen, lobes 7-10 mm, filaments attached ca 13.5-15 mm above base of corolla tube (ca. 40 % of tube length, anthers 4-4.6 x 1-1.5 mm; style poberulous to hirtellous, ca. 15-19 mm long, stigmatic lobes ca 3.5-4 mm. Capsules woody, narrowly ellipsoid to cylindrical, externally glabrous to slightly puberulous, 50-90 x 3-4.5 mm, endocarp 0.2-0.3 mm thin. Seeds oblong-fusiform (9-12 x 1.8-3 mm long.) with wings marginally fimbriate.

Distribution, habitat and phenology. *Ladenbergia pittieri* is found on foothills and lower slopes of the northesternmost Cordillera Oriental of Colombia and Venezuela, Guiana and Brazilian Shield at altitudes between 150 – 1500 m. (Fig 22). This species is little collected because it occurs in areas of difficult access. It has been collected in flower and fruit in March and October.

Diagnostic characters and discussion. *Ladenbergia pittieri* is characterizaded by having ovate to suborbicular (length/ width 1.5-1.7) leaf blades wich are chartaceous, cordate to rounded at base and acuminate at apex with tuft domatia in the abaxial side, a multiflora inflorescence with three to four lateral ordens, a small calyx limb (1.8-2.2 mm) with acute-obtuse lobes, corolla tube large (25-40 mm) and slender (ca. 2 mm wide) and narrowly capsules elongate (50-90 mm x 1.8-3 mm).

Steyermark (1974) compares *L. pittieri* with *L. lambertiana*, *L. lucens* and *L. amazonensis* from which it differs in its stile puberulous to hirtellous except of *L. lucens* (now considered *L. lambertiana*) and *L. lambertiana*, of wich is distinguished by calyx lobed acuminate to obtuse and corolla tube larger.

Andersson (1997) distinguished *L. pittieri* from *L. lambertiana* by its fused (vs free) stipules and the presence of a hirsute or villous indumentum along the sides of midrib and veins (vs glabrous or minutely strigulose).

Extensive herbarium work permits to show that an Andersson's view is inadecuate to understand these species; the stipules of *L. pitiieri* are fused only at the base without reach to the forming sheath around the petiole (free in the Andersson'view). The indument features of leaves result gradual variation and It is not a good character for delimitation of species. Therefore, *L. pittieri* differs from *L. lambertiana* in having chartaceous and ovate leaf blades with cordate base, corolla tube and fruit usually larger.

Collections of *L. glaciliflora* from Brazilian Cerrado show some characters that resemble a lot of *L. pittieri* such as chartaceous and ovate to suborbiculate leaf blades

with cordate base, flowers tubes with long corolla and fruits. However, *L. pittieri* can be distinguished based on pedicelate flowers, fruits longer than *L. graciliflora* and distributions patterns disjunct.

Examined material.

Colombia. Norte de Santander: Schlim 691 (BM, F, G, K, P). Amazonas: Rio Igara Parana, Sastre 2094 (P image!).

Venezuela. Aragua: Van der Werff & Ortiz 5733 (F, Mo, NY). Lara: Marcano Berti et al. 351-979 (Us). Mérida: Steyermark 56695 (F, NY), Valverde et al. 1274 (Mo), van der Werff & Ortis 5686 (F, MO). Trujillo: Steyermark 55653 (F), Steyermark 57038 (F, NY), Steyermark & Carreño Espinoza 111641 (MO, NY). Zulia: Bunting 7775 (NY), Bunting 10779 (NY), Davidse et al. 18611 (MO). Amazonas: Terr. Federal Amazonas, Atures, Rio Coro Coro, 600 m, Holst et al 3186 (MO). Tachira: Rio San Buena, 700-1000 m, 13 Mar 1980, Liesner et al 9619 (MO)

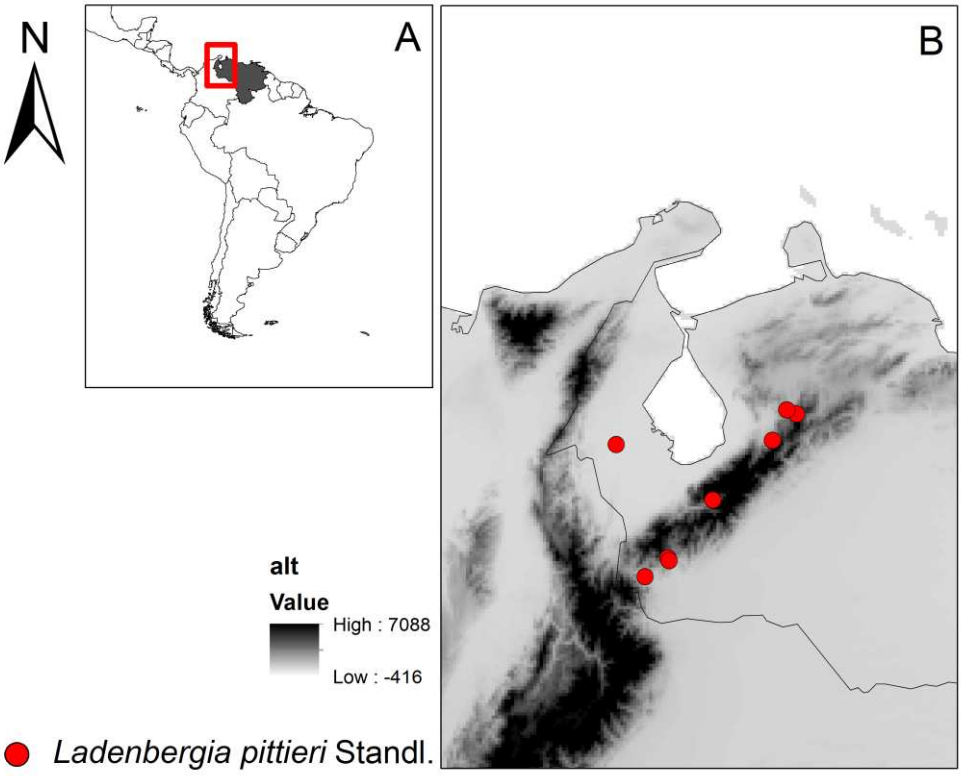

Fig 22. A. Colombia, Venezuela and South America. B. Enlarged map showing the distribution the *Ladenbergia pittieri* Standl.

