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Systématique et biogéographie du groupe Caesalpinia (famille Leguminosae)

par
Edeline Gagnon

Département des sciences biologiques
Centre sur la biodiversié
Institut de recherche en biologie végétale
Faculté des arts et sciences

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Résumé

Parmi les lignées des Caesalpinioideae (dans la famille des Leguminosae), l'un des groupes importants au sein duquel les relations phylogénétiques demeurent nébuleuses est le « groupe Caesalpinia », un clade de plus de 205 espèces, réparties présentement entre 14 à 21 genres. La complexité taxonomique du groupe Caesalpinia provient du fait qu'on n'arrive pas à résoudre les questions de délimitations génériques de *Caesalpinia* sensu lato (s.l.), un regroupement de 150 espèces qui sont provisoirement classées en huit genres. Afin d'arriver à une classification générique stable, des analyses phylogénétiques de cinq loci chloroplastiques et de la région nucléaire ITS ont été effectuées sur une matrice comportant un échantillonnage taxonomique du groupe sans précédent (~84% des espèces du groupe) et couvrant la quasi-totalité de la variation morphologique et géographique du groupe Caesalpinia. Ces analyses ont permis de déterminer que plusieurs genres du groupe Caesalpinia, tels que présentement définis, sont polyphylétiques ou paraphylétiques. Nous considérons que 26 clades bien résolus représentent des genres, et une nouvelle classification générique du groupe Caesalpinia est proposée : elle inclut une clé des genres, une description des 26 genres et des espèces acceptées au sein de ces groupes. Cette nouvelle classification maintient l'inclusion de douze genres (*Balsamocarpon*, *Cordeauxia, Guilandina, Haematoxylum, Hoffmanseggia, Lophocarpinia, Mezoneuron, Pomaria, Pterolobium, Stenodrepanum, Stuhlmannia, Zuccagnia*) et en abolit deux (*Stahlia* et *Poincianella*). Elle propose aussi de réinstaurer deux genres (*Biancaea* et *Denisophytum)*, de reconnaître cinq nouveaux genres (*Arquita*, *Gelrebia*, *Hererolandia*, *Hultholia* et *Paubrasilia*), et d'amender la description de sept genres (*Caesalpinia*, *Cenostigma*, *Coulteria*, *Erythrostemon*, *Libidibia*, *Moullava*, *Tara*). Les résultats indiquent qu'il y aurait possiblement aussi une 27^{e} lignée qui correspondrait au genre *Ticanto,* mais un échantillonage taxonomique plus important serait nécéssaire pour éclaircir ce problème.

Les espèces du groupe Caesalpinia ont une répartition pantropicale qui correspond presque parfaitement aux aires du biome succulent, mais se retrouvent aussi dans les déserts, les prairies, les savanes et les forêts tropicales humides. À l'échelle planétaire, le biome succulent consiste en une série d'habitats arides ou semi-arides hautement fragmentés et caractérisés par l'absence de feu, et abrite souvent des espèces végétales grasses, comme les Cactacées dans les

néo-tropiques et les Euphorbiacées en Afrique. L'histoire biogéographique du groupe Caesalpinia a été reconstruite afin de mieux comprendre l'évolution de la flore au sein de ce biome succulent. Ce portrait biogéographique a été obtenu grâce à des analyses de datations moléculaires et des changements de taux de diversification, à une reconstruction des aires ancestrales utilisant le modèle de dispersion-extinction-cladogenèse, et à la reconstruction de l'évolution des biomes et du port des plantes sur la phylogénie du groupe Caesalpinia. Ces analyses démontrent que les disjonctions trans-continentales entre espèces sœurs qui appartiennent au même biome sont plus fréquentes que le nombre total de changements de biomes à travers la phylogénie, suggérant qu'il y a une forte conservation de niches, et qu'il est plus facile de bouger que de changer et d'évoluer au sein d'un biome différent. Par ailleurs, contrairement à nos hypothèses initiales, aucun changement de taux de diversification n'est détecté dans la phylogénie, même lorsque les espèces évoluent dans des biomes différents ou qu'il y a changement de port de la plante, et qu'elle se transforme, par exemple, en liane ou herbacée. Nous suggérons que même lorsqu'ils habitent des biomes très différents, tels que les savanes ou les forêts tropicales humides, les membres du groupe Caesalpinia se retrouvent néanmoins dans des conditions écologiques locales qui rappellent celles du biome succulent.

Finalement, bien que la diversité des espèces du biome succulent ne se compare pas à celle retrouvée dans les forêts tropicales humides, ce milieu se distingue par un haut taux d'espèces endémiques, réparties dans des aires disjointes. Cette diversité spécifique est probablement sous-estimée et mérite d'être évaluée attentivement, comme en témoigne la découverte de plusieurs nouvelles espèces d'arbres et arbustes de légumineuses dans la dernière décennie. Le dernier objectif de cette thèse consiste à examiner les limites au niveau spécifique du complexe *C. trichocarpa,* un arbuste des Andes ayant une population disjointe au Pérou qui représente potentiellement une nouvelle espèce. Des analyses morphologiques et moléculaires sur les populations présentes à travers les Andes permettent de conclure que les populations au Pérou représentent une nouvelle espèce, qui est génétiquement distincte et comporte des caractéristiques morphologiques subtiles permettant de la distinguer des populations retrouvées en Argentine et en Bolivie. Nous décrivons cette nouvelle espèce, *Arquita grandiflora*, dans le cadre d'une révision taxonomique du genre *Arquita,* un clade de cinq espèces retrouvées exclusivement dans les vallées andines.

Mots-clés: taxonomie, systématique, biogéographie, biome succulent, *Caesalpinia*, délimitation d’espèces, délimitation de genres, Andes, forêts sèches tropicales

Abstract

Amongst the lineages of the Caesalpinioideae (in the family Leguminosae), one of the largest groups where phylogenetic relationships remains unclear is the Caesalpinia Group, a clade of ca. 200 species, currently considered to comprise between 14 and 21 genera. The taxonomic complexity of the Caesalpinia Group stems from persisting doubts on the generic delimitations within *Caesalpinia* sensu lato, a group of 150 species that are provisionally classified into eight genera. In order to establish a stable generic classification, phylogenetic analyses of five chloroplastic loci and the nuclear ribosomal ITS locus were carried out on a matrix containing an unprecedented taxonomic sampling of the Caesalpinia Group (~84% of species of this group included), with virtually all of the morphological variation and geographic distribution represented. These analyses allowed us to determine that several genera of the Caesalpinia Group, as currently defined, are polyphyletic or paraphyletic. We consider that there are 26 well-resolved clades that represent distinct genera, and a new generic classification system is proposed, which includes a key to genera, the description of the 26 genera and all species accepted within these groups. A total of twelve previously accepted genera are maintained in this classification (*Balsamocarpon*, *Cordeauxia, Guilandina, Haematoxylum, Hoffmanseggia, Lophocarpinia, Mezoneuron, Pomaria, Pterolobium, Stenodrepanum, Stuhlmannia,* and *Zuccagnia*), whereas two genea are abolished (*Stahlia* and *Poincianella*). In addition, two genera are re-instated (*Biancaea* and *Denisophytum*), five new genera are described, (*Arquita*, *Gelrebia*, *Hererolandia*, *Hultholia* and *Paubrasilia*), and the description of seven genera are emended (*Caesalpinia*, *Cenostigma*, *Coulteria*, *Erythrostemon*, *Libidibia*, *Moullava*, *Tara*). Our results also indicate that there could possible be a 27th lineage corresponding to the genus *Ticanto,* but an increased taxonomic sampling is needed to adequately address this issue.

The Caesalpinia Group has a pantropical distribution that corresponds almost perfectly to the geographical distribution of the Succulent Biome, but are also found in deserts, grassland prairies, savannahs, and tropical rainforests. On a planetary scale, the Succulent Biome consists of a series of semi-arid to arid habitats that are highly fragmented, and which are characterised by the absence of fire, such as deserts and dry forests. This biome often harbours succulent plant taxa, such as the Cactaceae in the Neotropics and the Euphorbiaceae in Africa. The biogeographical history of the Caesalpinia Group was reconstructed in order to gain insight into the evolution of the flora within this Succulent biome. This biogeographical portrait of this group was reconstructed using molecular dating analysis, diversification rate shifts tests, the reconstruction of ancestral areas using the dispersal-extinction-cladogenesis model (DEC), as well as through ancestral character reconstruction of the biomes and habits. These analyses demonstrate that intercontinental disjunctions between sister species belonging to the same biome are more frequent than the total number of biome shifts across the phylogeny, suggesting that there is a strong conservation of niches, and that it is easier to move than to switch to and evolve in a different biome. Furthermore, contrary to our initial hypothesis, no changes in diversification rates were detected in our phylogenies, even when species switched biomes or evolved a different plant habit, e.g. becoming lianas or herbaceous perennials. We suggest that even when members of the Caesalpinia Group inhabit different biomes, such as savannahs or tropical rainforests, they are still tracking local ecological conditions that are typical of the Succulent biome.

Finally, while total plant species diversity in the Succulent Biome does not compare to the diversity found in tropical rainforests, this biome distinguishes itself by a high number of endemic species, distributed in disjunct patches across the world. This species diversity is probably under-estimated and needs to be carefully re-evaluated, as shown in several recent descriptions of new tree and shrub species from the Succulent biome, all published in the last decade. The last objective of this thesis is to examine the species limits in *Caesalpinia trichocarpa,* a shrub from the Andes that has a disjunct population in Peru, which potentially represents a new species. Morphological and molecular analyses of populations occurring across the Andes, including Bolivia and Argentina, allow us to conclude that the populations in Peru represent a new species, which is genetically distinct and has subtle morphological characteristics that allow it to be distinguished from populations found in Argentina and Bolivia. We describe this news species, *Arquita grandiflora*, in a taxonomic revision of the genus *Arquita*, a clade of five species found exclusively in Andean valleys.

Keywords: taxonomy, systematics, biogeography, Succulent biome, *Caesalpinia*, delimitation of species, delimitation of genera, taxonomy, the Andes, seasonally dry tropical forest;

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Liste des abbréviations et sigles

AF ou Af: Africa

AS ou As: Asia

C: Coastal

CA: Central America

Car: Carribean

BAMM: Bayesian Analysis of Macroevolutionary Mixtures

BS : bootstrap support

CI : consistency index

DEC: dispersal-extinction-cladogenesis

G: Grassland

HPD: highest posterior density

LPWG : Legume Phylogeny Working Group

MCC : Mimosoideae-Caesalpinieae-Cassieae

Mccr : Maximum clade credibility

MCMC : Markov Chain Monte Carlo

ML: maximum likelihood

MP: maximum parsimony

MRCA: most recent common ancestor

NA ou Na: North America

PA: Australian-Pacific

PP : posterior probability

R: Rainforest

RI : retention index

P-E : Poincianella-Erythrostemon

S: Succulent

s.l. : sensu lato

s.s. : sensu stricto

SA ou Sa: South America

SDTF : seasonally dry tropical forest

SIC : simple indel coding

T: Temperate

TA_{N}: Annealing Temperature of PCR with standard TAQ;

TA_{PH} : annealing temperature of PCR with Phire polymerase;

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Introduction

La diversité des organismes vivants sur la terre et leur hétérogénéité à travers le temps et l'espace est un phénomène encore aujourd'hui difficile à expliquer pour les biologistes (Kreft & Jetz, 2007; Donoghue & Sanderson, 2015). En effet, pour mieux comprendre cette biodiversité et ainsi l'étudier dans son ensemble, il faut d'abord précisément la décrire, la nommer et connaître son histoire : une étape possible grâce à deux branches de la biologie, soit la systématique et la biogéographie.

La systématique correspond au domaine qui cherche à comprendre l'évolution des organismes biologiques à travers leurs relations phylogénétiques. À tort, la systématique est souvent confondue avec la classification des organismes et leur taxonomie : ce n'est en effet qu'une des applications possibles des analyses phylogénétiques (Baum & Smith, 2013). Les données avec lesquelles elle cherche à reconstruire ces liens phylogénétiques sont multiples, soient par la morphologie, l'ontogénie, la génétique, la chimie, etc.

La biogéographie est quant à elle une discipline qui cherche à comprendre la distribution de la biodiversité à travers la planète et les facteurs qui déterminent cette distribution. On distingue la biogéographie en deux sous-disciplines, soient la biogéographie historique et la biogéographie écologique (Wiens & Donoghue, 2004; Wen & al., 2013). La première cherche à comprendre comment différentes lignées d'organismes vivants ont évolué à travers le temps et l'espace, en tentant ainsi d'évaluer si différents processus terrestres - comme la tectonique des plaques, l'orogénèse ou l'apparition de barrières ou de ponts terrestres - ont eu un impact ou non sur la mobilité des espèces et leur diversification à travers différents continents et paysages (Morrone & Crisci, 1995). En revanche, la biogéographie écologique cherche à comprendre quels sont les facteurs environnementaux qui expliquent la répartition de cette diversité biologique à travers l'espace, incluant les conditions abiotiques (température, pluie, sols, feux, etc.), l'apparition de traits chez différentes lignées leur permettant de résister à certaines conditions de stress ou d'être plus compétitifs (l'évolution de la photosynthèse C4, par exemple), ainsi que les interactions inter-espèces (Wiens & Donoghue, 2004). De plus en plus, l'intégration de ces deux sous-disciplines de la biogéographie permettent de faire avancer les études macro-évolutionnaires de la diversité, grâce aux comparaisons empirique des histoires évolutives de différentes lignées, afin de comprendre comment les biomes passés et présents se sont formés, et comment ceux-ci risquent d'évoluer dans le futur (Ricklefs, 2006; Ricklefs & Jenkins, 2011; Donoghue & Edwards, 2014).

Dans cette optique, cette thèse s'intéresse à la systématique et la biogéographie du groupe Caesalpinia, un groupe de plantes de la famille des légumineuses qui se retrouve de manière prédominante dans des milieux arides à travers le globe. Cette introduction cherche donc à donner un cadre théorique à plusieurs questions centrales aux objectifs de cette thèse, notamment:

a) La définition du genre et de l'espèce, ainsi que les critères utilisés pour les délimiter et établir leur classification taxonomique;

b) Les patrons de diversification et les hypothèses biogéographiques chez les plantes tropicales, en particulier dans les milieux arides du biome succulent;

c) Une brève introduction au groupe Caesalpinia de la famille des Leguminosae, soulignant les raisons qui en font un groupe particulièrement intéressant à étudier au niveau de la systématique et de la biogéographie.

I. Le système de classification linnéen : du concept d'espèce à celui du genre

Le système de classification linnéen utilisé de nos jours peut être défini comme un système à rang hiérarchique. En ce sens, le nom du taxon réfère à sa position par rapports aux autres taxons dans le même système : il existe ainsi différentes classes hiérarchisées, soit plusieurs espèces dans un genre, plusieurs genres dans une famille, plusieurs familles dans un ordre, etc. Conséquemment, nommer un taxon implique aussi de comprendre son positionnement dans le système de classification et d'identifier ses relations par rapport aux autres taxons (Baum & Smith, 2013).

Ce système de nomenclature est initialement apparu sans inclure les notions d'évolution, dans un esprit très pragmatique visant à aisément décrire et mémoriser la diversité biologique (Stevens, 2002). Toutefois, aujourd'hui, il a été adapté pour également refléter les liens cladistiques qu'il existe entre les taxons étudiés. Les opinions sur ce système de classification continuent à diverger : certains chercheurs croient en effet que les rangs taxonomiques sont des catégories arbitraires et ne reflètent pas des entités naturelles (Coyne & Orr, 2004). D'autres pensent, au contraire, que ces catégories ne sont pas aléatoires et qu'elles produisent des classifications stables donnant de l'information sur les relations évolutives des espèces qui les composent (Diggs & Liscomb, 2002). Il s'agit là de la continuité du débat classique de la *Scala Naturae*, c'est-à-dire de la discussion à savoir si la nature et ses organismes vivants représentent un continuum ou au contraire, des entités discrètes que l'on peut aisément classer et catégoriser (Stevens, 2002). Nonobstant l'issue de ce débat, il est certain qu'un système de classification taxonomique est un outil essentiel pour définir et référer aux organismes vivants qui nous entoure. Le choix de nommer ces taxons d'une façon ou d'une autre reflète en effet notre compréhension de la diversité qui nous entoure et a un impact concret sur la perception de cette richesse, ainsi que la manière de l'exploiter et de la conserver (Mace, 2004).

La composition des noms des espèces est binomiale : un premier nom fait référence au genre et le deuxième à l'espèce. En ce sens, une bonne compréhension de ce en quoi consiste une espèce et un genre - et quels sont les critères qui nous permettent de délimiter ces deux catégories taxonomiques - est donc essentiel. Dans cette section, une révision des concepts et critères utilisés dans la délimitation d'espèce est présenté pour pouvoir les relier et contraster par la suite à la délimitation de genre.

i. Le concept d'espèce

Les espèces sont considérées comme l'unité fondamentale de la diversité évolutionnaire et sont d'intérêt pour les écologistes, les biologiques évolutionnaires, les systématiciens et les biologistes de la conservation (Coyne & Orr, 2004). Malgré tout, il n'existe toujours pas de consensus sur cette unité taxonomique fondamentale, et les concepts d'espèces font partis d'un vieux débat qui est encore aujourd'hui un sujet important de discorde (de Queiroz, 2007). Ce débat est étroitement lié aux différents critères qui sont utilisés pour délimiter ces groupes : en effet, différents concepts mènent à différents critères de délimitation et ainsi à l'identification de différentes espèces à partir des mêmes données empiriques. Il existe par ailleurs une panoplie de définitions d'espèce : Mayden (1997), par exemple, a identifié pas moins de 24 définitions différentes. Une façon simplifiée de les présenter consiste toutefois à les regrouper en deux grandes catégories : celles qui se basent sur le processus « mécanistique », c'est-à-dire sur une délimitation des espèces basée sur des analyses démontrant comment le processus de spéciation s'est accompli, et celles basées sur un concept historique de l'espèce, c'est-à-dire sur l'identification de groupes d'individus qui ont des ancêtres communs grâce à différents caractères génétiques et/ou morphologiques (Lucklow, 1995).