16. *Ladenbergia riveroana* (Wedd.) Standl. Publ. Field Mus. Nat. Hist., Bot. Ser. 7: 201. 1931. *Cascarilla riveroana* Wedd., Ann. Sci. Nat., Bot. Ser. 3, 10: 11 (1848).- Type: [Tafalla in] Pavon 587; Peru, Cajamarca, "Cascarillo Azahar macho […] de Jaen" 1805 (G lectotype designated by Andersson 1994; MA image! isolectotype; BM image!, P (03945922) image! both probable isolectotypes)

Nomenclatural Note: Andersson (1994) designated as the lectotype for this species a specimen deposited at the G herbarium, and mentioned as possible isolectotypes specimens deposited at herbaria P, BR, K. Here, I highlight some important data from Andersson's lectotypification. Weddell (1848) described *Cascarilla riveroana* and did not mention of the type locality, but, later, Weddell (1849) mentioned the type locality as Jaen, in Peru. He also reported two common names noted by Pavon, "azahar macho" and "azahar hembra", which correspond to the brevistylous and longistylous flowers, respectively, which are noted on the vouchers deposited in herbariums P, at British Museum and Lessert (Delessert). There are five vouchers identified as *Cascarilla riveroana* deposited at P and labeled by Weddell, from which Andersson only studied one labeled for Weddell and present uncertain locality. Between the other vouchers: one has Weddell's labeling, the type locality and an incomplete label of Pavon (vulgo "azahar macho", N 587, Ic 741) and the other has Weddell's label, the type locality and an incomplete label of Pavon (vulgo "azahar hembra", N 586, Ic 740). The vouchers deposited at the BM herbarium all have an incomplete label of Pavon, with locality information and the common name "Azahar". The voucher at the MA herbarium has an complete label of Pavon (vulgo "Azahar macho", N 587, Ic 741), and is identified with the invalid name *Chinchona ferruginea.* This MA specimen matches the lectotype at G that Andersson selected, and thus is clearly an isolectotype. Material deposited in P is inadequate to determine an isolectotype.

Tree 7-20 m tall. Young branches hirtellous to hirsute. Stipules interpetiolar shortly fused at the base, oblong in the basal portion with upper part acuminate ending generally at an apex, hirtellous externally and internally, 1.8-3 cm x 0.75-1.1 cm, with colleters arranged in two or three rows on the base 0.7-1.3 mm; petioles 2.5-7.5 cm long, puberulous to hirtellous; leaf blades not bullate, thick in texture, chartaceous

when dry, 14.5-35 x 7.-20 cm, elliptic-oblanceolate to broadly ovate (length/width 1.75-2.1), broadly cuneate or cordate at base, attenuate to acuminate at apex, secondary veins 12-19 pairs with arrangement weakly brochidodromous, slightly sulcate above, prominent beneath, tertiary venation +/- obscure above, distinct below with an opposite-percurrent arrangement generally, adaxial surface matte to nitid and puberulous to hirtellous, abaxial surface slightly to densely hirtellous throughout, margins slightly revolute, tuft domatia absent. Inflorescence terminal, branched in two to three orders, multi-flowered (generally + 100 flowers), broadly triangular in outline, axes densely hirtellous, peduncle 2.5-6 cm long, rachis 12-18.5 cm long with all axes discontinuous, higher order (2-3) axes, unequally contracted, bracts ovate to lanceolate. Flowers 5-merous, strongly fragant, nocturnal, distylous, subsessile to separated on pedicels 2-3 mm long or on axes in dichasial groups; hypanthium obconical, densely hirtellous, 2.5-3.2 x 1.8-2.3 mm, calyx limb 2.6-2.9 mm long with lobes generally obtuse and irregular 1.2-1.5 mm long, sparsely hirtellous outside, glabrous inside, colleters not seen; corolla salverform, pilose externally and glabrous inside, white, l tube in brevistylous flowers 18-26 mm, in diameter 2.3-2.9 mm, tube in longistylous flowers 14-15.5 mm, in diameter 2-2.2 mm, lobes in brevistylous flowers 7.5-9 mm long and in longistylous flowers 9-11 mm; filaments attached ca 18 mm above base of corolla tube (ca. 75 % of tube length) in brevistylous flowers and ca 9-11 mm above base of corolla tube (ca. 55-60 % of tube length) in longistylous flowers, anthers 4,2-5.5 x 1-1.2 mm; style glabrous, ca. 12-14.5 mm long in brevistylous flowers and 12.5-14 mm long in longistylous flowers, stigmatic lobes ca 3.1-4 mm. Capsules woody with dehiscence basipetal, narrowly oblong- cylindrical, externally puberulous to hirtellous, 25-65 x 5-7 mm, endocarp < 0.4 mm thin. Seeds oblong-fusiform, 12-19 x 2.5-3.5 mm, with wings marginally fimbriate (9 J-K).

Vernacular names: The names “azahar macho” “azahar hembra” were reported by Pavon (Weddell 1949). “shuipiu kumpajii” by aguaruna people in Peru (Alban, 2013).

Distribution, habitat and phenology. *Ladenbergia riveroana* is found in montane wet forest in southern Ecuador, in the provinces of Morona-Santiago and Zamora Chinchipe, and in northern to Central Peru, in the departaments of Amazonas,

Cajamarca, and Pasco, at 700 and 2200 msnm (Fig 23). It has been collected in flower and fruit in April and September.

Diagnostic Characters and Discussion. *Ladenbergia riveroana* is a tree characterized by its hirtellous, oblong stipules that are apparently interpetiolar but actually shortly fused at the base; generally ovate-oblong leaf blades that are densely hirtellous throughout beneath, with the base generally cordate to broadly cuneate; multi-flowered inflorescences (+ 100 flowers) with the branches hirtellous and branched to 2-3 orders; small corollas that are slender, pilose externally, and glabrous inside; hypanthium that is densely hirtellous externally; calyx limb slightly hirtellous externally with the inside glabrous and the lobes irregular and generally obtuse. Fruits woody, slender and thin.

Standley (1936), in the Rubiaceae treatment for Peru, distinguished *Ladenbergia riveroana* from the similar species *L. malacophylla* and *L. carua* based on the form of the leaf base, acute in *L. riveroana* vs rounded or subcordate in *L. malacophylla* and *L. carua*. However morphological characters of the shape of the leaves of *Ladenbergia* must be taken with care, keeping in mind that leaf shape may vary according to the growing position on the branches and the type of environment where they develop. The material studied in this analysis shows that *L. riveroana* has leaves with the base variably acute to cordate.

Andersson (1997) did not compare *L. riveroana* and *L. carua*, which posses similar indument, leaf shape and flower length. These two species can be separated by branching of the inflorescence (2-3 orders in *L. riveroana vs.* 1-2 orders in *L. carua*), the number of flowers of each inlforescence (more than 100 in *L. riveroana vs.* 19-39 in *L. carua*), the fruit shape (more globose and pyriform in *L. carua* vs. slender and larger in *L. riveroana*) and the endocarp (thin in *L. riveroana vs.* thick in *L. carua*).

Examined material.

Ecuador. Prov. Santiago-Zamora: Cerro Partidero, beetwen the rios Paute and Negro, 1234 m, 04 Nov 1944, Camp E-920A (NY). Prov. Morona-Santiago: Limon Indaza,

Cordillera de Huaracayo, east of Cordillera del Condor and rio Coangos, 1800 m, 24 Mar 2001, Neill & Manzanares 13166 (MO, GB); Cerro Paatin Nairt, 1220 m, 11 Oct 2002, Wisum et al 38 (MO). Prov. Zamora Chinchipe: Nangaritza, Cordillera del Condor region, above Pachicutza, 1800 m, 5 Dec 1990, Neill & Palacion 9527 (GB, QCNE, MO); upper Rio Nangaritza valley, 930 m, 25 Nov, 2005, Neill & Quizhpe 14927 (MO, NY); 900 m, 3 Dec, 1990, Neill 9492 (QCNE, MO); 930 m, 25 Nov 2005, Neill & Qhizhpe 14927 (GB, MO); Sector Hito el "Empalme", 1200 m, 8 Jun 2005, Quizhpe et al 1219 (MO, NY, US); Canton Miazi, 970 m, 20 Oct 1991, Palacios et al 8904 (QCNE, MO); Parque Nacional Podocarpus, 1100 m, Jan 1995, Palacios & Tirado 13317 (GB, MO); Las Orquideas Reserve, Neill et al 15207 (MO); Neill et al 15284 (MO). El Pangui, rio Wawaime tributary of rio Quimi, 1100 m, 10 Ago 2007, Neill et al 15539 (MO, NY). Yantzaza, Cerro Machinaza, 1700 m, 23 Jul 2005, Quizhpe 1689 (GB, MO, NY); Quizhpe 1550 (MO, NY); Qhizhpe 1601 (LOJA, MO, NY).

Peru. Amazonas: Luya, Jaipe, 1600-1700 m, 26 Jun 1991, Diaz & Campos 4477 (GB, MO); Diaz & Campos (MO). Cajamarca: San Ignacio, Huarango, Huarandoza, 1609 m, 19 May 2007, Perea & Flores 3150 (MO, NY); Perea & Flores 3493 (MO); Caserio Nuevo Mundo, 1500-1600, 19 Jul 1997, Campos & Nuñez 4197 (F, MO, NY); Campos & Nuñez 4604 (MO); Pino et al 193 (MO); San Jose de Lourdes, 1800 m, 22 Apr 1999, Vasquez et al 26168 (MO). Oxapampa: San Alberto, 1850 m, 10 Oct 1980, Diaz 1610 (MO); Chontabamba, 2100 m, 09 Ago 2002, Monteagudo et al 3627 (MO); 2060 m, 14 Sep 2007, Monteagudo et al 15476 (F, MO); Huancabamba, PNYCH, 1800 m, 29 Oct 2007, Monteagudo et al 15727 (F, MO); 1894 m, 24 Jul 2008, Monteagudo et al 16947 (MO); Tunqui, 1780 m, 24 Oct 2007, Monteagudo et al 15567 (GB, MO); Pozuzo, 700 m, 29 Sep 2007, Rojas et al 4657 (MO); 28 Dec 2007, Rojas & Ortiz 5126 (MO); 29 Sep 2007, Rojas et al 4657 (MO); 2000 m, 21 Sep 1984, Smith 8530 (MO); La Suiza Vieja, 2200 m, 23 Jun 2003, Van der Werff et al 17713 (MO); Van der Werff et al 20163 (GB, MO).

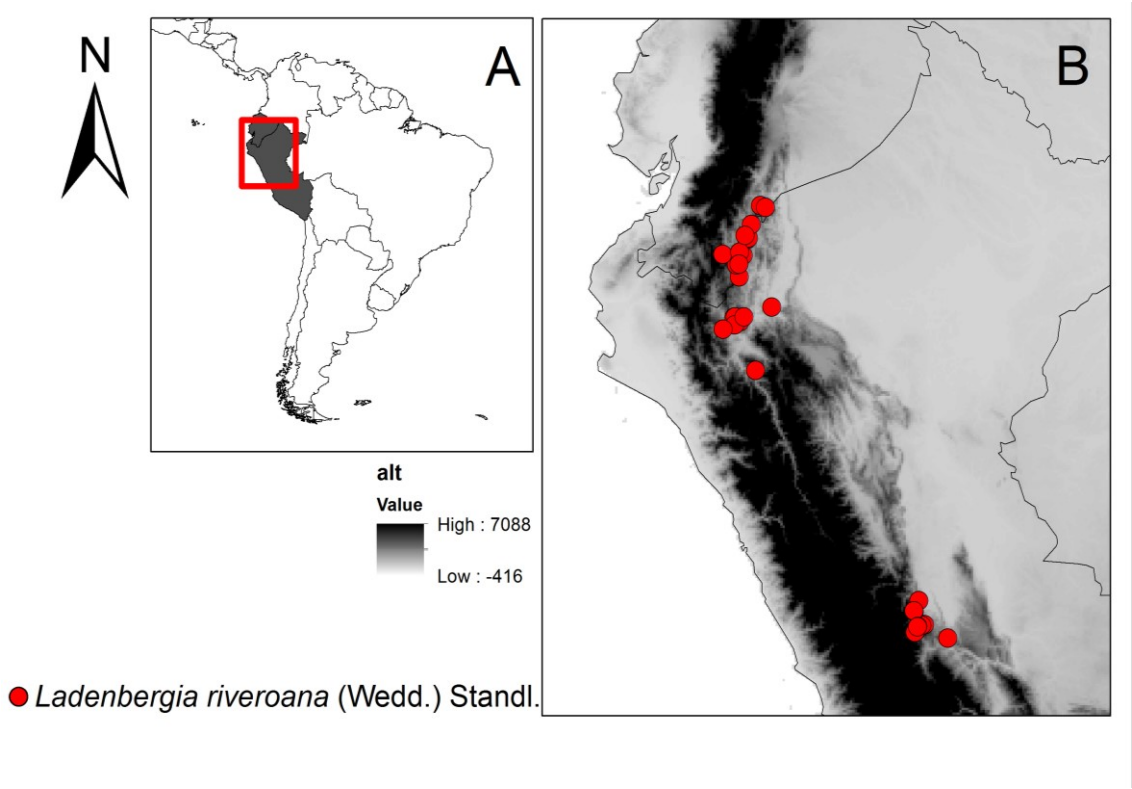

Fig 23. Peru, Ecuador and South America. B. Enlarged map showing the distribution the *Ladenbergia riveroana* (Wedd.) Standl.