D'un côté, le « concept d'espèces biologiques (Biological species concept) » (Mayr, 1995) et le « concept de cohésion des espèces (Cohesion species concept) » (Templeton, 1989) sont par exemple tous les deux basés sur l'identification de groupes d'individus ou de populations qui sont le résultat de processus biologiques. Pour Mayr, les espèces sont des groupes d'individus isolés reproductivement les uns des autres, alors que pour Templeton, il s'agit de groupes d'individus qui maintiennent leur intégrité par des mécanismes de cohésions génétiques et écologiques. Or, dans les faits, étudier ces mécanismes de cohésions génétiques, écologiques et les limites reproductives d'espèces peut être difficile (voire impossible pour des organismes à reproduction asexuées). Parallèlement, le « concept d'espèces évolutives (Evolutionary species concept) » (Wiley, 1978), et le « concept d'espèces phylogénétiques (Phylogenetic species concept) » (de Queiroz & Donoghue, 1988) tentent identifier des groupes de descendances communes (des clades monophylétiques (de Queiroz & Donoghue, 1988) ou des groupes avec une histoire évolutive partagée (Wiley, 1978)).

Ces deux catégories de classification soulèvent la possibilité que plusieurs mécanismes distincts peuvent mener au phénomène de spéciation chez les organismes vivants, lesquels sont inhérents à leurs différentes propriétés biologiques, à leur histoire évolutive, ainsi qu'à leurs dynamiques de reproduction distinctes. Un exemple classique est le rejet du concept d'espèce biologique par les botanistes, en raison du fait que les barrières de reproduction entre différentes espèces sont souvent faibles, tel que démontré par l'occurrence plus fréquente d'hybrides. La spéciation chez les plantes peut aussi se produire via différents évènements de polyploïdie, tels que chez les complexes d'espèces agamiques, ce qui donne un vrai défi pour les taxonomistes d'identifier des lignées discretes morphologiquement (Lucklow, 1995; Dickinson, 1999; Coyne & Orr, 2004). Néanmoins, une étude récente de Rieseberg & al. (2006) suggère que ces cas pourraient ne pas être représentatifs des plantes en général. Utilisant les données morphométriques de quelques 200 espèces de plantes, ils ont observé qu'elles correspondaient souvent à des groupes discrets d'individus morphologiquement similaires, et que, quand les données étaient disponibles, ces groupes morphologiques correspondaient à des lignées reproductives isolées.

Une autre contribution intéressante à ce débat complexe sur les concepts des espèces est la proposition d'un nouveau concept unifié de la théorie des espèces avec un seul concept central de l'espèce. Suivant cette logique, de Queiroz (2005, 2007) argumente que le débat entre les biologistes ne doit pas tourner autour de ce en quoi consiste une espèce, mais plutôt sur la façon de les délimiter. Selon lui, presque tous ces différents concepts ont un point commun : les espèces sont considérées comme des lignées de métapopulations qui évoluent séparément à travers le temps. Il suggère également que le désaccord entre les biologistes provient du fait que la séparation des lignées évolutionnaires prend une certaine période de temps, durant laquelle différents critères opérationnels (mécanismes, les patrons phylogénétiques, etc.) ont lieu à différentes échelles temporelles. En somme, ce que qui est perçu par plusieurs comme des concepts d'espèces en opposition serait en réalité différents indices pour un seul et même concept central de l'espèce. Ainsi, les critères opérationnels peuvent être considérés comme des propriétés secondaires qui s'accumulent tranquillement sous ce concept unifié de l'espèce. Cette proposition de de Queiroz fait écho à la proposition de Mayr (1957) d'adopter un concept d'espèce à deux niveaux hiérarchiques, c'est-à-dire 1) un principe primaire qui s'attarde à la théorie de la définition d'espèce et 2) des principes secondaires s'intéressant à la manière pratique et empirique de définir les espèces, en se basant sur ce principe primaire (discuté dans Hey, 2006).

ii. Le concept de genre

La définition la plus simple du genre est que celui-ci correspond une catégorie taxonomique située juste au-dessus du rang d'espèce dans le système de classification linnéen, correspondant ainsi à un groupe d'espèces. Tout comme pour le concept d'espèce, on s'attendrait alors à ce que les genres forment des groupes d'espèces morphologiquement discrets, puisque l'on invoque souvent le besoin d'avoir des synapomorphies ou des caractères diagnostiques pour identifier ces groupes génériques. En ce sens, Small (1989) fait référence au genre comme le produit de la *génériation*, un processus qui est une extension de la spéciation et qui mène à « l'établissement d'écarts morphologiques entre des groupes d'espèces inclus dans le genre et d'autres espèces ». La question demeure toutefois : combien de caractères sont nécessaires avant qu'un groupe d'espèces puisse officiellement être considéré comme un genre distinct? De plus, quels sont les processus qui mènent à ce que les espèces évoluent en groupes discrets?

Tel que mentionné précédemment, le genre n'est pas universellement perçu comme une unité évolutionnaire aussi significative que celle de l'espèce. Cette perception a par ailleurs changée à travers le temps. Par exemple, un sondage mené par Anderson (1940) pour déterminer les opinions d'une cinquantaine de biologistes sur le genre a démontré que deux fois plus de participants pensaient que les genres étaient des unités plus naturelles que les espèces et que la majorité pensait que les mêmes processus responsables de l'origine des espèces étaient impliqués dans l'origine des genres. Or, dans une version contemporaine de ce même sondage, Barraclough et Humphreys (2015) ont démontré que ces opinions sont maintenant renversées. Plus de la moitié des répondants d'un sondage mené sur 107 spécialistes ont indiqué que les espèces devraient étaient les unités évolutionnaires les plus réels. En contraste, moins d'un quart des répondants qui ont répondu que les genres étaient les unités évolutionnaires plus réels, et plus de la moitié des répondants n'ont pas nommé un processus qui expliquerait la création des genres.

Cette perception post-moderne du genre implique qu'il y a un manque de connaissances et un questionnement à savoir si l'on peut comprendre les processus évolutifs qui façonnent la diversité à une échelle plus grande que l'espèce. Sans ces réponses, on arrive inévitablement à la conclusion que le genre est un outil de communication, et que l'assignation du rang des genres au taxon est arbitraire puisqu'elle ne reflète pas des groupes « naturels », ce qui résulte en des unités qui ne sont pas réellement comparable au niveau de leur histoire évolutive. Il est ainsi difficile de dire si un niveau d'hiérarchie est plus significatif qu'un autre (Coyne & Orr, 2004).

Certains chercheurs défendent quant à eux l'idée que les genres peuvent être considérés comme des groupes d'espèces qui occupent une niche écologique particulière à travers le temps et qu'ils sont formés par les mêmes processus qui opèrent au niveau de la spéciation, tel que la sélection divergente et l'isolement reproductive, tel que le suggère Barraclough (2010). Cependant, ces processus peuvent seulement fonctionner dans un cadre où la spéciation est limitée et affectée par les taux d'extinction et de naissance des espèces. Ces deux facteurs sont à leur tour reliés à la géographie, à l'écologie et à la superficie d'un endroit, lesquelles déterminent le nombre d'espèce possible dans une région. La naissance, la diversification et l'extinction des genres seraient donc liés aux taux de spéciation et d'extinction des espèces, lesquels pourraient être limités par la conservation de niche entre espèces et à leur possibilité de dispersion à travers un paysage (Barraclough, 2010).

Toutefois, si cela est bel et bien le cas, comment pourrait-on détecter ces groupes? Barraclough (2010) suggère que des méthodes comparatives identifiant les groupes occupant des niches similaires pourraient être utiles. L'identification de regroupements significatifs d'espèces pourraient aussi être détectés dans ces phylogénies en utilisant des méthodes quantitatives développés pour délimiter les espèces en « barcoding » (Pons & al., 2006), une méthode qui a été développée et testée sur des phylogénies de mammifères (Humphreys & Barraclough, 2014).

Une autre approche également utilisée pour tester des hypothèses alternatives de délimitation générique a été réalisée chez *Orchis* s.l. et a eu recours à des croisements expérimentaux entre espèces pour déterminer les barrières de reproduction post-zygotiques au sein de la sous-tribu des Orchidinae (Scopece & al., 2010). Ces barrières reproductives entre espèces ont ensuite été comparées à trois classifications différentes, la première basée sur des patrons morphologiques menant à des groupes polyphylétiques, la deuxième basée sur le monophylétisme phylogénétique et la dernière étant un compromis entre les deux premières classifications, permettant aussi de nommer des groupes paraphylétiques au niveau du genre. Les résultats de Scopece & al., (2010) ont permis de démontrer que les barrières de reproduction post-zygotiques semblaient correspondre aux groupes définis par la classification basée sur le monophylétisme phylogénétique. Bien que cette approche soit intéressante par sa démonstration d'un processus évolutif semblant séparer et isoler des lignées d'espèces, elle serait très difficile, voire impossible à appliquer pour les genres à toutes les groupes de plantes ou d'animaux, ou les barrières reproductives sont plutôt entre les espèces.

Quels sont alors les critères qui sont les plus communément utilisés pour délimiter les genres? L'une des propriétés les plus désirables d'un système de classification est qu'il soit stable et qu'il permette de prédire facilement les relations phylogénétiques entre les taxons qui le constituent, c'est-à-dire en nommant des groupes d'organismes de manière à ce qu'il soit aisé de comprendre à quelles lignées appartiennent différents organismes (Orthia & al., 2005; Humphreys & Linder, 2009; Vences & al., 2013; Garnock-Jones, 2014). Afin d'établir ces classifications, l'approche la plus souvent utilisée correspond au concept phylogénétique des espèces, appliquée à une échelle taxonomique plus élevé, c'est-à-dire d'uniquement regrouper une espèce et tous ses descendants.

En pratique, bien que la majorité des études qui classifient les genres ne donnent pas d'explication précise quant aux critères qui sont considérées pour définir les genres, elles utilisent pour la plupart le critère de monophylétisme phylogénétique (Humphreys & Linder, 2009), c'est-à-dire que les genres doivent correspondre à des clades qui sont stables et bien supportés dans leurs analyses. L'un des autres avantages principaux de la monophylie est que l'hypothèse de séparation générique devient alors testable, ce qui n'est pas possible dans le cas du paraphylétisme, par exemple (Garnock-Jones, 2014). Idéalement, les genres doivent aussi être définis par des synapomorphies, qui facilitent la reconnaissance et l'identification des taxons sur le terrain. Plusieurs auteurs pensent que satisfaire ces deux critères de délimitations n'est pas toujours possible (Vences & al., 2013), parfois à cause de l'histoire évolutive réticulée de certains groupes qui mène l'homoplasie des caractères morphologiques (Linder & al., 2010). D'autres critères qui sont proposées incluent de minimiser les changements taxonomiques, et de tenir aussi en compte la distribution géographique et écologique des genres (Linder & al., 2010; Vences & al., 2013; Garnock-Jones, 2014).

II. Biogéographie du biome succulent et des forêts tropicales sèches saisonnières

i. Distribution et caractéristiques du biome succulent

La majorité des membres du groupe Caesalpinia se retrouve dans une série d'habitats arides, lesquels correspondent en large partie au biome succulent de Schrire & al. (2005), l'une des quatre grandes métacommunautés biogéographiques identifiée chez les légumineuses, les trois autres étant le biome tempéré, le biome des forêts tropicales humides et le biome des savannes (Lavin & al., 2004; Schrire & al., 2005; voir la figure 3.1 du chapitre 3). Ce biome est difficile à définir en comparaison avec d'autres biomes, tels que les forêts tropicales humides, car il peut être dominé par différents types de structures de végétations. Le biome succulent inclut en effet des milieux dominés par une canopée d'arbres décidus tout comme des milieux désertiques dominés par des arbustes, lianes et arbrisseaux fortement épineux.

Toutefois, quelques traits fondamentaux partagés entre ces habitats les distinguent des trois autres biomes. Tout d'abord, la saisonnalité pluviométrique du biome succulent est très prononcée, avec une saison sèche de 5 à 6 mois (avec moins de 100 mm de pluie), et un maximum de 1800 mm de précipitation par année (Pennington & al., 2009). Souvent confondu avec le biome des savannes, le biome succulent se différencie également par l'absence de feux et des sols plus fertiles. Ceci se traduit par une flore sensible aux fortes perturbations et une prédominance de taxons succulents telle que les Cactaceae dans les néotropiques, et les Euphorbiaceae et les Aizoaceae en Afrique (Schrire & al., 2005; Cowling & al., 2005). Finalement, ce biome se caractérise par l'absence de tolérance au froid et au gel. Les déserts, prairies et forêts sous-tropicales (tel que le Chaco sec au Paraguay et en Argentine) subissent des gels occasionnels sont donc exclus de ce biome (Schrire & al., 2005; Pennington & al., 2009).

À travers le globe, le biome succulent est très fragmenté en comparaison aux biomes tempéré, des forêst tropicales humides, et des savannes, se retrouvant dans des aires disjointes de tailles variées (voir figure 3.2 du chapitre 3). Celles qui sont les mieux étudiées correspondent aux forêts tropicales sèches saisonnières (FTSS) des néotropiques, qui contiennent 54,2% de la superficie mondiale de ce type de forêt (Miles & al, 2006). La distribution disjointe des FTSS forme un arc autour de l'Amazone, partant du Caatinga du Brésil, passant par la Bolivie, le Paraguay et l'Argentine et remontant dans les vallées andines du Pérou, de l'Équateur et de la Colombie. Elles se poursuivent au nord en Amérique Centrale et dans les Caraïbes. Au total, 21 noyaux floristiques ont ainsi été identifiés et cartographiés par Linares-Palomino & al. (2011, voir figure I).

Dans ces milieux, la famille la plus importante en terme d'espèces ligneuses est celle des Leguminosae (Bridgewater & al., 2003), sauf dans les Caraïbes et en Floride où la famille des Myrtaceae domine (Pennington & al., 2009). Dans les néotropiques, des recensements floristiques ont également démontré un haut taux de diversité béta entre ces différents aires (peu d'espèces partagées entre ces aires), ou les espèces endémiques à chaque aire sont généralement abondante (Trejo & Dirzo, 2002; Bridgewater & al, 2003; Oliveira-Filho & al., 2006; Linares-Palomino, 2006). Par exemple, l'étude la plus complète et la plus récente sur les affinités floristiques des FTSS à travers les néotropiques démontre que 8 des 21 noyaux floristiques de FTSS ont un pourcentage de taxons ligneux endémiques qui varie entre 31.3 à 65.5% (excluant ci le noyau insulaire des Caraïbes, contenant 77,5% de taxons endémiques ligneux; Linares-Palomino & al., 2011).