17. *Ladenbergia stenocarpa* (Lam.) Klotzsch. Getr. Dasrt. Gew. 14: ad tab. 15 (1846). *Cinchona stenocarpa* Lamb., III Cinchona 13 (1821). *Cascarilla stenocarpa* (Lamb.) Wedd., Ann, Sci. Nat., Sér. 3, 11: 271 (1849). *Buena stenocarpa* (Lamb.) Wedd., J. Linn. Soc. 11:186 (1869). Type: (Tafalla in) Pavón s.n.; Peru, Cajamarca '…ex Jaen in montibus Loxa. Quito" (BM lectotype designated by Andersson 1994: 22; G image!, MA image!, P image! with number 594, supposedly isolectotypes)

Shrub or tree 2 (-20) m tall. Young branches moderately puberulous. Stipules fused at ¼ forming sheath, ovate to oblong in the basal portion with upper part acuminate, generally glabrous to puberulous, 0.7-1.5 x 0.4-0.55 cm long; petioles 1.3-3.2 cm long, glabrous to sparcely puberulent; leaf blades plane, +/- thick in texture, +/- chartaceous when dry, 10-15 x 4.5-7.5 cm, elliptic to ovate (length/width 2-2.2), cuneate at base, acute to acuminate at apex, midvein above slightly sulcate, secondary veins prominulous above and slightly sulcate, prominent beneath, 9-12 pairs with arrangement brochidodromous, tertiary venation obscure to slightly impressed above,

slightly distinct below with pattern alternate percurrent, adaxial surface matte to nitid, glabrous, abaxial surface with midrib and veins sparsely puberulous to +/- hirsute, sometimes also with bristly hairs along margin of midrib, intervenous surface glabrous or minutely strigulose, margin plane, tuft domatia present. Inflorescence terminal, branched in two to four orders, multi-flowered (ca. 90 flowers), broadly triangular in outline, axes puberulous, peduncles 2-4 cm, rachis 7-10 cm long composed by 2-3 nodes with axes articulated, dichasial, bracts lanceolate, acuminate, generally deciduous. Flowers 5-merous, strongly fragant, nocturnal, distylous, sessile to subsessile or on short axes in dichasial congested groups of 3-6; hypanthium obconical, glabrous to puberulous, ca. 2-2.5 x 1.8-2 mm, calyx limb 1.8-2.5 mm long, lobes deeply generally acute, 0.5-1.8 mm long, sparsely puberulous outside, glabrous inside, colleters evident in the sinus; corolla salverform, white, tube in brevistylous flowers 10-14 mm, in diameter 1.2-1.8 mm, tube in longistylous flowers 8.5-9.5 mm, in diameter 2-2.5 mm, lobes in brevistylous flowers 8-10 mm and in longistylous flowers 5.5-7 mm, filaments attached ca 4.5-5 mm above base of corolla tube (ca. 50 % of tube length) in longistylous flowers and ca 1.3-2 mm above base of corolla tube (ca. 20 % of tube length) in brevistylous flowers, anthers 4.7-6 x 1-1.5 mm; style glabrous, ca. 1.5-1.7 mm long in brevistyls flowers and 7.5-7.7 mm long in longistyls flowers, stigmatic lobes ca 1.2-1.5 mm. Capsules woody, narrowly ellipsoid to cylindrical, externally glabrous to slightly puberulous, 15-60 x 4.5-6.5 mm, endocarp 0.2-0.3 mm thin. Seeds oblong-fusiform (11-13 x 1.8-3.2 mm long.) with wings marginally fimbriate (Fig 26).

Distribution, habitat and phenology. *Ladenbergia stenocarpa* is found on eastern slopes of the Andes in northernmost Peru and southernmost Ecuador; it grows at altitudes between 800 and 1400 msnm in sandy rocky soils (Fig 24). This species is little collected because it occurs in areas of difficult access. It has been collected in flower and fruit in February- March and July- October.

Diagnostic Characters and Discussion. *Ladenbergia stenocarpa* is characterizaded by having elliptic (length/ width 2-2.2) leaf blades wich are +/- narrowly cuneate at base and acute to acuminate at apex with tuft domatia in the abaxial side, a multiflora

inflorescence with two to four lateral ordens, a small calyx limb (1.8-2.5 mm), rather small corolla (tube ca. 14 mm) and rather thin capsules (15-60 mm x 4.5-6.5 mm).

Andersson (1994) compares *L. stenocarpa* with *L. oblongifolia*, from which it differs in its proporcionally narrower leaf blades (vs rounded in *L. oblongifolia*) wich are cuneate in the base (vs broadly cuneate to rounded) and acute to acuminate (vs obtuse to rounded in *L. oblongifolia*) in the apex.

L. stenocarpa resembles at *L. acutifolia* in the form and size of the leaf blades and small flowers but can be distinguished by presence of the tuft domatia (vs absent in *L. acutifolia*), inflorescences with two – four orden lateral (vs two to three in *L. acutifolia*), corolla tube villosulous in the outside (vs glabrous to slightly puberulous in *L. acutifolia*) and capsules slender usually larger (15-60 mm in *L. stenocarpa* vs 25-40 mm in *L. acutifolia*).

Examined material.

Ecuador. Zamora-Chinchipe: Cantón Nangaritza, Cordillera del Cóndor, hill about 2 km downstream from Campamento Shaime along Río Nangaritza,900-1200 m, 15 Feb 1994, van der Weff et al. 13083 (GB), Fuentes et al 1047 (MO), Quizhpe et al 651 (MO). Estacion Cientifica San Francisco, 1800-2200, 05 Oct 2001, Wolff 74 (MO). Sucumbios: Sinangoe Station, 1400-1500 m, 12 Aug 2001, Aguinda 1638 et al (MO).

Peru. Amazonas: Prov. Condorcanqui, Cerro Kampankis, 1345 m, 08 Aug 2011, Huamantupa et al 15450 (MO, F). Bagua, Aramango, 1650 m, 15 Dec 2001, Vasquez et al 27385. Cajamarca: San Ignacio, Huarango, Nuevo Mundo, 1500-1600 m, Campos & Nunez 4189 (MO)

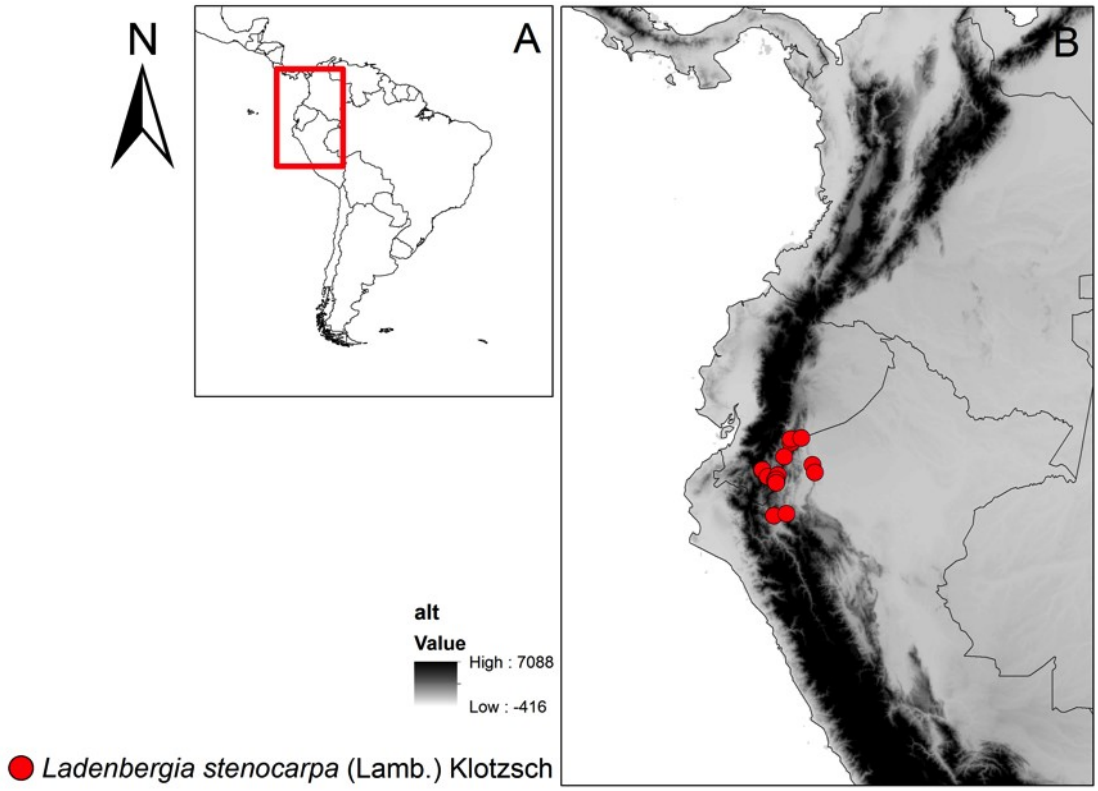

Fig 24. Peru, Ecuador and South America. B. Enlarged map showing the distribution the *Ladenbergia stenocarpa* (Lam.) Klotzsch.

18. *Ladenbergia undata* Klotzsch. Getr. Darst. Gew. 14: ad tab. 15 (1846). *Cascarilla undata* (Klotzsch) Wedd., Ann. Sci. Nat., Sér. 3, 10: 2 (1848). *Cinchona undata* (Klotzch) Kartens, Fl. Columb. 1: 131 (1861). *Buena undata* (Klotzsch) Weed. J. Linn. Soc. 11: 187 (1969). Type: Moritz 963; Venezuela, Mérida, Vicinity of Mérida (B holotype, destroyed; K ex herb. Bentham, lectotype designated por Andersson (1997); BM image!, G image!, HBG image!, K image!, ex herb. Hooker isotypes; NY probable isotype without number, S posible isotypes ascribed to "Dr. Sonder").

Shrub to Tree 9-15 m tall. Young branches ferrugineous-tomentose. Stipules interpetiolar fused at the base forming the sheath, oblong - rounded in the basal portion with upper part obtuse, hirtellous externally and glabrous internally, 3.7 – 4.5 cm x 1.4 -1.5 cm, with colleters arranged in two or three rows on the base 0.5-1.2 mm; petioles 2-4.5 cm long, hirsute to glabrescent; leaf blades bullate, thick in texture, chartaceous when dry, 5.5-27 x 3.5.-11 cm long, broadly oblong-ovate to broadly oblong (length/width 1.5-2.5), cordate or rounded at base, acuminate to rounded at

apex, secondary veins 10-16 pairs with arrangement weakly brochidodromous, slightly sulcate above, prominent beneath, tertiary venation +/- obscure above, distinct below with an opposite-percurrent arrangement generally, adaxial surface matte to nitid and puberulous to hirtellous, abaxial surface slightly to densely hirtellous throughout, margins slightly revolute, tuft domatia absent. Inflorescence terminal, branched in one to two orders, few-flowered (generally 9-28 flowers), broadly triangular in outline, axes hirtellous to hirsute, peduncle 1-4.8 cm, rachis 5-12 cm long composed by 2-3 nodes with axes articulated, dichasial, bracts lanceolate, hirsute, generally deciduous. Flowers 5-merous, coarse, strongly fragant, nocturnal, distylous, subsessile or pedicellate 2-3 mm long on short axes in dichasial congested groups of 3-6; hypanthium obconical, hirsute with trichomes ferrugineous, ca. 4-6 mm x 4-4.5 mm long, calyx limb 3.5-10 mm long, lobes irregular and generally rounded-obtuse, 3.7-7 mm long, hirsute outside, glabrous inside, with colleters in the sinus; corolla salverform, white, tube in brevistylous flowers 18-22 mm, in diameter 4-7.5 mm, longistylous flowers not seen, lobes flowers 15-17 mm, filaments attached ca 13 mm above base of corolla tube (ca. 70 % of tube length), anthers 6-6.5 x 1-1.5 mm; style glabrous, ca. 10-12 mm long, stigmatic lobes ca 3-3.8 mm. Capsules woody, oblong, hirtellous, 45-50 x 7-10 mm, endocarp 0.5-0.7 mm thick. Seeds oblong-fusiform 11-12 x 3.5-4 mm long with wings marginally fimbriate (Fig 7 I-P).

Distribution, habitat and phenology. *Ladenbergia undata* is found in the northeastern Andes of Colombia and Venezuela. There is few records on herbarium and floristic list, habit in wet forest at altitudes between 1650-2800 m (Fig 25). It has been collected in flower and fruit in April and May.

Diagnostic Characters and Discussion.

Ladenbergia undata is characterized by its chartaceous and +/- bullate leaf blades, which are densely hirtellous beneath, by its flower fleshy with long (3.5-10 mm) calyx with long (3,7-7 mm) lobes, fruit with endocarp thick (0.5-0.7) and by wide seed (3.5-4 mm).

Ladenbergia undata is morphological related to *L. bullata* due to its surface bullate leaf blades but it differs in having form and indumentum beneath diferent (rounded and hirtellous to hirsute in *L. undata* vs elliptic to lanceolate and glabrous to puberulous in *L. bullata*), form calyx lobed (rounded in *L. undata* vs acute in *L. bullata*) and texture the endocarp fruit (thick in *L. undata* vs thin in *L. bullata*).

Additional collections studied.

Colombia. Norte de Santander: Cuatrecasas et al. 12571 (F), Engel s.n. (F). Santander: Killip & Smith 15990 (F, NY).

Venezuela. Mérida: Bernardi 456 (NY), 2160 (G, NY), 3128 (G), Linden 1410 (BM, F, G, K, P), Steyermark 56040 (F, MO), 56105 (F ster.), 56107, 56178 (F, MO, NY), 56178 (F), 56179, 56670 (F ster.), 56671 (F, NY both ster.)