L'idée que les FTSS des néotropiques puissent être considérées comme des îles continentales est par ailleurs renforcée par la comparaison avec des îles comme les Galapagos, où 43% des plantes vasculaires sont endémiques (Tye, 2000). En effet, bien que les FTSS sont des habitats hautement dégradés (moins de 2% des FTSS d'origine en Amérique centrale et 3,2% du Caatinga brésilien sont jugés encore vierges (Janzen, 1988; de Queiroz, 2006)), il est possible que le pourcentage de taxons endémiques soit sous-estimé. Plusieurs publications récentes ont en effet décrit un grand nombre d'espèces cryptiques ou qui n'avaient jamais été recensées dans les Andes, en Amérique centrale et au Brésil. Chez les Leguminosae, ceci inclut notamment *Mimosae jaenensis* (Särkinen & al., 2011), *Caesalpinia celendiniana, Caesalpinia pluviosa* var. *maraniona, Mimosa lamolina* (Lewis & al., 2010), *Coursetia greenmanii* (de

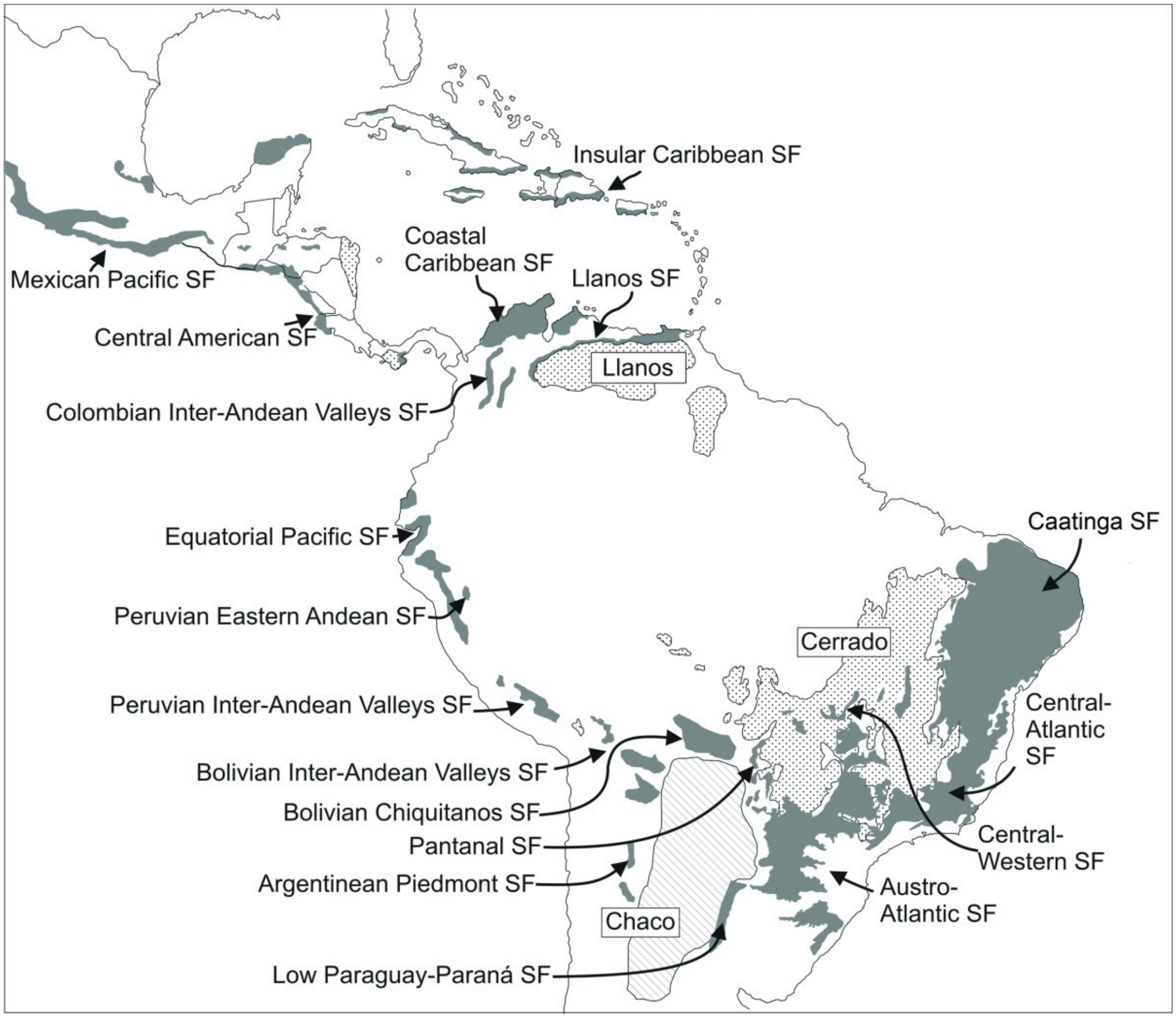

Figure I. Noyaux floristiques des forêts tropicales sèches saisonnières, tiré de Linares-Palomino & al. (2011). Les aires foncées représentent les forêts tropicales sèches saisonnières, alors que les aires pointillées correspondent à différentes savannes (Cerrado du Brésil et Llanos de la Colombie) et les aires correspondent au Chaco, une forêt sèche tempérée du Paraguay, de la Bolivie et de l'Argentine. L'abbréviation SF signifie « Seasonal Forest ».

Stefano & al. 2010), *Coursetia caatinga* (de Queiroz & Lavin, 2011), *Poisonnia eriantha* (Pennington & al., 2011), *Maraniona lavinii* (Hughes & al, 2004), *Parkinsonia perduviana* (Hughes & al., 2003) et *Caesalpinia oyamae* (Sotuyo & Lewis, 2007).

La présence du biome succulent de Schrire et al. (2005) en Afrique et en Asie est un sujet qui demeure incertain, en raison des grandes variations floristiques et physionomiques entre ces continents (Lock, 2006; Pennington & al., 2009; Dexter & al., 2015). Schrire et al. (2005) considère toutefois que le biome succulent se retrouve aussi en Afrique et s'étend en Arabie Saoudite jusqu'au Nord de l'Inde, en raison de la présence d'habitats partageant des conditions de pluviosité similaires, caractérisés par l'absence de feu et qui ont une forte présence de taxons succulents; ces milieux correspondrait au « Thicket biome » (discuté en détail par Cowling & al., 2005). Les plus grands fragments du biome succulent en Afrique incluraient ainsi la corne d'Afrique, dont la région du « Somalia-Masai » de White (1983), le sud-ouest du Madagascar, ainsi que les parties de la Namibie et l'ouest de l'Afrique du Sud qui contiennent le « Succulent-Karoo » et le « Nama-Karoo ». Ces régions seraient reliées par un « corridor aride », composées de petites aires protégées du feu dans les savannes (tels que des affleurements rocheux, des zones riveraines ou des termitières, selon Cowling & al., 2005).

En comparaison, Schrire & al. (2005) considèrent que le biome succulent est largement absent de l'Asie (à l'exception de l'Inde), en raison de l'absence d'habitats secs dominés par les lignées succulentes. Toutefois, certains auteurs considèrent que certaines forêts de moussons particulièrement sèches de l'Asie du Sud-Est, soumises aussi à une forte saisonnalité de la pluviosité, pourraient être considérées comme faisant partie de ce biome (Pennington & al., 2009). Ces forêts incluraient alors les « monsoon vine thickets » du nord de l'Australie (Bowman, 2000), ainsi que des formations végétales similaires répandues à travers les îles indonésiennes et la péninsule indochinoise. Toutefois, des études plus approfondies sont nécessaires pour déterminer s'il existe réellement des similitudes entre ces milieux ou si ces formations végétales sont en réalité régies par des conditions ou dynamiques écologiques distinctes.

ii. Hypothèses biogéographiques

Plusieurs hypothèses ont été proposées pour expliquer les patrons de diversité observés chez la famille des Légumineuse dans le biome succulent sur une échelle globale, ainsi que spécifiquement pour les néotropiques, où le biome succulent a été le mieux documenté. Il a été observé chez les Leguminosae, que différents clades ont tendance à évoluer au sein de biomes particuliers, suggérant que la conservation des niches et les changements de niches entre clades sont des facteurs importants dans les structures de diversification phylogénétiques (Schrire & al., 2005). En outre, des analyses de vicariance effectuées avec les quatre biomes, ou métacommunautés biogéographiques, ont mené à l'observation que les clades qui ont évolué dans le biome succulent semblent être les lignées sœurs des clades occupant le biome des Savannes et des Forêts tropicales humides. Ceci supporte la théorie selon laquelle la famille des Leguminosae serait apparue pour la première fois dans des environnement arides, et non pas humides (Raven & Polhill, 1981), une hypothèse qui serait en accord avec la distribution des fossiles de la famille et les adaptations morphologiques clés qui la caractérisent (McKey, 1994; Schrire & al., 2005). Ceci suggère aussi que le biome Succulent est ancien et qu'il agirait comme une source d'espèces pour les autres biomes, car il est moins fréquent de trouver des lignées des forêts tropicales humides et des savannes comme groupe frère de lignées occupant le biome succulent (Schrire & al., 2005).

Se basant sur la distribution actuelle du biome succulent à travers le monde et sur l'emplacement des fossiles des Leguminosae, Schrire & al. (2005) ont proposé un scénario biogéographique qui pourrait expliquer l'origine de la famille des Léguminosae, baptisé « l'hypothèse de la mer de Tethys », faisant référence à un large plan d'eau qui existait durant l'Éocene (56-43 Ma) et qui traversait l'équateur et séparait les continents des deux hémisphères. La famille des Leguminosae serait alors apparue le long d'une ceinture d'habitats arides tropicaux localisée autour de cette mer et se serait par la suite dispersée vers les pôles, dans les régions boréo-tropicales et tempérés. Cet environnement tropical aride aurait ensuite été déplacé et fragmenté par les mouvements tectoniques et les changements climatiques, résultant dans la distribution actuelle du biome succulent.

À l'échelle néotropicale, d'autres hypothèses biogéographiques ont aussi été proposé pour expliquer les forts niveaux d'endémisme entre aires disjointes du biome succulent, incluant l'hypothèse de « l'arc Pléistocène ». Cette idée est basée sur l'observation qu'un certain nombre d'arbres, tel que *Anadenathera colubrina* et *Geoffroea spinosa* (deux taxons des Leguminosae), présents à travers l'arc de FTSS autour de l'Amazonie. Une des explications proposées pour ce patron floristique proposée est que le biome succulent aurait possiblement eu une distribution élargie dans le passé récent (Prado & Gibbs, 1993). Ceci mène à la proposition selon laquelle le biome succulent aurait pu être plus répandu durant les périodes les plus sèches du Pléistocène et que les baisses de température à la fin de cette époque auraient mené à la contraction de ce biome, entrainant ainsi l'isolation et ultimement la diversification de cette flore (Prado & Gibbs, 1993; Pennington & al., 2000).

Toutefois, des études récentes ont présenté des résultats qui ne supportent pas cette théorie. Tout d'abord, peu d'indices paléo-palynologiques et géomorphologiques soutiennent l'hypothèse d'un biome succulent plus répandu à cette époque, en raison de la rareté de fossiles provenant de milieux secs en Amérique du Sud et de la difficulté à identifier et à distinguer les FTSS des savannes dans des études paléo-palynologiques se basant sur des modèles climatiques (Mayle & al., 2004; Mayle, 2006). Aussi, une étude sur la biogéographie cladistique et la datation moléculaire de neuf genres de plantes typiques de la flore néotropicale des FTSS d'Amérique du Nord et du Sud n'a pas trouvé de patrons de vicariance communs, et a obtenu des dates de divergences des espèces suggèrent plutôt des origines tertiaires et quaternaires (Pennington & al., 2004). Ces résultats suggèrent donc une origine plus ancienne que le Pléistocène des espèces du FTSS, menant à l'hypothèse que les aires disjointes actuelles sont peut-être des vestiges, beaucoup plus stables et isolées qu'estimé précédemment. Les patrons de diversité dans le biome succulent seraient donc le résultat d'un processus évolutif de plus longue durée.

Suite à l'échec des hypothèses de vicariance pour expliquer les patrons de distribution des espèces au sein du biome succulent (Schrire & al., 2005; Pennington & al., 2004), les systématiciens de la famille des Leguminosae ont cherché des explications alternatives aux hypothèses classiques de biogéographie historique, s'intéressant notamment aux différences de structure phylogénétique de la biodiversité au sein de différents biomes. Par exemple, le haut taux d'endémicité au sein de la FTSS se traduit par une forte structure géographique au sein des lignées phylogénétiques, un phénomène rarement observé chez les lignées se spécialisant dans les biomes des Forêts tropicales humides et des Savannes, où les espèces ont généralement des distributions géographiques larges mais ne sont pas nécessairement abondantes localement. Les exemples incluent notamment le genre *Inga* ainsi que des arbres de la sous-famille des Papilionoideae, pour lesquels des études phylogénétiques ont démontré très peu de structure géographiques à l'intérieure du genre (Lavin, 2006). Par ailleurs, les espèces génétiquement rapprochées auraient une tendance plus forte à se retrouver au sein du même territoire, tel que le démontre une étude où 19 espèces d'*Inga* ont été étudiées dans un hectare de forêt tropicale humide d'Amérique du Sud (Valencia & al., 1994; Richardson & al., 2001). Cette faible structure géographique au sein des phylogénies se traduit aussi par des indices de diversité béta moins élevés dans les forêts tropicales humides, en comparaison au haut taux retrouvé dans les FTSS, tel que discuté dans la section précédente. Suivant cette logique, des études sur la composition floristique des forêts de l'Amazonie de l'ouest du Pérou ont relevé que les 825 arbres de la famille des Léguminosae sur le territoire d'étude avait des distributions tellement larges que les espèces les plus communes pouvaient être retrouvées aussi loin qu'en Équateur, avec comme résultat des indices de diversité béta très faibles (Pitman & al. 1999, 2001). Ceci contraste fortement avec les patrons retrouvés chez les lignées de Leguminosae du biome succulent, où il est rare de trouver plus d'une espèce du même genre dans la même communauté floristique, tel que démontré par des études de *Coursetia* et *Poisonnia* (Lavin, 2006).

Ces différences entre les structures phylogénétiques de différents biomes pourraient être expliquées par des processus écologiques qui opèrent différemment au sein des communautés, tel que proposé dans le cadre de la théorie écologique neutre associée aux études phylogénétiques de la composition des communautés (Hubbell, 2001; Webb & al., 2002). Ces deniers s'intéressent aux patrons d'assemblage, aux abondances relatives et à la diversité des espèces au sein de communautés écologiques semblables, qui sont connu comme des méta-communautés. Pour commencer, la répartition très fragmentée du biome succulent, combinée avec l'idée que la conservation des niches empêche les lignées des méta-communautés avoisinantes de s'établir facilement, fait en sorte que les communautés du biome succulent sont isolées et ont des taux d'immigration de nouvelles espèces très faibles. Ces faibles taux sont par ailleurs accentués par la faible perturbation et la stabilité des FTSS, lesquelles restreignent l'établissement de nouvelles espèces, tel qu'en témoigne la croissance et la persistance des plantes succulentes dans l'absence de feu (Lavin & al., 2004). Au cours du temps, la combinaison de ces conditions avec la dérive génétique mène à l'établissement et la domination de certaines lignées dans une région, ce qui à son tour restreint les possibilités pour une espèce similaire ou proche parente de s'établir dans la même région. Ceci ferait en sorte que les communautés ont des structures phylogénétiques faibles, avec très peu de cas de spéciation sympatriques. En contraste, pour les méta-communautés qui sont moins isolés et fragmentées, telles que les forêts tropicales humides, les taxons de ces milieux ont une plus grande facilité de se disperser et de s'établir à des distances plus éloignées de leur parents. De plus haut taux d'immigration local serait donc attendu dans ces communautés, particulièrement dans les cas ou ces milieux subiraient des pertubations régulières (e.g. ouverture dans la canopée de la forêt tropicale humide), menant à de plus haut taux d'extinction local. Conséquemment, dans ces cas les résultats inverses sont attendus, c'est-à-dire des communautés avec de fortes structures phylogénétiques, avec beaucoup d'espèces proche parentes capables de se côtoyer et des espèces qui sont peu abondantes ou rares (Lavin & al., 2004; Lavin, 2006; Lavin & Matos-Beyra, 2008).

Ultimement, les patrons de diversité sont probablement expliqués par une combinaison de ces processus écologiques qui influencent les taux d'extinction et de spéciation au sein d'une communauté, ainsi que par des changements géologiques et climatiques. Ces derniers peuvent aussi influencer les taux d'extinctions et de spéciations par la contraction et l'expansion de différentes communautés à travers le temps. Par exemple, Linares-Palomino (2006) suggère que l'orogénèse des Andes est probablement responsable de l'isolation et des différences floristiques observées entre les noyaux floristiques des FTSS boliviennes et argentines et des FTSS péruviennes et équatoriennes. L'orogénèse des Andes a aussi mené à l'apparition de nouveaux habitats alpins, qui ont présenté des opportunités écologiques qui ont mené à la radiation d'espèces pré-adaptées à ce type d'habitat (Hughes & Atchison, 2015), tel que démontré chez le genre *Lupinus* de la sous-famille des Papilionoideae (Drummond & al., 2012), des membres de la famille des Valerianaceae (Bell and Donoghue, 2005), ainsi que chez le genre *Bartsia* des Orobanchaceae (Uribes-Convers & Tank, 2015). En incorporant des informations plus détaillés sur les relations phylogénétiques des espèces typiques à l'histoire géologique de différentes régions et en utilisation des méthodes développés récemment pour les études biogéographiques (tel que présenté par Wen & al., 2013), incluant la modélisation des niches écologiques, il peutêtre possible de discerner et d'identifier les facteurs écologiques et historiques les plus importants pour expliquer les patrons de diversification du biome succulent.

La taxonomie problématique de *Caesalpinia* sensu lato

Malgré le fait que la famille des Leguminosae est la troisième plus grande famille d'angiosperme, avec 751 genres et près de 19,500 espèces, il ne reste environ que 11 % des genres (ou près de 83 genres) qui n'ont pas été échantillonnés dans les études phylogénétiques publiées à ce jour (Lewis & al., 2005; LPWG, 2013). Les résultats des analyses phylogénétiques publiées dans les dernières années ont démontré que la sous-famille des Caesalpinioideae est un groupe polyphylétique qui doit être divisé en plusieurs sous-familles (dont la meilleure façon de procéder est présentement en train d'être débattue au sein de la communauté des systématiciens des Leguminosae) (Bruneau & al., 2008; LPGW, 2013). L'envers de la médaille est qu'il existe encore beaucoup de groupes pour lesquels les connaissances phylogénétiques doivent encore être éclaircies au niveau des espèces et des genres, dû au fait qu'il reste encore beaucoup d'espèces qui n'ont jamais été échantillonée dans les études phylogénétiques reliées à la famille des Légumineuses (LPWG, 2013). L'un de ces groupes dont les relations phylogénétiques demeurent méconnues est le groupe Caesalpinia, un clade de c. 205 espèces qui se retrouve majoritairement dans des milieux tropicales arides. Bien qu'il compte parmi l'un des plus grands clades en termes du nombre d'espèces au sein de la tribu des Caesalpinieae (sensu Lewis & al., 2005), le nombre de genres au sein du groupe Caesalpinia demeure incertain. L'histoire taxonomique du groupe Caesalpinia semble également longue et complexe et a été décrite en détail par Lewis (1998).

En somme, le défi pour arriver à une classification stable du groupe Caesalpinia découle d'une incertitude des délimitations génériques au sein d'un groupe de 150 espèces, *Caesalpinia* sensu lato. Sa distribution étendue à travers le globe, la difficulté d'identifier des caractères morphologiques diagnostiques pour différents groupes et un haut taux d'homoplasie morphologique (Lewis & Schrire, 1995) ont en effet mené à une absence de consensus chez les botanistes quant au nombre de genres que l'on devrait reconnaitre au sein de *Caesalpinia* s.l. Ceci est en outre illustré par le fait qu'il subsiste en ce moment 30 synonymes génériques pour ce groupe (Lewis, 1998). Par exemple, certains auteurs, tels que Bentham (1865), ont considéré *Caesalpinia* comme un large genre divisé en plusieurs sections, alors que Britton et Rose (1930) ont reconnu jusqu'à 14 genres en se basant pour leur classification sur des différences morphologiques provenant pour la majorité des fruits. La classification la plus récente du groupe Caesalpinia (Lewis, 2005) propose quant à elle de diviser *Caesalpinia* sensu lato en neuf genres, pour un total de 21 genres dans le groupe Caesalpinia. Toutefois la délimitation exacte de ces genres demeure incertaine et Lewis (2005) admet qu'un bon nombre d'espèces asiatiques et africaines ne semblent appartenir à aucun des genres proposés.

De nombreuses études cladistiques morphologiques et moléculaires du groupe Caesalpinia ont également tenté de mieux comprendre les relations phylogénétiques au sein de *Caesalpinia* s.l. (Kantz & Tucker, 1994; Kite & Lewis 1994; Lersten & Curtis, 1994, 1996; Rudall & al., 1994; Lewis & Schrire, 1995; Kantz, 1996; Simpson & Miao, 1997; Herendeen & al. 2003; Gasson & al. 2009). Toutefois, les conclusions de ces études demeurent limitées en raison de l'absence d'une phylogénie claire et résolue et du fait que l'échantillonnage taxonomique dans ces groupes était généralement insuffisant, empêchant ainsi la représentation complète de la variation morphologique au sein du groupe Caesalpinia. Les rares études avec un échantillonnage taxonomique suffisant et représentatif (Simpson & al., 2003; Nores & al., 2012) ont toutefois utilisé des marqueurs moléculaires peu informatifs ne permettant pas de résoudre les liens phylogénétiques au sein du groupe. Pour surmonter ces défis, les études présentées dans cette thèse comprennent un grand nombre d'espèces représentatives et analysent un nombre suffisamment important de marqueurs génétiques pour obtenir des arbres phylogénétiques résolus et statistiquement robustes afin d'évaluer les limites génériques au sein du groupe Caesalpinia.

L'absence de compréhension des relations phylogénétiques et de l'évolution du groupe Caesalpinia nous prive d'un modèle pour comprendre l'évolution d'un groupe qui affectionne les climats arides à une échelle globale. Par exemple, Schrire & al. (2005) ont émis l'hypothèse que *Caesalpinia* sensu stricto, tel que défini par Lewis (2005) et qui contiendrait une quinzaine d'espèces, est un clade dont la distribution géographique actuelle à travers l'Amérique du sud, l'Amérique centrale, les Caraïbes, l'Afrique, la péninsule arabe et l'Inde serait la représentation des restants d'un type de végétation sec ayant persisté à travers le Tertiaire, et qui était possiblement répandu autour de la mer de Téthys au début de l'époque Éocène. Résoudre les liens phylogénétiques et la taxonomie du groupe Caesalpinia permettrait de vérifier si les espèces du genre *Caesalpinia s.s.* et d'autres lignées, occupant aussi des milieux arides similaires à travers le globe, sont réellement ou non des espèces anciennes, vestiges d'une végétation sèche qui aurait ses origines aussi loin que le Tertiaire.

Lavin & al. (2004) et Schrire et al. (2005) ont aussi émis l'hypothèse selon laquelle les dynamiques de diversifications entre clades de légumineuses occupant différents biomes sont affectées par des facteurs différents, et que l'évolution vers un autre biome a un rôle important dans les taux de spéciation et d'extinction au sein de la famille des légumineuses. Koenen & al. (2013) ont cherché à étudier ces taux de diversification dans différents clades de la famille des Leguminosae, représentatifs de ces différents biomes : leurs résultats, bien qu'encore préliminaires, semblent démontrer qu'un clade typique du biome succulent des néotropiques, soit le genre *Robinia,* a un taux de diversification beaucoup plus lent, voir quasiment négatif, en comparaison avec d'autres clades évoluant dans d'autres biomes. Ceci contraste fortement avec d'autres groupes de Leguminosae qui ont connu des augmentations importantes dans leur taux de diversification suite à leur adaptation et évolution vers d'autres biomes, telles que les genres *Calliandra* et *Mimosa* qui ont évolués plusieurs fois vers le biome des Savannes (Simon & al., 2009; Koenen & al., 2013). Ces différentes dynamiques de diversification observées entre groupes évoluant au sein de différents biomes pourraient aussi être intéressant aussi à étudier dans le groupe Caesalpinia. Bien que la majorité des espèces du groupe poussent typiquement dans des habitats du biome succulent, il compte aussi des espèces qui poussent dans les forêts tropicales humides et les savannes de l'Amérique du Sud, de l'Afrique et de l'Asie, ainsi que dans des déserts et des prairies faisant partie du biome Tempéré de Schrire et al. (2005) en Amérique du Nord et en Amérique du Sud.

III. Objectifs de recherche

Afin de mieux comprendre la systématique et la biogéographie des taxons du groupe Caesalpinia, les quatre chapitres de cette thèse répondent aux objectifs de recherche suivants :

(1) Établir un système de classification générique pour le groupe Caesalpinia

Le premier objectif de cette thèse est d'évaluer si la classification générique actuelle du groupe Caesalpinia correspond ou non des groupes monophylétiques qui sont définis par des synapomorphies ou des combinaisons de caractères diagnostiquables. Pour vérifier si *Caesalpinia* s.l. devrait effectivement être divisé en huit genres (sensu Lewis, 2005), la première étape est donc de reconstruire des phylogénies en utilisant des marqueurs génétiques informatifs, avec une représentation adéquate de toute la variation morphologique et géographique au sein du groupe Caesalpinia. Les patrons phylogénétiques ainsi reconstruits seront par la suite comparé à la morphologie des espèces pour mieux déterminer comment délimiter les genres au sein de ce groupe.

Le chapitre 1 (Gagnon et al. 2013) présente une analyse phylogénétique préliminaire basée sur le gène chloroplastique *rps16*, et démontre que la classification actuelle du groupe en 21 genres est insatisfaisante. Afin de répondre à ce manque, le chapitre 2 présente les résultats de nouvelles analyses sur le jeu complet de données des six marqueurs génétiques séquencés pour reconstruire les relations phylogénétiques du groupe Caesalpinia. En accord avec ces résultats, une description de tous les genres du groupe Caesalpinia est présentée, ainsi qu'une clé dichotomique d'identification aux genres, et les diagnoses pour des nouveaux genres, des genres re-instaurés et des genres amendés. L'objectif est de chercher à inclure dans ce synopsis toutes les espèces acceptées pour chaque genre lorsque la taxonomie est suffisamment claire pour le permettre, ainsi que les transferts aux genres appropriés des noms d'espèces, lorsque nécessaire.

(2) Reconstruire l'histoire biogéographique du groupe Caesalpinia

Le deuxième objectif de cette thèse cherche à éclaircir l'histoire biogéographique du groupe Caesalpinia, afin de déterminer si la distribution pantropicale de ce groupe est le résultat d'une origine ancienne liée à l'évolution d'une végétation sèche autour de la mer de Téthys à l'époque Éocène, ou si c'est le résultat de dispersion de longue distance plus récente. Les phylogénies présentées font ressortir des patrons géographiques, qui incluent d'impressionnantes disjonctions intercontinentales entre l'Afrique, l'Amérique du Sud et l'Amérique du Nord, parfois même entre espèces sœurs. À travers des analyses de datation molélculaire et des reconstructions d'aires ancestraux, nous déterminons si les disjonctions - ou encore la naissance de nouvelles lignées chez le groupe Caesalpinia - sont corrélées ou non avec des phénomènes d'ordre géographique et climatique (la dérive des continents, des périodes d'assèchement climatiques, etc.).

Par ailleurs, ce document cherche à déterminer si ces disjonctions ont lieu au sein du même biome, ou s'il est fréquent pour les taxons de changer de biome quand ils se sont dispersés vers de nouveaux continents. Ceci permettra d'évaluer l'hypothèse de la conservation des niches, qui suggère qu'il est plus facile pour les espèces végétales de s'établir dans des habitats similaires mais lointains, que d'acquérir au cours de l'évolution les caractéristiques nécessaires pour s'adapter à des biomes géographiquement voisins mais écologiquement différents.

Finalement, comme certains taxons du groupe Caesalpinia occupent aussi les biomes des savanes, des milieux tempérés chauds et des forêts tropicales humides, il est intéressant de déterminer si les taxons qui évoluent dans ces autres biomes ont des taux de diversification différents des espèces retrouvées dans les biomes succulents, tel qu'observé à l'échelle de la famille des Légumineuses (Koenen et al., 2013). Suivant cette même logique, cette thèse chercher à déterminer si le port des plantes (arbustif, herbacé ou lianescent) est associé ou non à certains types de biomes et à des changements de taux de diversification, en reconstruisant l'évolution ancestrale du port et des biomes à travers la phylogénie.

(3) Décrire une nouvelle espèce du Pérou et faire la révision d'un nouveau genre

Le troisième objectif de cette thèse consiste à évaluer s'il existe ou non une espèce cryptique au sein de *Caesalpinia trichocarpa,* une espèce arbustive qui est présentement répartie dans des vallées disjointes en Argentine, en Bolivie et au Pérou. Des missions de collectes botaniques récentes ont en effet permis de constater que les populations au Pérou, séparées par plus de 1350 km, comportent des différences morphologiques qui pourraient indiquer qu'elles représentent une espèce cryptique, c'est-à-dire qu'elles sont morphologiquement très similaires, mais génétiquement distinctes.

Afin de tester cette hypothèse, des analyses moléculaires et morphologiques détaillées ont été effectuées à partir de quatre marqueurs chloroplastiques et nucléaires, ainsi que sur 31 caractères morphologiques qualitatifs et quantitatifs. Ces jeux de données proviennent d'un échantillonnage dense des populations de plusieurs individus de *Caesalpinia trichocarpa*, suite à des missions de récoltes au Pérou et en Argentine et la consultation de nombreux spécimens de plusieurs herbiers à travers le monde (K, MO, NY, US, USM, CORD, CTES, SI). Par ailleurs, ce document cherche aussi à déterminer le statut générique de *Caesalpinia trichocarpa* ainsi que de certaines espèces apparentées, dont quatre espèces se retrouvant dans les Andes (*C. ancashiana*, *C. celendiniana* et *C. mimosifolia*). Plus spécifiquement, il s'agit de déterminer si ces espèces représentent un genre distinct et s'il est possible de le caractériser et de le distinguer morphologiquement. Considérant les résultats de nos différentes analyses, des changements taxonomiques sont apportés à travers le cadre d'une révision taxonomique de ces espèces andines.

Chapitre 1: A molecular phylogeny of Caesalpinia sensu lato: increased sampling reveals new insights and more genera than expected

Edeline Gagnon[1], Colin E. Hughes[2], Gwilym P. Lewis[3], Jeny Solange Sotuyo[4] and Anne Bruneau[1]

1. Institut de recherche en biologie végétale and Département de sciences biologiques, Université de Montréal, H1X 2B2, Montréal, Canada;
2. Institute of Systematic Botany, University of Zürich, 8008, Zürich, Switzerland;
3. Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, United Kingdom;
4. Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Tercer Circuito s/n, Ciudad Universitaria, Delegación Coyoacán, Apartado Postal 70-233, 04510 México, D.F. Mexico

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1.1 Résumé/ Abstract

Résumé

Caesalpinia sensu lato (s.l.), est un groupe pantropical de près de 150 espèces d'arbres, d'arbustes et de lianes, qui se retrouvent en majorité dans des habitats arides du biome succulent (sensu Schrire & al., 2005), telles que les forêts saisonnières sèches de l'Amérique Central, de l'Amérique du Sud, ainsi que des Caraïbes. La délimitation traditionnelle de *Caesalpinia* s.l. en fait l'un des plus grands genres au sein de la tribu des Caesalpinieae, mais plus récemment, sept genres ont été re-instaurés par Lewis (2005), soit *Coulteria, Erythrostemon, Guilandina, Libidibia, Mezoneuron, Poincianella,* et *Tara,* réduisant *Caesalpinia* s.s. à quelques espèces. La validité de ces genres re-instaurés est questionnée, car leur monophylétisme n'a jamais été testé adéquatement en utilisant des données moléculaires. L'incertitude entourant la délimitation des genres de *Caesalpinia* s.l. empêche d'établir une classification générique stable pour le groupe Caesalpinia, qui inclut *Caesalpinia* s.l. et 13 autres genres. Pour résoudre ces problèmes de classification au sein *Caesalpinia* s.l. et le groupe Caesalpinia, nous présentons une nouvelle phylogénie basée sur des séquences chloroplastiques de *rps16,* et qui inclut un échantillonnage taxonomique dense de 18 des 21 genres du groupe Caesalpinia et 98 des 150 espèces de *Caesalpinia* s.l. Nos résultats supportent le monophylétisme de cinq des genres re-instaurés par Lewis (2005), mais suggèrent que trois autres genres (incluant *Caesalpinia* s.s.) sont non-monophylétiques et leur délimitation devrait être revue. Par ailleurs, trois nouveaux clades sont identifiés au sein de *Caesalpinia* s.l., et de plus amples études morphologiques seront nécessaires pour déterminer s'ils devraient être reconnus comme des genres distincts. Les incertitudes concernant la délimitation de certains clades sont discutées en relation avec la variation morphologique retrouvée au sein de *Caesalpinia* s.l.

Mots-clés: *Caesalpinia* sensu lato, groupe Caesalpinia, taxonomie, delimitation générique, Caesalpinioideae, Leguminosae

Abstract

Caesalpinia sensu lato (s.l.), in its broadest circumscription, is a pantropical group of c.150 species of trees, shrubs and lianas many of which grow in arid habitats of the Succulent Biome (sensu Schrire & al., 2005), and especially in the seasonally dry tropical forests of Central and South America and the Caribbean. As traditionally circumscribed, *Caesalpinia* s.l. was one of the largest genera in tribe Caesalpinieae, but seven generic segregates, namely *Coulteria, Erythrostemon, Guilandina, Libidibia, Mezoneuron, Poincianella* and *Tara* were reinstated by Lewis (2005), greatly reducing the number of species remaining in *Caesalpinia* sensu stricto (s.s.) Nevertheless, doubts remain regarding the monophyly and delimitation of some of these segregate genera, which have not been thoroughly tested using molecular data, and this has hindered the establishment of a comprehensive generic classification of the broader Caesalpinia Group as a whole. Here we present a new phylogeny of the Caesalpinia Group, based on plastid *rps16* sequences and dense taxon sampling including 18 of the 21 genera of the Caesalpinia Group and 98 of the c.150 species of *Caesalpinia* s.l. Our results support the monophyly of five of the genera reinstated by Lewis, but the three other genera (including *Caesalpinia* s.s.) are non-monophyletic and need to be re-evaluated. Furthermore, three robustly supported newly discovered clades within *Caesalpinia* s.l. potentially merit recognition as distinct genera pending complete investigation of diagnostic morphological characters. Uncertainties concerning the delimitation of some clades are discussed especially in relation to the extensive morphological variation found within *Caesalpinia* s.l.

Keywords: *Caesalpinia* sensu lato, Caesalpinia Group, Taxonomy, Generic delimitation, Caesalpinioideae, Leguminosae

1.2 Introduction

Caesalpinia sensu lato (Leguminosae subfamily Caesalpinioideae), as traditionally circumscribed, is a pantropical group of about 150 species of trees, shrubs and lianas that mostly grow in seasonally dry and semi-arid habitats of the Succulent biome (sensu Schrire et al., 2005) and especially in seasonally dry tropical forests (SDTF) in the Neotropics. The genus in its broadest sense not only needs taxonomic revision at the species level, but also reorganisation at the intra-generic level. While both morphological and molecular phylogenetic analyses (Lewis & Schrire, 1995; Simpson & Miao, 1997; Simpson & al., 2003; Bruneau & al., 2008; Manzanilla & Bruneau, 2012; Nores & al., 2012) have clearly demonstrated that *Caesalpinia* s.l. is not monophyletic, the lack of a densely sampled and robustly supported phylogeny has left many doubts about how many genera should be recognised and how they should be delimited.

Caesalpinia s.l. is part of the larger informal Caesalpinia Group of tribe Caesalpinieae, which has a long and complex taxonomic history (reviewed by Lewis, 1998, 2005). In brief, the number of genera in the Caesalpinia Group has been modulated by the varying size of the genus Caesalpinia, both in terms of its species and generic nomenclatural composition, with 25 generic names having been, at one time or another, placed in synonymy under a broadly circumscribed Caesalpinia s.l.

The informal Caesalpinia Group proposed by Polhill & Vidal (1981) originally comprised 16 genera, including the then broadly circumscribed genus *Caesalpinia*. This group was considered to be one of the most distinctive of the nine informal generic groups in the Caesalpinieae tribe, based on a set of morphological characters that included the presence of a lower cucullate sepal on the calyx, as well as the highest occurrence and diversity of spines, thorns, trichomes and secretory structures within the tribe. Based largely on these characters, Polhill & Vidal (1981) also included *Conzattia*, *Lemuropisum* and *Parkinsonia* in the Caesalpinia Group, but these three genera were subsequently shown to belong to the Peltophorum Group (Lewis & Schrire, 1995; Bruneau & al., 2001; Haston & al., 2005). Within their Caesalpinia Group, Polhill & Vidal (1981) also recognised a number of genera with consistently pinnate (rather than bipinnate) leaves, including *Cenostigma*, *Cordeauxia*, *Stahlia*, *Stuhlmannia*, and *Zuccagnia*.