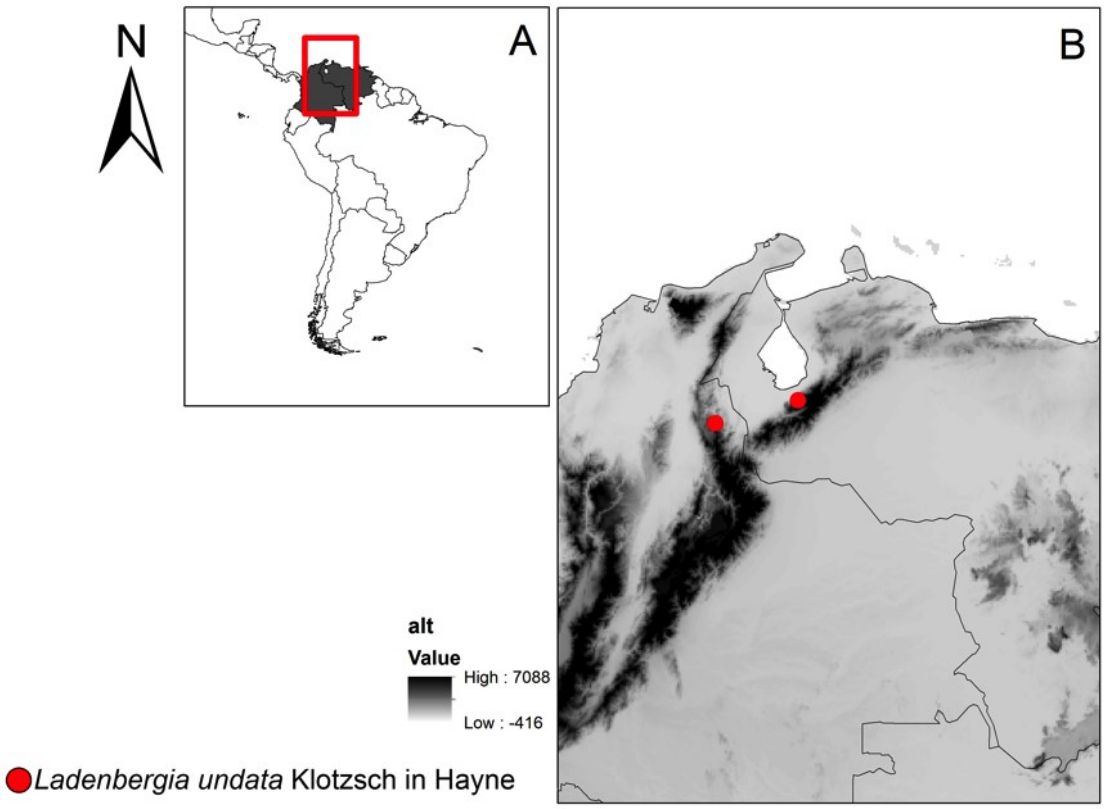

Fig 25. Colombia, Venezuela and South America. B. Enlarged map showing the distribution the *Ladenbergia undata* Klotzsch

ACKNOWLEDGMENTS.

I thank the directors and curators of the herbaria MO, NY, F, USM, MOL, HOXA, UEC, CR, USJ, INB, RB, R, G, UB, CEN, as well as Gustavo Shimizu, João do Carmo, Nállarett Dávila, Joaquina Albán and Claes Persson for their help with taxonomic problems; Suzana Costa for assistance with maps; and Robin Foster, Jurgen Homeier, Jhon Janovec for sending photos of *Ladenbergia* and allies. I am also grateful to Alba Arvelaez, Rosa Ortiz, Fernanda Cabral, Jhon Pruski, Carmen Ulloa and Mary Stiffler for diverse help and assistance during my stay in Missouri Botanical Garden, and to Maria A. Zuñiga and Esteban Jiménez in Costa Rica.