More recently, Lewis (2005) proposed the reinstatement of eight genera, including *Caesalpinia* s.s. (Table 1.1 in bold) from within *Caesalpinia* s.l., bringing the number of recognised genera in the Caesalpinia Group to 21. As noted by Lewis (2005), the monophyly of these reinstated genera remains to be tested, firm generic boundaries must be determined to ensure correct generic placement of all species of *Caesalpinia* s.l., and morphological support and diagnosability need to be established for each genus. To date, no adequately sampled and robust molecular phylogeny has been available to test the proposed genus-level classification of the Caesalpinia Group. Furthermore, there are some 15 species, mainly Asian taxa, of uncertain generic affinities that are presently unassigned to any segregate genus. Lewis (2005) pointed out that it was critical for these Asian taxa to be included in molecular analyses before they could be assigned to any one genus with confidence, and before a comprehensive new generic system for the Caesalpinia Group could be established.

Caesalpinia s.l. encapsulates the difficulties and dilemmas surrounding generic delimitation. To date it has been difficult, due to inadequate sampling of either morphological or molecular data, to establish stable groups that have predictive taxonomic value, in the sense that this permits reliable prediction of specific attributes for taxa that have not been characterised or formally described (Humphreys & Linder, 2009). This is one of the main difficulties in the classification of *Caesalpinia* s.l.: the apparent lack of obvious diagnostic morphological synapomorphies for some genera that would provide a clear basis for assigning to genera species that have not been sampled in molecular phylogenies. This is partly due to high levels of homoplasy for many morphological characters in *Caesalpinia* s.l. As a result, certain authors, including Bentham (1865), considered *Caesalpinia* to be a single large polymorphic genus best divided at the infrageneric level into several sections. Others have argued that *Caesalpinia* should be separated into several genera based on specific subsets of morphological characters. For example, Britton and Rose (1930) recognised 16 genera from within *Caesalpinia* s.l. based mostly on fruit characters. A number of in-depth morphological, phytochemical and anatomical studies have presented diverse new evidence for phylogenetic analysis and generic delimitation,

Table 1.1 Generic delimitation of *Caesalpinia* s.l. proposed by Lewis (2005). In bold, genera reinstated by Lewis (2005). Geographic distribution: Africa (AF), Asia (AS), Carribean, Central America (CA), North America (NA), South America (SA).

Generic names	**# species**	**Synonyms**	**Geographic distribution**
Balsamocarpon Clos.	1		SA
Cenostigma Tul.	2		SA
Cordeauxia Hemsl.	1		AF
Hoffmannseggia Cav.	24	*Larrea* Ortega, *Larrea* auct. Cav., *Moparia* Britton & Rose	NA, SA
Pomaria Cav.	16	*Melanosticta* DC., *Cladotrichium* Vogel	NA, SA, AF
Haematoxylum L.	4	*Cymbosepalum* Baker, *Haematoxylon* L.	CA, SA, AF
Lophocarpinia Burkart	1		SA
Moullava Adans.	1	*Watagea* Dalzell	As
Pterolobium R.Br. ex Wight & Arn.	11	*Cantuffa* J.F.Gmel., *Reichardia* Roth	Af, AS
Stenodrepanum Harms	1		SA
Stuhlmannia Taub.	1		AF
Stahlia Bello	1		Caribbean
Zuccaginia Cav.	1		SA
Coulteria Kunth	9-10	*Guaymasia* Britton & Rose, *Brasilettia* sensu Britton & Rose	CA
Tara Molina	3	*Russellodendron* Britton & Rose, *Nicargo* Britton & Rose	SA, CA
Erythrostemon (Hook.) Klotzsch	13	*Schrammia* Britton & Rose	SA
Poincianella Britton & Rose	~35		CA
Guilandina L.	7–18	*Bonduc* Mill., *Caesalpinia* subgenus *Guilandina* (L.) Gillis & Proctor	Pantropical
Libidibia (DC.) Schltdl.	6–8	*Caesalpinia* sect. *Libidibia* DC.	CA, SA
Mezoneuron Desf.	26	*Mezoneurum* DC., *Caesalpinia* subgenus *Mezoneuron* Desf. Ex Herendeen & Zarucchi	AS, AF
Caesalpinia L., sensu stricto	~25	*Poinciana* L., *Brasilettia* (DC.) Kuntze	CA, SA, Carribean
Unplaced Old World Taxa	~15	*Biancaea* Tod., *Campecia* Adans., *Cinclidocarpus* Zoll., *Ticanto* Adans., *Caesalpinia* sect. *Sappania* DC., *Caesalpinia* sect. *Nugaria* DC., *Caesalpinia* sect. *Cinclidocarpus* (Zoll.) Benth.& Hook. f.	AS, Af

but none have achieved the comprehensive taxon sampling needed to definitively support the division of *Caesalpinia* s.l. These include studies on floral development and ontogeny (Kantz & Tucker, 1994; Rudall & al., 1994; Kantz, 1996), phytochemistry of non-protein amino acids in seeds (Kite & Lewis, 1994), leaf anatomy and secretory structures (Lersten & Curtis, 1994, 1996; Rudall & al., 1994; Herendeen & al., 2003), and wood anatomy (Gasson & al., 2009).

The other challenge is that species of the Caesalpinia Group and *Caesalpinia* s.l. occur on all five continents, and it has thus been difficult to obtain fresh leaf material or DNA samples of all relevant taxa. Furthermore, many species are locally abundant, but narrowly distributed endemics, particularly those that grow in SDTF (Linares-Palomino, 2006; Pennington & al., 2009; Linares-Palomino & al., 2011), some of them only described within the last decade (*Caesalpinia celendiniana, Caesalpinia pluviosa* var. *maraniona*, Lewis & al., 2010; *Caesalpinia oyamae*, Sotuyo & Lewis, 2007), requiring highly targeted fieldwork to obtain material. Previous molecular and morphological phylogenetic studies have focused either on higher-level relationships and employed sparse species-level sampling (Simpson & Miao, 1997; Lewis and Schrire, 1995; Haston et al., 2005; Bruneau et al., 2008; Manzanilla & Bruneau, 2012; Nores & al., 2012;), or have focused on particular segregates by producing phylogenies with denser species level sampling either within *Caesalpinia* s.l. or the broader Caesalpinia Group (e.g., *Hoffmannseggia*, Simpson & al., 2004, 2005; *Pomaria*, Simpson & al., 2006). The recent phylogenetic study by Nores et al. (2012), based on sequences from the plastid regions *trnL–trnF* and *matK*, as well as morphology, included representatives of all genera of the informal Caesalpinia Group (sensu Lewis, 2005), and established the placements of the four monospecific genera, *Balsamocarpon, Lophocarpinia, Stenodrepanum* and *Zuccagnia*. They also compiled a more extensive sampling of *Caesalpinia* s.l. (51 species) based on plastid *trnL–trnF* region sequences from Genbank. However, even this denser taxon sampling remains insufficient to address generic delimitation issues across *Caesalpinia* s.l. as a whole. Furthermore, no previous phylogenetic studies have sampled the type species of *Caesalpinia* sensu stricto, *Caesalpinia brasiliensis* L., nor the types of other genera proposed for reinstatement by Lewis (2005), making it difficult to ascertain to what extent clades that have been recovered truly correspond to the proposed classification.

The overall objective of this study is to clarify phylogenetic relationships within *Caesalpinia* s.l. and the higher level informal Caesalpinia Group as a whole, and specifically to test the monophyly of the Lewis (2005) segregate genera and evaluate whether other well-supported clades within *Caesalpinia* s.l. merit recognition as distinct genera. Given the remarkable morphological variation across *Caesalpinia* s.l., it is essential to sample specimens as widely as possible, both taxonomically and geographically. We use the densely sampled molecular phylogenetic hypothesis based upon a variable plastid marker to discuss possible morphological synapomorphies or sets of diagnostic characters for the robustly supported clades recovered in our analyses.

1.3 Material and methods

1.3.1 Taxonomic sampling

In this study, we sample 276 accessions representing 120 species (98 from *Caesalpinia* s.l.) from 18 of the 21 genera belonging to the informal Caesalpinia Group (sensu Lewis, 2005). The phylogenetic positions of three monospecific genera missing from our sampling, *Lophocarpinia, Stahlia,* and *Stenodrepanum*, were previously investigated by Nores & al. (2012) and Simpson & al. (2003). Our sample includes type species for all the genera sampled from the Caesalpinia Group (Table 1.2; type species marked *) except *Mezoneuron* (*Mezoneuron glabrum* Desf.) As far as possible, multiple accessions from different localities per species were included. Material was sampled from herbarium specimens or field-collected silica-dried leaf samples from wild and cultivated plants. Locality details, herbarium vouchers and GenBank numbers for all accessions are listed in Table 1.2. An additional 11 sequences from Haston & al. (2005) and Marazzi & al. (2006) were downloaded from Genbank.

As outgroup, we included 56 sequences from Genbank (Haston & al., 2005; Marazzi & al., 2006; Marazzi & Sanderson, 2010) and 17 new sequences that were generated de novo, that encompassed the tribe Caesalpinieae (28 genera), as well as the more distantly related *Poepiggia procera* (Dialiinae clade), which was used to root the trees (Table 1.2). This extensive outgroup was included to verify if all species hypothesized to belong to *Caesalpinia* s.l. fall within the Caesalpinia Group rather than elsewhere in tribe Caesalpinieae, as suggested for example for *Cenostigma* (Simpson & al., 2003).

1.3.2 Molecular methods

DNA was extracted using: (1) a modified CTAB protocol (Joly & Bruneau, 2006); (2) QIAGEN DNeasy Plant Mini Kit (Mississauga, ON, Canada), following the manufacturer's instructions; or (3) a 4% MATAB protocol (Ky & al., 2000).

The plastid region *rps16* was selected based on screening for ease of amplification and adequate phylogenetic resolution of the ten most variable chloroplast markers from Shaw & al. (2005, 2007) in an initial sample of ten Caesalpinia s.l. species (Babineau & al., 2013–in this issue). The locus was amplified using primers rps16F and rps2R (Oxelman & al., 1997) in reaction volumes of 50 µl, with 1× Taq DNA polymerase buffer without MgCl2 (Roche Diagnostics, Indianapolis, IN, USA), 3.0 mM MgCl2, 200 µM of each dNTP (Fermentas, Burlington, ON, Canada), 0.4 µM of each primer, 3 µg bovine serum albumin (New England Biolabs, Ipswich, MA, USA), 0.03% tween-20, 3% pure DMSO, one unit of Taq polymerase, and 50–300 ng of genomic DNA. The PCR consisted of an initial denaturing step of 5 min at 80 °C, followed by 35 cycles of these three steps: a denaturing step of 45 s at 94 °C, an annealing step of 45 s at 53 °C, and an elongation step of 60 s at 72 °- C seconds. The final elongation step was 7 min at 72 °C.

For more difficult samples, we used a nested PCR with a second amplification of a 1/10 dilution of the original PCR product, identical PCR conditions, and replacing the primers with R851 and F68 (Babineau, 2013).

All PCR amplification products were submitted to Genome Quebec (Montreal, Canada), where they were purified and sequenced with Big Dye Terminator 3.1 chemistry on an ABI 3730×l DNA Analyzer (Applied Biosystems, Carlsbad, CA, USA). Chromatograms were assembled and visually inspected using Geneious (version 5.6-6.0.1-5, Biomatters, Auckland, New Zealand). Because the nested PCR technique can sometimes lead to non-specific amplification, sequences were submitted to a BLAST search (Altschul & al., 1990) and eliminated if they did not correspond to Leguminosae sequences in Genbank.

1.3.3 Phylogenetic analyses

Sequences were aligned, inspected and manually adjusted in Geneious. Gaps were coded using simple indel coding (SIC; Simmons & Ochoterena, 2000), implemented in SeqState 1.4.1 (Müller, 2005). Only indels that did not represent autapomorphies were retained.

Both maximum parsimony and Bayesian phylogenetic analyses were performed and the resulting trees compared. Maximum parsimony analysis was performed in PAUP* (Swofford, 2003) using a two-step analysis procedure (Davis & al., 2004) with an initial 1000 replicates of random addition sequence, with tree bisection-reconnection branch swapping, retaining the five most parsimonious trees at each replicate, followed by a second heuristic search with the same settings, starting from the trees in memory, retaining a maximum of 100,000 trees. To assess branch support, 10,000 bootstrap replicates were performed, with one tree retained per replicate.

Bayesian analysis was conducted in MrBayes3.2 (Ronquist & al., 2012), with the data partitioned between the DNA sequence matrix and SIC gap matrix. Jmodeltest 2 (Darriba & al., 2012) was used to estimate the best evolutionary model for the DNA matrix, which was identified as the GTR + I + G model according to the Aikake Criterion. The F81 model was specified for the indel matrix. The analysis was run on a server (Réseau Québécois de Calcul de Haute Performance (RQCHP), Université de Montréal, Canada) with two parallel runs of eight Markov Chain Monte Carlo (MCMC) chains each, four swaps per swapping cycle, and trees sampled every 1000 generations. The stop criterion was set to an average standard deviation of split frequencies that dropped to below the critical value 0.01. After observing results with Tracer v. 1.5 (Rambaut & Drummond, 2007) and ensuring that effective sample sizes were sufficient, the burn-in fraction was set to 10%.

Table 1.2 Accessions included in this study. Species of the Caesalpinia Group are classified sensu Lewis (2005), and the number of species sampled over the total number of species recognised in the genus is given in parentheses. Type species for genera in the Caesalpinia Group are preceded by an asterisk (*). Collector names and numbers (and herbarium acronym) of voucher specimens are listed for all material that was taken from herbarium specimens and for the voucher specimens of seed collections and silica-dried leaf samples, if known. Accession numbers are provided for published sequences downloaded directly from Genbank: Haston & al. (2005), Marazzi & al. (2006), and Marazzi & Sanderson (2010).

Genus (no. of species sampled/total no. species) ***Species***	**Voucher specimen (Herbarium)**	**Collection Locality**	**Genbank accession number**
OUTGROUP			
Acrocarpus fraxinifolius Wight & Arn.	Faden 74/1314 (K: Krukoff), Haston V200301 (RNG)	Kenya	AY899741
Acrocarpus fraxinifolius Wight & Arn	Manos 1416 (DUKE)	China, cultivated	KF522306
Arapatiella emarginata R.S. Cowan	Thomas 10913 (K)	Brazil	AY899746
Arcoa gonavensis Urb.	Jiménez 3522 (JSBD)	Dominican Republic	KF522309
Batesia floribunda Spruce ex Benth.	Ricker et al. 11 (K)	Peru	AY899745
Bussea sakalava Du Puy & R. Rabev.	Capuron 23.331_SF (K)	Madagascar	AY899766
Cassia javanica L.	Fougère-Danezan 6 (MT)	Singapore, cultivated	KF522255
Cassia fistula L.	Marazzi & Flores BM177 (MEXU, Z)	Mexico, cultivated	AM086915
Ceratonia oreothauma Hillc. & al.	Munton 16 (K)	Oman	KF522310
Ceratonia siliqua L.	Wieringa & Janzen 3477 (WAG)	Greece	KF522311
Cercidium andicola Griseb.	Hughes & Forrest 2313 (K)	Bolivia	AY899779
Chamaecrista acosmifolia (Benth.) H.S.Irwin & Barneby	Conceiçao & Marazzi AC1129 (HUEFS, Z)	Brazil	AM086584
Chamaecrista desvauxii (Collad.) Killip	Marazzi et al. BM013 (Z, CTES, PY)	Paraguay	AM086911
Chamaecrista nictitans Moench	Klitgaard et al. 686 (K)	Ecuador	KF522254
Chamaecrista nictitans Moench	Marazzi et al. BM034 (Z, CTES, PY)	Paraguay	AM086912

Chamaecrista serpens Greene	Marazzi & Flores BM179 (Z, CTES, PY)	Mexico	AM086913
Colvillea racemosa Bojer ex Hook.	Haston V200302 (RNG)	Madagascar	KF522247
Colvillea racemosa Bojer ex Hook.	Lewis *et al*. 2147 (K)	Madagascar	AY899794
Conzattia chiapensis Miranda	López 7571 (MEXU)	Mexico	KF522249
Conzattia multiflora (B.L. Rob.) Standl.	Du 600 (K),Haston V200303 (RNG)	Mexico	AY899785
Conzattia multiflora (B.L. Rob.) Standl.	Hughes 1824 (MEXU)	Mexico	KF522244
Conzattia multiflora (B.L. Rob.) Standl.	Sahagun sn (RNG)	Mexico	AY899786
Delonix baccal (Chiov.) Baker f.	Gillett 13717 (K)	Kenya	AY899792
Delonix brachycarpa (R. Vig.) Capuron	Phillipson 3081 (FHO)	Madagascar	AY899790
Delonix elata (L.) Gamble	Wood Y/74/449 (BM)	Yemen	AY899787
Delonix elata (L.) Gamble	Friss et al. 8579 (K)	Ethiopia	KF522246
Delonix floribunda (Baill.) Capuron	Randriarimalala 16A (K)	Madagascar	AY899791
Delonix pumila Du Puy, Phillipson & R. Rabev.	Miller et al. 6147 (K)	Madagascar	AY899793
Delonix regia (Bojer ex Hook.) Raf.	du Puy et al. M578 (K)	Madagascar	AY899788
Delonix regia (Bojer ex Hook.) Raf.	Jodrell Acc. No. 06483 (K: Krukoff) Haston V200304 (RNG)	Mexico	AY899789
Delonix regia (Bojer ex Hook.) Raf.	Marazzi & Flores BM179 (MEXU, Z)	Mexico, cultivated	AM086916
Delonix regia (Bojer ex Hook.) Raf.	Phillipson et al. 3778 (K)	Madagascar, cultivated	KF522248
Gleditsia sinensis Lam.	Keith 58 (Hilliers Arboretum), Haston V200305 (RNG)	cultivated	AY899744
Gleditsia sinensis Lam.	Marazzi BM188 (Z)	Switzerland, cultivated	AM086917
Gleditsia triacanthos L.	Marazzi BM189 (Z)	Switzerland, cultivated	AM086918
Gymnocladus chinensis Baill.	Herendeen II-V-02-1 (US)	USA, cultivated	KF522308
Gymnocladus dioica (L.) Koch	P 495609 (USDA), Haston V200306 (RNG)	cultivated	AY899743
Heteroflorum sclerocarpum M. Sousa	Hughes 1845 (FHO)	Mexico	AY899784
Heteroflorum sclerocarpum M. Sousa	Hughes 1849 (FHO, MEXU)	Mexico	KF522245

Jacqueshuberia loretensis R.S. Cowan	Rimachi Y 9050 (NY)	Peru	AY899761
Jacqueshuberia purpurea Ducke	de Lima 3273 (NY, INPA)	Brazil	AY899762
Lemuropisum edule H. Perrier	Willings sn (K)	Madagascar	AY899795
Melanoxylon brauna Schott	Noscheler 10 (K)	Brazil	AY899757
Moldenhawera brasiliensis Yakovlev	de Carvalho sn (NY)	Brazil	AY899759
Moldenhawera luschnathiana Yakovlev	de Sant'Ana 595 (NY)	Brazil	AY899760
Parkinsonia aculeata L.	Hawkins 94/5 (FHO)	Mexico	AY899772
Parkinsonia aculeata L.	Contreras 1136 (FCME)	Mexico	KF522243
Parkinsonia africana Sond.	Kolberg sn (OFI)	South Africa	AY899780
Parkinsonia anacantha Brenan	Adamson EA12869 (FHO)	Kenya	AY899781
Parkinsonia florida (Benth. ex A. Gray) S. Watson	Hawkins 101 (FHO)	Mexico	AY899775
Parkinsonia florida (Benth. ex A. Gray) S. Watson	Hawkins 126 (FHO)	Mexico	AY899776
Parkinsonia florida (Benth. ex A. Gray) S. Watson	Hughes 1562 (FHO)	Mexico	AY899777
Parkinsonia microphylla Torr.	Hawkins 127 (FHO)	Mexico	KF522250
Parkinsonia peruviana C.E. Hughes, Daza & Hawkins	Hughes 2022 (FHO)	Peru	AY899771
Parkinsonia praecox (Ruiz & Pav.) Hawkins	Hawkins 36 (FHO)	Mexico	AY899778
Parkinsonia raimondoi Brenan	Thulin 4135 (FHO)	Somalia	AY899783
Parkinsonia scioana (Chiov.) Brenan	Hassan 63 (FHO)	Somalia	AY899782
Parkinsonia texana (A. Gray) S. Watson	Hawkins 151/152/153 (FHO)	Mexico	AY899774
Peltophorum africanum Sond.	Kornas 2861 (FHO)	Zambia	AY899768
Peltophorum dubium (Spreng.) Taub.	Hughes 1685 (FHO)	Mexico	AY899769
Peltophorum pterocarpum (DC.) Backer ex K. Heyne	Grierson & Long 2884 (E)	Bhutan	AY899770
Peltophorum pterocarpum (DC.) Backer ex. K. Heyne	Goyder 3719 (K)	Australia	KF522242
Poeppiga procera Presl	Klitgaard 65 (K)	Brazil	AY899740
Pterogyne nitens Tul.	Pennington 244 (FHO)	Brazil	AY899747
Recordoxylon speciosum (R. Ben.) Normand & Mariaux	de Lima 3333 (NY)	Brazil	AY899756
Schizolobium parahyba (Vell.) S.F. Blake	Hughes 1880 (FHO)	Mexico	AY899767
Senna covesii (A. Gray) H.S. Irwin & Barneby	Marazzi BM297 (ARIZ)	USA, cultivated	HM236885
Senna spectabilis (DC.) H.S. Irwin & Barneby	Marazzi et al. BM029 (PY, CTES, Z)	Paraguay	AM086983

Senna sp.	Bruneau 1287 (MT)	Mexico	KF522256
Tachigali densiflora (Benth.) L.F.Gomes da Silva & H.C. Lima	de Carvalho 4095 (K)	Brazil	AY899763
Tachigali myrmecophila Ducke	Cowan 38220 (K)	Brazil	AY899764
Tetrapterocarpon geayi Humbert	Noyes 1049 (K)	Madagascar	AY899742
Umtiza listeriana Sim.	Schrire 2602 (K)	South Africa	KF522307
Vouacapoua macropetala Sandwith	Breteler 13793 (WAG)	French Guiana	AF365110
CAESALPINIA GROUP			
Balsamocarpon Clos (1/1 species)			
**Balsamocarpon brevifolium* Clos.	Baxter DCI 1869 (E)	Chile	KF522135
**Balsamocarpon brevifolium* Clos.	Taylor 745 (K)	Chile	KF522136
Caesalpinia L. sensu stricto (18/~25 species)			
**Caesalpinia brasiliensis* L.	Leonard & Leonard 13904 (US, K)	Haiti	KF522092
Caesalpinia bahamensis Lam.	Baker B27 (K)	Bahamas	KF522091
Caesalpinia bahamensis Lam.	Michael 8975 (MEXU)	Bahamas	KF522093
Caesalpinia barahonensis Urb.	Ekman 5965 (K)	Haiti	KF522094
Caesalpinia bracteata Germish.	Van Hoepen 2018 (K)	South Africa	KF522258
Caesalpinia buchii Urb.	Acevedo-Rodriguez et al. 8522 (US, K)	Dominican Republic	KF522115
Caesalpinia cassioides Willd.	Hughes et al. 2023 (FHO)	Peru	KF522097
Caesalpinia cassioides Willd.	Hughes et al. 2228 (FHO)	Peru	KF522098
Caesalpinia cassioides Willd.	Hughes et al. 2641 (FHO)	Peru	KF522095
Caesalpinia cassioides Willd.	Pennington et al. 789 (E)	Peru	KF522096
Caesalpinia dauensis Thulin	Gilbert et al. 7695 (K)	Ethiopia	KF522266
Caesalpinia erianthera Chiov.	Friis et al. 4698 (K)	Somalia	KF522123
Caesalpinia erianthera Chiov.	Radcliffe-Smith 5518 (K)	Oman	KF522122
Caesalpinia erianthera Chiov.	Thulin & Mohamed 6941 (K)	Somalia	KF522125
Caesalpinia erianthera Chiov.var. *erianthera*	Thulin 5557 (K)	Somalia	KF522118
Caesalpinia erianthera var. *pubescens* Brenan	Boulos et al. 17000 (K)	Yemen	KF522117
Caesalpinia glandulosopedicellata R. Wilczek	Bamps & Malaisse 8647 (K)	Zaire	KF522261
Caesalpinia madagascariensis (R.Vig) Senesse	Bruneau 1348 (MT)	Madagascar	KF522119

Caesalpinia madagascariensis (R.Vig) Senesse	Lewis et al. 2158 (K)	Madagascar	KF522120
Caesalpinia oligophylla Harms.	Hassan 70 (FHO, K)	Somalia	KF522262
Caesalpinia pauciflora (Griseb.) C. Wright	Ekman 9703 (K)	Cuba	KF522124
Caesalpinia pauciflora (Griseb.) C. Wright	Liogier & Liogier 20521 (NY)	Hispaniola	KF522116
Caesalpinia pulcherrima (L.) Sw.	Cox 1 , RBG Liv.Coll. 1975-3028 (K)	cultivated	KF522174
Caesalpinia pulcherrima (L.) Sw.	Fougère-Danezan 19 (MT)	Singapore, cultivated	KF522172
Caesalpinia pulcherrima (L.) Sw.	Lewis &Hughes 1715 (K)	Guatemala	KF522171
Caesalpinia pulcherrima (L.) Sw.	Montreal Botanical Garden 7089-92 (MT)	Canada, cultivated	KF522173
Caesalpinia rubra (Engl.) Brenan	de Winter 3164 (K)	South Africa	KF522260
Caesalpinia rubra (Engl.) Brenan	Oshikoto 1917BD (K)	Namibia	KF522259
Caesalpinia sessilifolia S. Watson	Hinton 24737 (MEXU)	Mexico	KF522121
Caesalpinia stuckertii Hassl.	Beck 9443 (NY)	Bolivia	KF522126
Caesalpinia stuckertii Hassl.	Kaprovickas 4626 (K)	Argentina	KF522127
Caesalpinia trothae subsp. *erlangeri* (Harms) Brenan	Beckett & White 1711 (K)	Somalia	KF522263
Caesalpinia trothae subsp. *erlangeri* (Harms) Brenan	Thulin & Warfa 5816 (K)	Somalia	KF522267
Caesalpinia trothae subsp. *erlangeri* (Harms) Brenan	Vollesen & Hassan 4873 (K)	Somalia	KF522264
Caesalpinia trothae subsp. *trothae* Harms	Bidgood et al. 559 (K)	Tanzania	KF522265
Cenostigma Tul. (2/2 species)			
**Cenostigma macrophyllum* Tul.	Coradin et al. 6306 (K)	Brazil	KF522053
**Cenostigma macrophyllum* Tul.	Thomas 9615 (K)	Brazil	KF522069
Cenostigma macrophyllum Tul.	de Queiroz 9147 (HUEFS)	Brazil	KF522037
Cenostigma tocantinum Ducke	Klitgaard & de Lima 88 (K)	Brazil, cultivated	KF522071
Cenostigma tocantinum Ducke	Klitgaard s.n. (INPA)	Brazil	KF522070
Cordeaxia Hemsl. (1/1 species)			
**Cordeauxia edulis* Hemsl.	Gillett & Beckett 23305 (K)	Somalia	KF522083
**Cordeauxia edulis* Hemsl.	Hassan 232 (FHO, K)	Somalia	AY899748
**Cordeauxia edulis* Hemsl.	Kuchar 17803 (K)	Somalia	KF522084

Coulteria Kunth (7/9-10 species)			
**Coulteria mollis* Kunth	Way NMLW 28 (K)	Venezuela	KF522187
Coulteria platyloba (S. Watson) N. Zamora	Gagnon & Marazzi, EG2010.007 (MT)	USA, cultivated	KF522175
Coulteria platyloba (S. Watson) N. Zamora	Lorea Lozada 685 (MEXU)	Mexico	KF522183
Coulteria platyloba (S. Watson) N. Zamora	MacQueen 178 (K)	Mexico	KF522178
Coulteria platyloba (S. Watson) N. Zamora	Steinmann 3199 (INIREB, K)	Mexico	KF522184
Caesalpinia colimensis F.J.Herm.	Sousa 6163 (K)	Mexico	KF522176
Caesalpinia pringlei (Britton & Rose) Standl.	Cruz Duran 926 (MEXU)	Mexico	KF522180
Caesalpinia pumila (Britton & Rose) F.J.Herm.	Gagnon & Marazzi EG 2010.014 (MT)	USA, cultivated	KF522182
Caesalpinia pumila (Britton & Rose) F.J.Herm.	Lewis et al. 2067 (K)	Mexico	KF522177
Caesalpinia pumila (Britton & Rose) F.J.Herm.	Nabhan et al. 1988 (MEXU)	Mexico	KF522185
Caesalpinia velutina (Britton & Rose) Standl.	Hughes et al. 2087 (FHO)	Mexico	KF522189
Caesalpinia velutina (Britton & Rose) Standl.	Lewis 1797 (NY)	Mexico	KF522179
Caesalpinia velutina (Britton & Rose) Standl.	Tenorio 296 (MEXU)	Mexico	KF522191
Caesalpinia velutina (Britton & Rose) Standl.	Torres 1590 (MEXU)	Mexico	KF522186
Caesalpinia velutina (Britton & Rose) Standl.	Way et al. JIC 22176 (K)	Mexico	KF522190
Caesalpinia violacea (Mill.) Standl.	Lewis et al. 1763 (NY)	Mexico	KF522188
Caesalpinia violacea (Mill.) Standl.	Tenorio 4442 (MEXU)	Mexico	KF522181
Erythrostemon (Hook.) Klotzsch (13/13 species)			
**Erythrostemon gilliesii* Klotzsch	Marazzi et al. BM131 (CTES, Z)	Argentina	AM086914
**Erythrostemon gilliesii* Klotzsch	Spellenberg 12701 (MT)	USA, cultivated	KF522296
Erythrostemon calycina (Benth) L.P.Queiroz	Giuletti 2045 (HUEFS)	Brazil	KF522304
Erythrostemon calycina (Benth) L.P.Queiroz	Lewis & Andrade 2003 (K)	Brazil	AY899749
Erythrostemon calycina (Benth) L.P.Queiroz	Lewis & Andrade 1885 (K)	Brazil	KF522303

Caesalpinia ancashiana Ulibarri	Hughes et al. 3021 (MT, Z)	Peru	KF522164
Caesalpinia ancashiana Ulibarri	Hughes et al. 3025 (MT, Z)	Peru	KF522166
Caesalpinia ancashiana Ulibarri	Hughes et al. 3026 (MT, Z)	Peru	KF522165
Caesalpinia ancashiana Ulibarri	Hughes et al. 3027 (MT, Z)	Peru	KF522169
Caesalpinia ancashiana Ulibarri	Hughes et al. 3065 (MT, Z)	Peru	KF522168
Caesalpinia ancashiana Ulibarri	Hughes et al. 3070 (MT, Z)	Peru	KF522167
Caesalpinia ancashiana Ulibarri	Lewis & Klitgaard 2266 (K)	Ecuador	KF522170
Caesalpinia angulata (Hook & Arn.) Baill.	Brownless et al. 591 (E)	Chile	KF522288
Caesalpinia angulata (Hook & Arn.) Baill.	Nee 37585 (K)	Chile	KF522287
Caesalpinia argentina Burkart	Hughes et al. 2460 (FHO)	Bolivia	KF522289
Caesalpinia argentina Burkart	Pennington et al. 13323 (K)	Bolivia	KF522290
Caesalpinia caudata (A. Gray) Fisher	Simpson I-IV-01-3 (TEX)	USA	KF522298
Caesalpinia celendiniana G.P. Lewis & C.E. Hughes	Hughes et al. 2210 (FHO)	Peru	KF522148
Caesalpinia celendiniana G. P. Lewis & C.E. Hughes	Hughes et al. 3097 (MT, Z)	Peru	KF522149
Caesalpinia celendiniana G.P. Lewis & C.E. Hughes	Hughes et al. 3102 (MT, Z)	Peru	KF522147
Caesalpinia coluteifolia Griseb.	Gagnon et al. EG207 (MT)	Argentina	KF522291
Caesalpinia coluteifolia Griseb.	Gagnon & Atchison EG223 (MT)	Argentina	KF522292
Caesalpinia coulterioides Griseb. Emend. Burkart	Gagnon & Atchison EG209 (MT)	Argentina	KF522285
Caesalpinia exilifolia Griseb.	Gagnon et al. EG201 (MT)	Argentina	KF522295
Caesalpinia exilifolia Griseb.	Gagnon et al. EG202 (MT)	Argentina	KF522294
Caesalpinia exilifolia Griseb.	Gagnon & Atchison EG219 (MT)	Argentina	KF522293
Caesalpinia fimbriata Tul.	Hughes et al. 2441 (FHO)	Bolivia	KF522284
Caesalpinia fimbriata Tul.	Hughes et al. 2466 (FHO)	Bolivia	KF522286
Caesalpinia fimbriata Tul.	Wood 10627 (K)	Bolivia	KF522211
Caesalpinia fimbriata Tul.	Solomon & Nee 16062 (NY)	Bolivia	KF522297
Caesalpinia mimosifolia Griseb.	Gagnon et al. EG203 (MT)	Argentina	KF522160
Caesalpinia mimosifolia Griseb.	Gagnon & Atchison EG211 (MT)	Argentina	KF522159

Caesalpinia mimosifolia Griseb.	Särkinen et al. 2006 (FHO)	Argentina	KF522161
Caesalpinia trichocarpa Griseb.	Hughes et al. 2442 (FHO)	Bolivia	KF522162
Caesalpinia trichocarpa Griseb.	Hughes et al. 3041 (MT, Z)	Peru	KF522152
Caesalpinia trichocarpa Griseb.	Hughes et al. 3042 (MT, Z)	Peru	KF522154
Caesalpinia trichocarpa Griseb.	Hughes et al. 3047 (MT, Z)	Peru	KF522150
Caesalpinia trichocarpa Griseb.	Hughes et al. 3056 (MT, Z)	Peru	KF522158
Caesalpinia trichocarpa Griseb.	Hughes et al. 3057 (MT, Z)	Peru	KF522155
Caesalpinia trichocarpa Griseb.	Hughes et al. 3063 (MT, Z)	Peru	KF522157
Caesalpinia trichocarpa Griseb.	Hughes et al. 3155 (MT, Z)	Peru	KF522156
Caesalpinia trichocarpa Griseb.	Hughes et al. 3156 (MT, Z)	Peru	KF522153
Caesalpinia trichocarpa Griseb.	Lewis & Klitgaard 2166 (K)	Argentina	KF522163
Caesalpinia trichocarpa Griseb.	Särkinen et al. 2225 (FHO)	Peru	KF522151
Guilandina L. (5/7-18 species)			
*_Guilandina bonduc_ L.	Bruneau 1342 (MT)	Madagascar	KF522062
*_Guilandina bonduc_ L.	van Balooy s.n., Krukoff coll. (K)	Malaysia	KF522063
Guilandina major L.	Herendeen & Pooma 30-IV-1999-1 (US)	USA, cultivated	KF522253
Caesalpinia minax Hance	Li Shi Jin 802 (CAS, IBSC)	China	KF522131
Caesalpinia minax Hance	Living collection National Botanic Garden of Belgium 19645275(BR)	China, cultivated	KF522132
Caesalpinia murifructa Gillis & Proctor	Gillis 13096 (K)	Bahamas	KF522064
Caesalpinia volkensii Harms	Archbold 2861 (K)	Tanzania	KF522065
Caesalpinia volkensii Harms	Friis et al. 3516 (K)	Ethiopia	KF522066
Caesalpinia volkensii Harms	Somers s.n., RBG Liv.Coll. 1978-891 (K)	Kenya	KF522067
Haematoxylum L. (3/4 species)			
*_Haematoxylum campechianum_ L.	Bruneau 1313 (MT)	Mexico	KF522200
*_Haematoxylum campechianum_ L.	du Puy et al. M356 (K)	Madagascar	KF522208