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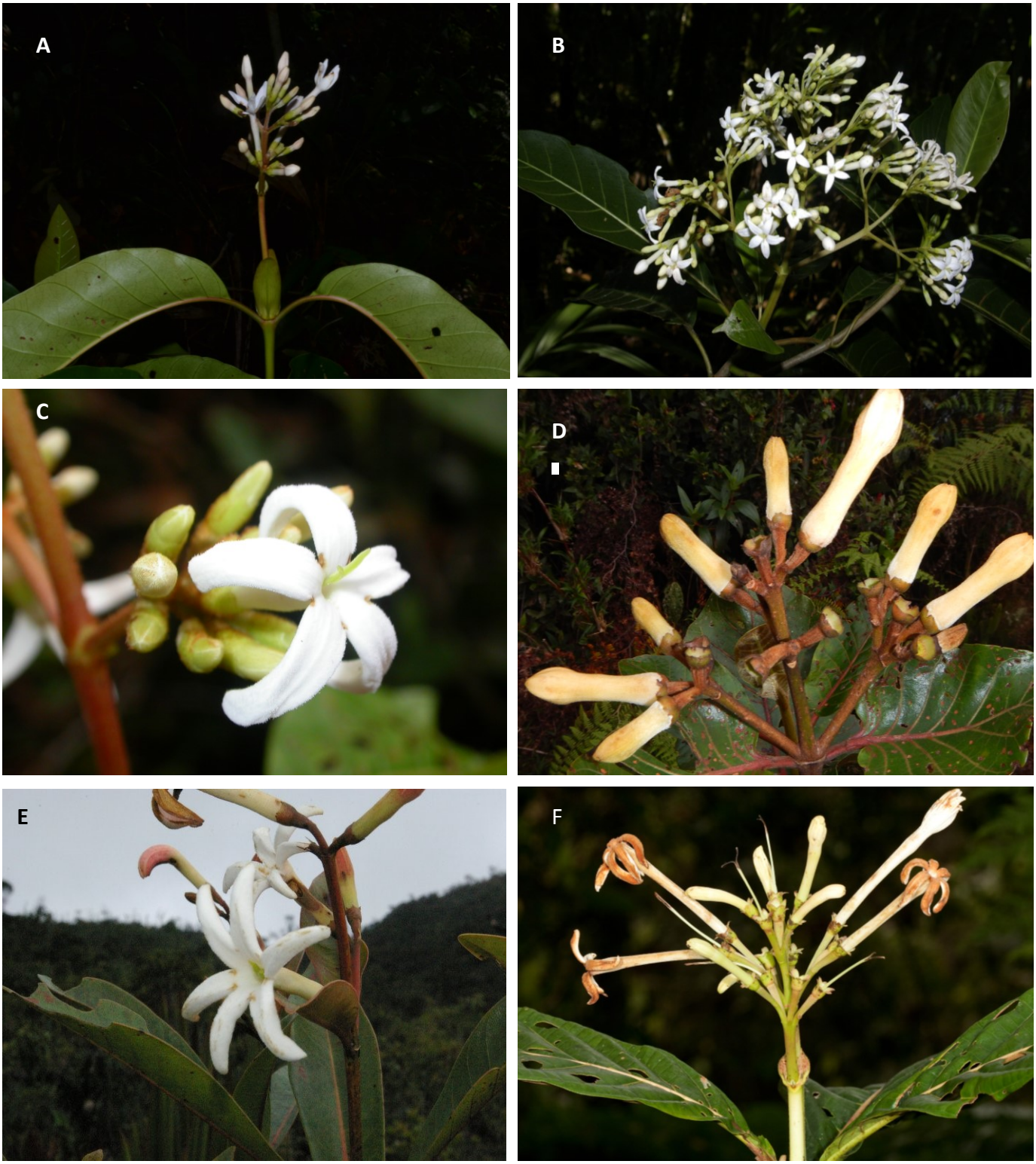
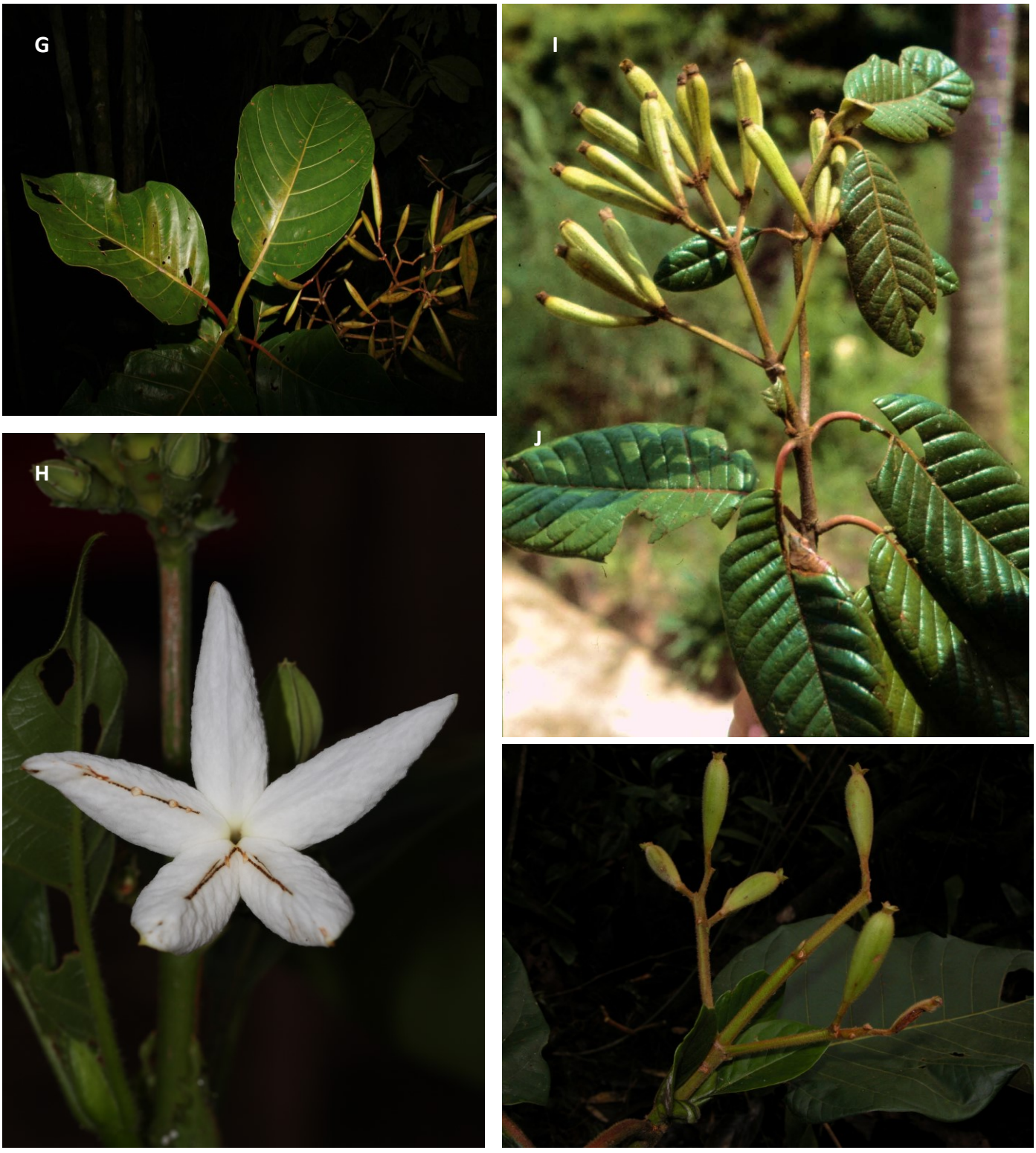
APPENDIX I. LIST OF ACCEPTED SPECIES.