**Haematoxylum campechianum* L.	Hughes 1273 (FHO)	Guatemala	AY899754
**Haematoxylum campechianum* L.	Miller & Morello 8849 (MO)	Dominica	KF522201
Haematoxylum brasiletto H. Karst.	Bernandes et al. 891 (MO)	Colombia	KF522209
Haematoxylum brasiletto H. Karst.	Gagnon & Marazzi EG2010.011 (MT)	USA, cultivated	KF522207
Haematoxylum dinteri Harms	Sucheach s.n. (OFI), Haston V200308 (RNG)	Namibia	AY899755
Haematoxylum brasiletto H. Karst.	Gagnon & Marazzi EG2010.013 (MT)	USA, cultivated	KF522206
Haematoxylum brasiletto H. Karst.	Lewis et al. 2057 (FHO)	Mexico	AY899753
Hoffmannseggia Cav. (7/24 species)			
**Hoffmannseggia glauca* (Ortega) Eifert	Gagnon & Marazzi EG2010.05 (MT)	USA	KF522214
**Hoffmannseggia glauca* (Ortega) Eifert	Gagnon & Marazzi EG2010.19 (MT)	USA	KF522212
**Hoffmannseggia glauca* (Ortega) Eifert	Spellenberg 12699 (MT)	USA	KF522213
Hoffmannseggia aphylla (Phil.) G.P.Lewis & Sotuyo	Gardner & Knees 6503 (E)	Chile	KF522146
Hoffmannseggia aphylla (Phil.) G.P.Lewis & Sotuyo	Gardner & Knees 6557 (E)	Chile	KF522144
Hoffmannseggia microphylla Torr.	Holmgrenn 6505 (NY)	USA	KF522145
Hoffmannseggia miranda Sandwith	FLSP 945 (NY)	Peru	KF522239
Hoffmannseggia miranda Sandwith	Hughes & Daza 2358 (FHO)	Peru	KF522240
Hoffmannseggia prostrata DC.	Hughes & Daza 2359 (FHO)	Peru	KF522241
Hoffmannseggia viscosa Hook.& Arn.	Eastwood et al. RJE35 (FHO)	Peru	KF522138
Hoffmannseggia viscosa Hook.& Arn.	Hughes et al. 2221 (FHO)	Peru	KF522137
Hoffmannseggia viscosa Hook.& Arn.	Simpson 22-II-00-3 (TEX)	Peru	KF522139
Libidibia (DC.) Schltdl. (6/6-8 species)			
**Libidibia coriaria (Jacq.) Schltdl.*	Fougère-Danezan 20 (MT)	Singapore, cultivated	KF522109
**Libidibia coriaria (Jacq.) Schltdl.*	Hughes 1495 (K)	Mexico	AY899750
**Libidibia coriaria (Jacq.) Schltdl.*	Hughes et al. 2163 (FHO)	Mexico	KF522107

Libidibia ferrea (Mart. ex Tul.) L.P.Queiroz	Fougère-Danezan 21 (MT)	Singapore, cultivated	KF522105
Libidibia ferrea (Mart. ex Tul.) L.P.QueirozG.P.Lewis	Lewis et al. 1623 (K)	Brazil	KF522114
Libidibia glabrata (Kunth) Castellanos & G.P. Lewis	Delgado 2097 (MEXU)	Peru	KF522103
Libidibia glabrata (Kunth) Castellanos & G.P. Lewis	Eastwood et al. RJE84 (FHO)	Peru	KF522102
Libidibia glabrata (Kunth) Castellanos & G.P. Lewis	Lewis & Lozano 3043 (K)	Ecuador	KF522101
Libidibia glabrata (Kunth) Castellanos & G.P. Lewis	Särkinen et al. 2151 (FHO)	Peru	KF522104
Libidibia paraguariensis (Parodi) G.P.Lewis	Hughes et al. 2307 (FHO)	Bolivia	KF522110
Libidibia paraguariensis (Parodi) G.P.Lewis	Hughes et al. 2475 (FHO)	Bolivia	KF522111
Libidibia paraguariensis (Parodi) G.P.Lewis	Lewis & Klitgaard 2170 (K)	Argentina	KF522112
Libidibia paraguariensis (Parodi) G.P.Lewis	Zardini & Velazquez 19907 (K)	Paraguay	KF522113
Libidibia punctata (Willd.) Britton	Cardenas 4071 (K)	Venezuela	KF522106
Libidibia sclerocarpa (Standl.) Britton & Rose	Lewis & Hughes 1778 (K)	Mexico	KF522108
Mezoneuron Desf. (11/26 species)			
Mezoneuron andamanicum Prain	Herendeen 29-IV-1999-1 (US)	Thailand	KF522305
Mezoneuron benthamianum Baill.	Ern 2602 (K)	Togo	KF522196
Mezoneuron benthamianum Baill.	Morton & Jarr SL3295 (K)	Sierra Leone	KF522195
Mezoneuron benthamianum Baill.	Vigne 3487 (FHO)	Ghana	KF522197
Mezoneuron cucullatum (Roxb.) Wight & Arn.	Grierson & Long 3623 (K)	Bhutan	KF522194
Mezoneuron deverdiana Guillaumin	McPherson 6211 (K)	New Caledonia	KF522078
Mezoneuron hildebrandtii Vatke	Lewis et al. 2137 (K)	Madagascar	KF522198
Mezoneuron kavaiensis (H. Mann) Hillbr.	Lorence & Wagner 8904 (NTBG)	Hawaii, U.S.A.	KF522192
Mezoneuron scortechinii F. Muell.	Wieringa et al. 4195 (WAG)	Australia	KF522077
Mezoneuron sumatranum (Roxb.) Wight & Arn.	Beaman 9642 (NY, MO)	Malaysia	KF522199
Mezoneuron sp.	Pullen 7619 (K)	New Guinea	KF522193

Caesalpinia erythrocarpa Pedley	Schodde 2246 (K)	New Guinea	KF522257
Caesalpinia nitens (F.Muell ex Benth.) Pedley	Bean 18033 (MO)	Australia	KF522076
Moullava Adans. (1/1 species)			
**Moullava spicata (Dalzell) Nicolson*	Critchett 11/79 (K)	Zambia, cultivated	KF522252
Poincianella Britton & Rose (27/~35 species)			
**Poincinaella mexicana* (A. Gray) Britton & Rose	Hughes et al. 1606 (NY, FHO)	Mexico	KF522218
**Poincinaella mexicana* (A. Gray) Britton & Rose	Delgado 01-2114 (MEXU)	Mexico	KF522219
**Poincinaella mexicana* (A. Gray) Britton & Rose	Lewis s.n., Kew Living Coll. 1973-21714 (K)	Mexico	KF522215
**Poincinaella mexicana* (A. Gray) Britton & Rose	Gagnon & Marazzi EG2010.015 (MT)	USA, cultivated	KF522217
Poincianella aff. mexicana	Contreras s.n. (MEXU)	Mexico	KF522227
Poincianella acapulcensis (Standl.) Britton & Rose	Lott 3205 (K)	Mexico	KF522233
Poincianella acapulcensis (Standl.) Britton & Rose	MacQueen et al. 406 (K)	Mexico	KF522235
Poincianella bracteosa (Tul.) L.P. Queiroz	Carvalho-Sobrinho 218 (HUEFS)	Brazil	KF522035
Poincianella bracteosa (Tul.) L.P. Queiroz	de Queiroz 7845 (HUEFS)	Brazil	KF522036
Poincianella bracteosa (Tul.) L.P. Queiroz	de Queiroz 10085 (HUEFS)	Brazil	KF522079
Poincianella caladenia (Standl.) Britton & Rose	Contreras 2868 (MEXU)	Mexico	KF522234
Poincianella caladenia (Standl.) Britton & Rose	Lewis et al. 2072 (K)	Mexico	KF522228
Poincianella eriostachys (Benth.)Britton & Rose	Hughes 1832 (K)	Mexico	AY899751
Poincianella eriostachys (Benth.)Britton & Rose	Lewis et al. 1799 (K)	Mexico	KF522029
Poincianella exostemma (DC.) Britton & Rose	Contreras s.n. febrero 2000 (MEXU)	Mexico	KF522237
Poincianella exostemma (DC.) Britton & Rose *subsp. exostemma*	Bruneau 1317 (MT)	Mexico	KF522221
Poincianella exostemma (DC.) Britton & Rose *subsp. exostemma*	Lewis & Hughes 1712, RBG Liv.Coll. 1989-3073 (K)	Guatemala	KF522224

Poincianella exostemma (DC.) Britton & Rose *subsp. exostemma*	Lewis & Hughes 1753 (K)	Guatemala	KF522222
Poincianella gaumeri (Greenm.) Britton & Rose	Calzada 19333 (K, MEXU)	Mexico	KF522030
Poincianella gaumeri (Greenm.) Britton & Rose	Hughes 492 (K)	Mexico	KF522034
Poincianella gaumeri (Greenm.) Britton & Rose	Lewis & Hughes 1762 (K)	Mexico	KF522044
Poincianella laxa (Benth.) Britton & Rose	Delgado 2337 (MEXU)	Mexico	KF522274
Poincianella laxiflora (Tul.) L.P. Queiroz	de Queiroz 7063 (HUEFS)	Brazil	KF522051
Poincianella melanadenia (Rose) Britton & Rose	Hughes et al. 2074 (FHO)	Mexico	KF522276
Poincianella melanadenia (Rose) Britton & Rose	Hughes et al. 2091 (FHO)	Mexico	KF522275
Poincianella melanadenia (Rose) Britton & Rose	Contreras 7369 (MEXU)	Mexico	KF522277
Poincianella microphylla (Mart. ex. G. Don) L.P. Queiroz	Coradin et al. 5941 (K)	Brazil	KF522040
Poincianella microphylla (Mart. ex. G. Don) L.P. Queiroz	de Queiroz 9060 (HUEFS)	Brazil	KF522039
Poincianella nelsonii Britton & Rose	Contreras & Sotuyo s.n. (MEXU)	Mexico	KF522300
Poincianella nelsonii Britton & Rose	Sotuyo, s.n., RBG Liv.Coll. 2002-3577(K)	Mexico	KF522301
Poincianella palmeri (S. Watson) Britton & Rose	Gagnon et al. EG2010.010 (MT)	USA, cultivated	KF522230
Poincianella palmeri (S. Watson) Britton & Rose	Gagnon et al. EG2010.023 (MT)	USA, cultivated	KF522229
Poincianella palmeri (S. Watson) Britton & Rose	Lewis 2064 (K)	Mexico	KF522232
Poincianella palmeri (S. Watson) Britton & Rose	Lewis et al. 2065 (K)	Mexico	KF522231
Poincianella pannosa (Standl.) Britton & Rose	Gentry 4365 (MEXU)	Mexico	KF522283
Poincianella pannosa (Standl.) Britton & Rose	Lewis 2051 (K)	Mexico	KF522282
Poincianella phyllanthoides (Standl.) Britton & Rose	Nee 32666 (K)	Mexico	KF522220
Poincianella phyllanthoides (Standl.) Britton & Rose	Steinmann 3718 (INIREB, MEXU)	México	KF522216
Poincianella placida (Brandegee) Britton & Rose	Lewis et al. 2032 (K)	Mexico	KF522273

*Poincianella placida (*Brandegee) Britton & Rose	Lewis 2046 (K)	Mexico	KF522272
Poincianella pluviosa (DC.) L.P.Queiroz	de Queiroz 12795 (HUEFS)	Brazil	KF522049
Poincianella pluviosa (DC.) L.P.Queiroz	Wood et al. 26552 (K)	Bolivia	KF522047
Poincianella pluviosa (DC.) L.P. Queiroz var. *pluviosa*	Nee 40000 (K)	Bolivia	KF522054
Poincianella pluviosa (DC.) L.P. Queiroz var. *pluviosa*	Wood 8838 (K)	Bolivia	KF522052
Poincianella pluviosa var. sanfranciscana (G.P. Lewis) L.P. Queiroz	Lewis & Andrade 1896 (K)	Brazil	KF522050
Poincianella pyramidalis (Tul.) L.P.Queiroz	Dorea 117 (HUEFS)	Brazil	KF522041
Poincianella pyramidalis (Tul.) L.P.Queiroz	de Queiroz 9020 (HUEFS)	Brazil	KF522042
Poincianella pyramidalis (Tul.) L.P.Queiroz	Mori & Boom 14207 (K)	Brazil	KF522038
Poincianella standleyii Britton & Rose	Contreras 2745 (K)	Mexico	KF522236
Poincianella yucatanensis (Greenm.) Britton & Rose*subsp. yucatanensis*	Lewis 1765 (K)	Mexico	KF522280
Poincianella yucatanensis (Greenm.) Britton & Rose*subsp. yucatanensis*	Lewis & Hughes 1766 (NY, K)	Mexico	KF522281
Caesalpinia coccinea G.P. Lewis &J.L. Contr.	Lewis 1802 (K)	Mexico	KF522225
Caesalpinia coccinea G.P. Lewis & J.L. Contr.	Lewis 1803 (K)	Mexico	KF522226
Caesalpinia echinata Lam.	Filgueiras 3391 (NY)	Brazil, cultivated	KF522099
Caesalpinia echinata Lam.	Lewis et al. 1624 (K)	Brazil	KF522072
Caesalpinia echinata Lam.	Miranda 76 (HUEFS)	Brazil	KF522100
Caesalpinia epifanioi J.L.Contr.	Contreras 2309 (K)	Mexico	KF522278
Caesalpinia epifanioi J.L.Contr.	Sotuyo & Sotuyo 20 (MEXU)	Mexico	KF522279
Caesalpinia hintonii Sandwith.	Sotuyo 46 (MEXU)	Mexico	KF522270
Caesalpinia hughesii G.P. Lewis	Lewis et al. 1795 (K)	Mexico	KF522223
Caesalpinia macvaughii J.L. Contr.&G.P. Lewis	Sotuyo et al. 8 (MEXU)	Mexico	KF522299
Caesalpinia macvaughii J.L. Contr.&G.P. Lewis	Sotuyo et al. 54 (MEXU)	Mexico	KF522269
Caesalpinia macvaughii J.L. Contr.&G.P. Lewis	Steinmann 3175 (INIREB, K, MEXU)	Mexico	KF522268

Caesalpinia marginata Tul.	Dubs 1746 (K)	Brazil	KF522045
Caesalpinia marginata Tul.	Wood et al. 26514 (K)	Bolivia	KF522048
Caesalpinia marginata Tul.	Wood et al. 26561 (K)	Bolivia	KF522046
Caesalpinia nicaraguensis G.P. Lewis	Hawkins & Hughes 4 (K)	Nicaragua	KF522302
Caesalpinia oyamae Sotuyo & G.P. Lewis	Hawkins & Hughes 23 (FHO, MEXU)	Mexico	KF522210
Caesalpinia pluviosa var. *maraniona* G.P.Lewis & C.E. Hughes	Hughes et al. 2215 (FHO)	Peru	KF522033
Caesalpinia pluviosa var. *maraniona* G.P.Lewis & C.E. Hughes	Hughes et al. 3105 (MT)	Peru	KF522032
Caesalpinia pluviosa var. *maraniona* G.P.Lewis & C.E. Hughes	Pennington et al. 793 (E, K)	Peru	KF522031
Caesalpinia pluviosa var. *maraniona* G.P.Lewis & C.E. Hughes	Särkinen et al. 2191 (FHO)	Peru	KF522043
Caesalpinia yucatanensis subsp. *chiapensis* G.P. Lewis	Hughes 1353 (FHO)	Mexico	KF522271
Pomaria Cav. (4/16 species)			
**Pomaria glandulosa* Cav.	Ventura & López 9294 (TEX)	Mexico	KF522088
Pomaria jamesii (Torr. & A. Gray) Walp.	Gagnon & Marazzi EG2010.020 (MT)	USA	KF522089
Pomaria jamesii (Torr. & A. Gray) Walp.	Higgins 17628 (NY)	USA	KF522090
Pomaria rubicunda (Vogel) B.B. Simpson & G.P. Lewis	Biganzoli et al. s.n. (NY)	Argentina	KF522085
Pomaria rubicunda var. *hauthallii* (Harms) B.B. Simpson & G.P Lewis	Ibarrola 1750 (US)	Argentina	KF522087
Pomaria stipularis (Vogel) B.B. Simpson & G.P. Lewis	Jonsson 1002a (A)	Brazil	KF522086
Pterolobium (1/11 species)			
**Pterolobium stellatum* (Forssk.) Brenan	Herendeen 17-XII-97-9 (US)	Tanzania	KF522238
Tara Molina (3/3 species)			
**Tara spinosa* (Molina) Britton & Rose	Eastwood et al. RJE36 (FHO)	Peru	KF522128
**Tara spinosa* (Molina) Britton & Rose	Hughes 2360 (FHO)	Peru	KF522129