Number	Distribution	Circunscription *sensu* Chilquillo (2016)	Circunscription *sensu* Andersson (1997)
1	Andes	*Ladenbergia acutifolia* (Ruiz & Pav.) Klotzsch.	*Ladenbergia acutifolia* (Ruiz & Pav.) Klotzsch.
2		*Ladenbergia bullata* (Wedd.) Standl.	*Ladenbergia bullata* (Wedd.) Standl.
3		*Ladenbergia carua* (Wedd.) Standl.	*Ladenbergia carua* (Wedd.) Standl.
4		*Ladenbergia crassifolia* (DC.) Standley (= *Ladenbergia franciscana* C. M. Taylor)	***Ladenberia ferruginea* Standl.**
5		*Ladenbergia discolor* K. Schum.	*Ladenbergia discolor* K. Schum.
6		*Ladenbergia heterophylla* (Wedd.) Standl.	*Ladenbergia heterophylla* (Wedd.) Standl.
7		*Ladenbergia klugii* L. Andersson (= *Ladenbergia ferruginea* Standl.)	*Ladenbergia klugii* L. Andersson.
8		*Ladenbergia lehmanniana* L. Andersson.	*Ladenbergia lehmanniana* L. Andersson.
9		*Ladenbergia macrocarpa* (Vahl) Klotzsch.	*Ladenbergia macrocarpa* (Vahl) Klotzsch (=*Ladenbergia crassifolia* (DC.) Stand.)
10		*Ladenbergia moritziana* Klotzsch.	*Ladenbergia moritziana* Klotzsch.
11		*Ladenbergia muzonensis* (Goudot) Standl.	*Ladenbergia muzonensis* (Goudot) Standl.
12		*Ladenbergia oblongifolia* (Mutis) L. Andersson.	*Ladenbergia oblongifolia* (Mutis) L. Andersson.
13		*Ladenbergia pavonii* (Lamb.) Standl.	*Ladenbergia pavonii* (Lamb.) Standl.
14		*Ladenbergia pittieri* Standl.	*Ladenbergia pittieri* Standl.
15		*Ladenbergia riveroana (Wedd.)* Standl.	*Ladenbergia riveroana (Wedd.)* Standl.
16		*Ladenbergia stenocarpa* (Lam.) Klotzsch.	*Ladenbergia stenocarpa* (Lam.) Klotzsch.
17		*Ladenbergia undata* Klotzsch.	*Ladenbergia undata* Klotzsch.
18		***Ladenbergia fosteri* E. Chilquillo**	*Ladenbergia graciliflora* K. Schum.
19	Other regions	*Ladenbergia pauciflora* L. Andersson	*Ladenbergia pauciflora* L. Andersson
20		*Ladenbergia cujabensis* Klotzsch	*Ladenbergia cujabensis* Klotzsch
21		*Ladenbergia buntingii* Steyerm.	*Ladenbergia buntingii* Steyerm.
22		*Ladenbergia rubiginosa* L. Andersson	*Ladenbergia rubiginosa* L. Andersson
23		*Ladenbergia nubigena* L. Andersson	*Ladenbergia nubigena* L. Andersson
24		*Ladenbergia hexandra* (Pohl) Klotzsch	*Ladenbergia hexandra* (Pohl) Klotzsch
25		*Ladenbergia amazonensis* Ducke	*Ladenbergia amazonensis* Ducke
26		*Ladenbergia lambertiana* (A. Braun ex Mart.) Klotzsch	*Ladenbergia lambertiana* (A. Braun ex Mart.) Klotzsch
27		*Ladenbergia paraensis* Ducke	*Ladenbergia paraensis* Ducke
28		*Ladenbergia graciliflora* K. Schum.	*Ladenbergia chapadensis* S. Moore
29		*Ladenbergia brenesii* Standl.	*Ladenbergia brenesii* Standl.
30		*Ladenbergia magdalenae* L. Andersson	*Ladenbergia magdalenae* L. Andersson
31		*Ladenbergia laurifolia* Dwyer	*Ladenbergia laurifolia* Dwyer
32		***Ladenbergia epiphytica* L. Andersson (Dubious species)**	*Ladenbergia epiphytica* L. Andersson
33		***Ladenbergia obovata* L. Andersson (Dubious species)**	*Ladenbergia obovata* L. Andersson
34		***Ladenbergia dwyeri* L. Andersson (Dubious species)**	*Ladenbergia dwyeri* L. Andersson

APPENDIX II.



A. *Ladenbergia discolor* K. Schum. B. *Ladenbergia stenocarpa* (Lamb.) Klotzsch. C. Longystylous flowers of *Ladenbergia klugii* L. Andersson. D. *Ladenbergia macrocarpa* (Vahl) Klotzsch. E. *Ladenbergia crassifolia* (Pav. ex DC.) Standl. F. *Ladenbergia heterophylla* (Wedd.) Standl.



G. *Ladenbergia oblongifolia* (Humb. ex Mutis) L. Andersson. H. Flowers of *Ladenbergia muzonensis* (Goudot) Standl. I. Branch with infrutescense of *Ladenbergia undata* Klotzsch. J. Branch with infrutescense of *Ladenbergia carua* (Wedd.) Standl.

CONSIDERAÇÕES FINAIS.

O estudo filogenético com uma amostragem abrangente do gênero *Ladenbergia* utilizando três marcadores moleculares (ITS, *trn*L e *rps*16) permitiu corroborar a monofilia do gênero e a sua relação com *Remijia*. Além disso, foi possível propor hipóteses sobre as relações de algumas especis dentro do gênero como: *L. hexandra* e *L. cujabensis*, espécies que ocorrem no cerrado e sudeste do Brasil; *L. amazonensis* e *L. graciliflora*, espécies restritas a habitats amazônicos; *L. carua* e *L. bullata*, espécies que habitam os Andes tropicais do sul; *L. riveroana* e *L. stenocarpa*, espécies que ocorrem em habitats com solos de arenisco nos Andes Centrales do Sul e *L. oblongifolia* espécie amplamente distribuída nos Andes a qual se relaciona com *L. heterophylla*, *L. pavonii* e *L. dwyeri* as quais se distribuem em os Andes do Norte e America Central.

No entanto, uma maior amostragem de táxons é necessária para obtenção de uma filogenia mais completa para o gênero. Além disso, novas regiões precisam ser exploradas que permitam proporcionar uma melhor resolução das relações no nível de espécie. Estudos futuros poderiam incluir sequenciamento de nova geração do genoma nuclear e do cloroplasto com finalidade de obter uma filogenia melhor resolvida, sendo esta a base para testar hipóteses biogeográficas sobre a origem e dispersão do gênero.

A abordagem taxonômica aqui apresentada mostra um tratamento taxonômico detalhado que inclui descrições, chave taxonômica e aspectos ecológicos das especies do gênero *Ladenbergia* que ocorrem nos Andes. Foram esclarecidas alguns problemas taxonomicos correntes nestas espécies mas também se apontam outros problemas de delimitação, como é o caso de *L. heterophylla* e especies afines (*L. obovata*, *L. epiphytica* e *L. dwyeri*) e *L. crassifolia* e seus morfotipos presentes a longo de sua distribuçao. Estudos futuros que incluam uma revisão taxonômica para todas as espécies do gênero é necessario. A geração de hipóteses filogenéticas com uma maior representação de indivíduos pertencentes a espécies de difícil delimitação também é necessário, de forma a testar a validade destas espécies ou se constituem parte da varição gradual de espécies mais amplas.

À luz dos nossos resultados, seria interessante dar início a estudos anatômicos, citológicos e ecológicos que forneçam informações ao respeito do desenvolvimento, biologia reprodutiva e habitat onde ocorrem as espécies de *Ladenbergia*, o que ajudaria a ter uma visão completa sobre o grupo e permita melhorar o entendimento das espécies.

ANEXO 1. Declaração referente a bioética e/ou biossegurança.

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DECLARAÇÃO

Em observância ao **§5º do Artigo 1º da Informação CCPG-UNICAMP/001/15**, referente a Bioética e Biossegurança, declaro que o conteúdo de minha Dissertação de Mestrado, intitulada "***Filogenia do gênero Ladenbergia Klotzsch (Rubiaceae: Cinchoneae) e taxonomia atualizada das espécies que ocorrem nos Andes Tropicais***", desenvolvida no Programa de Pós-Graduação em Biologia Vegetal do Instituto de Biologia da Unicamp, não versa sobre pesquisa envolvendo seres humanos, animais ou temas afetos a Biossegurança.

Assinatura: _____
Nome do(a) aluno(a): Eder Augusto Chilquillo Torres

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Nome do(a) orientador(a): André Olmos Simões

Data: 21-01-2016

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Campinas, 21 de janeiro de 2016

Assinatura : _____
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