**Tara spinosa* (Molina) Britton & Rose	Nee 45494 (MO)	Australia, cultivated	KF522130
Caesalpinia cacalaco Humb. & Bonpl.	Gagnon & Marazzi EG2010.022 (MT)	USA, cultivated	KF522202
Caesalpinia cacalaco Humb. & Bonpl.	Soto Nuñez 13682 (MEXU)	Mexico	KF522312
Caesalpinia cacalaco Humb. & Bonpl.	Walker s.n., RBG Liv.Coll. 1986-6481 (K)	Mexico	KF522203
Caesalpinia vesicaria L.	Hawkins & Hughes 11 (FHO)	Nicaragua	KF522204
Caesalpinia vesicaria L.	Lewis & Hughes 1768 (K)	Mexico	KF522205
Stuhlmannia Taub. (1/1 species)			
**Stuhlmannia moavi* Taub.	Keraudren-Aymonin & Aymonin 25628 (MO)	Madagascar	KF522060
**Stuhlmannia moavi* Taub.	Luke 3710 (MO, K)	Tanzania	KF522061
**Stuhlmannia moavi* Taub.	Luke & Robertson 2336 (K)	Kenya	KF522058
**Stuhlmannia moavi* Taub.	Robertson 7509 (K)	Kenya	KF522059
**Stuhlmannia moavi* Taub.	Tanner 3167 (K)	Tanzania	AY899765
Zuccagnia Cav. (1/1 species)			
**Zuccagnia punctata* Cav.	Fortunato 5545 (MO)	Argentina	KF522142
**Zuccagnia punctata* Cav.	Galleto et al. 171 (CORD)	Argentina	KF522141
**Zuccagnia punctata* Cav.	Guglianone et al. 1668 (K, SI)	Argentina	KF522143
**Zuccagnia punctata* Cav.	Lutz 136 (NY)	Argentina	KF522140
Unassigned Old World taxa (6/~15 species)			
Caesalpinia crista L.	Herendeen 1-V-99-3 (US)	Thailand	KF522073
Caesalpinia crista L.	Wieringa et al. 4199 (WAG)	Australia, cultivated	KF522074
Caesalpinia decapetala (Roth) Alston	Marazzi BM137 (Z)	Switzerland, cultivated	AM086910
Caesalpinia decapetala (Roth) Alston	Hughes et al. 2227 (FHO)	Peru, cultivated	KF522081
Caesalpinia decapetala (Roth) Alston	Hooper & Gandhi 2429 (US)	India, cultivated	KF522080
Caesalpinia decapetala (Roth) Alston	Herendeen & Mbago 19-XII-97-1 (US)	Tanzania	KF522082
Caesalpinia mimosoides Lam.	Larsen et al. 44653 (MO)	Thailand	KF522251
Caesalpinia oppositifolia Hattink	Lugas 607 (K)	Malaysia	KF522056
Caesalpinia oppositifolia Hattink	Lugas 921 (K)	Malaysia	KF522055
Caesalpinia parviflora Prain	van Beusekom et al. 3977 (K)	Thailand	KF522057
Caesalpinia vernalis Benth.	Li Shi Jin 787 (CAS, IBSC)	China	KF522075

Caesalpinia welwitschiana (Oliv.) Brenan	Bidgood et al. 2913 (K)	Tanzania	KF522133
Caesalpinia welwitschiana (Oliv.) Brenan	Malaisse 13658 (K)	Zaire	KF522134

1.4 Results

The aligned *rps16* matrix of 349 sequences had a total length of 1138 base pairs. Missing characters at the ends of sequences, caused by the nested PCR, were coded as missing, and represented 2.59% of the data. Within the Caesalpinia Group, sequence lengths varied from 378 to 834 bp, resulting in the inferences of 73 indels. A total of 64 characters were removed due to alignment ambiguities resulting from polymorphic nucleotide repeats making a final combined matrix of 1147 characters. A total of 564 characters were constant, 196 characters were variable but uninformative, and 387 (33.74%) were parsimony-informative.

The parsimony analysis resulted in the maximum 100,000 equally most parsimonious trees (length 1536 steps, CI 0.43, RI 0.86). The Bayesian analysis reached an average standard deviation of split frequencies of 0.009967 after 5,200,000 generations.

In both the strict consensus parsimony tree and the Bayesian majority rule consensus, the Caesalpinia Group is supported as monophyletic within the tribe Caesalpinieae (results not shown, BS: 74%, PP: 1.0), while *Caesalpinia* s.l. is clearly non-monophyletic (Fig. 1.1). While almost all clades corresponding to genera or putative genera were identical and had moderate to good support from the Bayesian and parsimony analyses, there is a lack of resolution and support for the backbone of the tree, which thus reveals very little about inter-clade relationships within the Caesalpinia Group. Nonetheless, the recovered topologies from the Bayesian and parsimony consensus trees were highly congruent, the only major difference being that *Tara* is supported as sister to *Coulteria* in the Bayesian phylogeny (albeit with very weak support, PP 0.53), whereas these two groups do not occur together in the parsimony analysis. Other minor differences in topology also lack support (e.g. *Caesalpinia* s.s. forms a polytomy with the *Cenostigma*-Poincianella B and *Pomaria*-Caesalpinia trichocarpa clades in the Bayesian tree, whereas in the parsimony tree it is sister to these two clades, plus Libidibia, Balsamocarpon and the core P-E Group; one accession of *Cenostigma* (*Cenostigma macrophyllum*, Thomas 9615, K) falls outside of the *Cenostigma*-Poincianella B Group in the Bayesian tree). Given the high congruence between the two trees, we present the strict consensus parsimony topology, but show both bootstrap and Bayesian posterior probability support values on branches (Fig. 1.2). It is interesting to note that although the parsimony strict consensus tree is more resolved than the Bayesian consensus, for certain nodes deeper in the phylogeny, which lack bootstrap support in the parsimony strict consensus, Bayesian support is high.

Of the eight genera (including *Caesalpinia* s.s.) proposed by Lewis (2005), five are monophyletic: *Coulteria* (BS: 73%, PP: 0.99), *Tara* (BS: 84%, PP: 1.0), *Libidibia* (BS: 95%, PP: 1.0), *Guilandina* (BS: 54%, PP: 1.0), and *Mezoneuron* (BS: 72%, PP: 1.0). The remaining three genera, *Poincianella*, *Erythrostemon* and *Caesalpinia* s.s. are not supported as monophyletic. While a core Poincianella-Erythrostemon Group is recovered, part of *Erythrostemon* (here designated the C. trichocarpa clade, BS: 98%, PP: 1.0) forms a distinct clade, sister to *Pomaria*, and part of *Poincianella* is nested within *Cenostigma*, albeit with low BS and PP. *Caesalpinia echinata*, tentatively placed in the Poincianella-Erythrostemon Group by Lewis (2005), is not placed in this clade, but its position is unresolved. Species of *Caesalpinia* s.s. (as circumscribed by Lewis, 2005) are placed in three distinct and highly supported monophyletic groups: *Caesalpinia* s.s., amended here to include a reduced number of species (BS:78%, PP:1.0); the Caesalpinia trothae clade (BS:100%, PP:1.0); and the Caesalpinia erianthera clade (BS:96%, PP:1.0; Figs. 1.1 & 1.2). Two previously unassigned Old World species are placed within a clade comprising the genus *Pterolobium*; three species form a distinct clade, here designated the Caesalpinia decapetala clade (BS: 74%, PP: 1.0), which is sister to the clade comprising *Pterolobium* plus *Mezoneuron*; and three species (*Caesalpinia welwitschiana*, *Caesalpinia mimosoides* and *Moullava spicata*) remain unresolved within a large polytomy.

1.5 Discussion

Here we present the most comprehensively sampled and well resolved phylogeny of the informal Caesalpinia Group published to date. Wide and representative taxon sampling, combined with use of a more variable plastid DNA sequence locus, has yielded better phylogenetic resolution than in previous studies (e.g. Bruneau & al., 2001, 2008; Simpson et al., 2003; Manzanilla & Bruneau, 2012; Nores et al., 2012). Despite the general lack of resolution and support across the backbone of the phylogeny, it is clear that *Caesalpinia* s.l. is not supported as monophyletic (Fig. 1.1).

While relationships amongst the major clades remain largely unresolved or weakly supported in our analyses, precluding detailed inferences about sister group relationships, our expanded phylogeny suggests that there are potentially many more genera in the Caesalpinia Group. Previous studies looking at character evolution within the Caesalpinia Group need to be reconsidered. For example, the recent phylogenetic analysis by Nores et al. (2012), with one representative of each of the genera of the Caesalpinia Group sensu Lewis (2005) (with the exception of *Guilandina* (see Section 4.3 below)), based on an analysis of *trnL–trnF* and *matK* sequences, as well as morphological data, supported the idea that species with idioblasts form a clade distinct from species that lack idioblasts and commonly have glandular secretory structures. This observation was first made by Lersten & Curtis (1994, 1996), who noted that external glandular trichomes and internal secretory cavities were found predominantly in leaflets of specific Neotropical genera (*Balsamocarpon*, *Cenostigma*, *Erythrostemon*, *Hoffmannseggia*, *Libidibia*, *Poincianella*, *Pomaria*), whereas idioblasts were mainly present in the other groups (*Caesalpinia* s.s., *Coulteria*, *Cordeauxia*, *Haematoxylum*, *Guilandina*, *Mezoneuron*, *Moullava*, *Pterolobium*, *Stuhlmannia*, *Tara*). Future analyses with stronger resolution of the backbone will need to re-examine if the inclusion of the new clades found here upholds this pattern of mutually exclusive clades with distinct leaf anatomical structures.

Our analyses support the monophyly of three genera that are clearly distinct from *Caesalpinia* s.l.: *Haematoxylum*, *Pomaria*, and *Hoffmannseggia*. Four monospecific genera *Zuccagnia*, *Balsamocarpon*, *Cordeauxia*, and *Stuhlmannia*, for which we sampled multiple individuals, also formed distinct clades, which did not nest in other genera of *Caesalpinia* s.l. Contrary to Simpson & al. (2003), we find that the two species of *Cenostigma* are placed in the Caesalpinia Group, as found by Manzanilla & Bruneau (2012), but in a clade with *Poincianella* pro parte (Poincianella B), rather than nested within *Mezoneuron* (see Section 4.6.3). Nores & al. (2012) found strong support for the monospecific *Lophocarpinia* as sister to *Haematoxylum*, and for *Stenodrepanum* as sister to *Hoffmannseggia* within a *Balsamocarpon-Hoffmannseggia-Zuccagnia* clade, the latter also supported in our analyses.

Here we review in detail all clades containing species from the eight genera reinstated from within *Caesalpinia* s.l. by Lewis (2005), including the five genera that are clearly supported as monophyletic in our analyses, as well as a set of nine new clades arising from the nonmonophyly of three of the genera (*Caesalpinia* s.s., *Poincianella*, and *Erythrostemon*) recognised by Lewis (2005) and the inclusion of previously unsampled Old World taxa. We provide a discussion of diagnostic morphological characters for each clade, whether these newly discovered clades should be considered as distinct genera, and whether they require new generic names.

1.5.1 *Tara* and *Coulteria*

Previous phylogenetic studies based on morphological, molecular and phytochemical data have suggested that *Tara* and *Coulteria* are closely related and potentially sister groups (Kite & Lewis, 1994; Simpson et al., 2003; Bruneau & al., 2008; Manzanilla & Bruneau, 2012; Nores & al., 2012). Although both *Tara* and *Coulteria* form strongly supported monophyletic groups in our analysis (Fig. 1.2A, B), thus supporting the resegregation of these genera by Lewis (2005), lack of resolution and support preclude making any firm inferences about their relationships to each other. Both genera have a distinctive cucullate lower sepal with a fimbriate margin, suggesting a pseudocopulatory insect pollination syndrome. However, the fruits of *Tara* are thick and indehiscent, and seeds are subglobose to globose, while *Coulteria* has thin, laterally compressed, subchartaceous fruits and laterally compressed seeds. In addition, certain species of *Coulteria* are known to be dioecious (G.P. Lewis, pers. obs., J.L. Contreras, pers.

comm.). The wood anatomy of the three species of *Tara* is distinctive, characterised by non-storied, heterocellular rays and axial parenchyma and indistinct growth rings (Gasson & al., 2009). Although species of *Coulteria* have a more variable wood anatomy, of the five species investigated to date (from a total of eight), all share the presence of prismatic crystals in ray cells and chambered axial parenchyma.

1.5.2 *Libidibia*

As found in other studies (Bruneau & al., 2008; Manzanilla & Bruneau, 2012; Nores & al., 2012), *Libidibia* forms a robustly supported (BS: 97%, PP: 1.0) monophyletic group, supporting the reinstatement of the genus by Lewis (2005). Species of *Libidibia* are unarmed trees, with impari-bipinnate leaves, and terminal paniculate or racemose inflorescences, and occur in disjunct areas of seasonally dry tropical forest across the Neotropics, from Mexico and the Antilles to Colombia, Venezuela, Ecuador, Peru, Paraguay, Brazil, Bolivia and Argentina. With the exception of the type species, *Libidibia coriaria*, all other species of the genus have smooth bark with a patchwork pattern of white, grey and green, described as "leopard-skin bark" (Lewis, 2005). Flowers are typically yellow (the standard petal usually with reddish orange insect guides on the inner surface), with microscopic tentacle-like papillate trichomes on the standard petal surface (Lewis, 2005), while fruits are dark brown to black, tannin-rich, woody and indehiscent. All *Libidibia* species have a distinctive wood anatomy, well defined by short-storied homocellular rays and axial parenchyma, and lacking prismatic crystals in the ray cells and growth rings (Gasson & al., 2009). A number of species, including *Libidibia ferrea*, *Libidibia punctata* and *Libidibia coriaria*, possess dark punctate glands on the abaxial surface of their leaflets, although the quantity of these glands is variable (pers. obs.). The type species, *L. coriaria*, is somewhat atypical for the group as it has rough fissured bark rather than the leopard-skin pattern of all other species, white (not yellow) flowers that lack the papillate trichomes, and tightly curled indehiscent fruits. While we did not manage to sequence the *rps16* locus from *Stahlia monosperma* due to nucleotide repeats, preliminary phylogenetic analyses based on plastid *trnD-trnT* sequences (results not shown) suggest that *Stahlia* is related to the

Libidibia clade, as previously suggested (Simpson et al., 2003; Nores et al., 2012). Although *Stahlia*, a tree endemic to Puerto Rico and the Dominican Republic, appears morphologically unique with its pinnate leaves and a bright red, sub-fleshy, oval to orbicular fruit, its floral morphology, indehiscent fruit, and dark punctuate glands on the abaxial leaflet surfaces show strong similarities to *Libidiba*. Based on these morphological and genetic affinities, we consider that *Stahlia* should be transferred to the genus *Libidibia* (Fig. 1.3).

1.5.3 *Guilandina*

Our results support *Guilandina* as a monophyletic group (Fig. 1.2A, BS: 54%, PP: 0.99) that includes the type species *Guilandina bonduc* L. and hence the reinstatement of the genus as proposed by Lewis (2005) and others (see below). Few species of Guilandina have been included in previous phylogenetic analyses (Bruneau & al., 2008; Manzanilla & Bruneau, 2012; Nores & al., 2012), and thus the status of the genus has remained uncertain. In addition, confusion was caused because previous studies (Bruneau & al., 2001, 2008; Manzanilla & Bruneau, 2012; Nores & al., 2012) have mistakenly included *Caesalpinia crista* as an exemplar of *Guilandina*. *Guilandina crista* Small was published as a name that included in synonymy *C. crista* L., *G. bonduc* L. and *Guilandina bonducella* L., but we can see in our results that the multiple accessions of *G. bonduc* and *C. crista* we sampled are not closely related, the latter species placed in a clade with *Pterolobium stellatum* and a species from *Caesalpinia* sect. *Nugaria* (Fig. 1.2A; see Section 1.5.7 below).

Guilandina is a pantropical genus of lianas and scandent shrubs characterised by unisexual flowers (morphologically the flowers of at least some species appear to be hermaphrodite, but lack pollen in the anthers and are thus cryptically pistillate; Gillis & Proctor, 1974), few-seeded, oval-shaped dehiscent fruits, and are often armed with rigid trichomes or prickles. The seeds are hard and globose and adapted for long-distance oceanic dispersal by flotation (Britton & Rose, 1930; Polhill & Vidal, 1981; Lewis, 2005). *Guilandina* is one of the most morphologically and chemically (Bell, 1981) distinctive segregates of *Caesalpinia* s.l., prompting recognition as a subgenus of *Caesalpinia* (Gillis & Proctor, 1974; Polhill & Vidal, 1981), or reinstatement to generic rank (e.g., Verdcourt, 1979). Despite the clear morphological diagnosability of *Guilandina* as a genus, taxonomic work is needed to resolve species delimitation and associated nomenclatural problems to produce a new species-level taxonomic revision. Species-level phylogenies of *Guilandina* may prove to be challenging and complex, as putative hybrids are thought to occur in the Caribbean region (G.P. Lewis, pers. obs.) and all species have the potential to disperse long distances in water, as found for other pantropical plant species with sea-drifted seeds, e.g. *Hibiscus tilliaceae* and allies in the Malvaceae (Takayama & al., 2006); and a number of legume species: *Canavalia rosea* and allies (Vataranpast & al., 2011), *Entada*, and the *Vigna marina-luteola* complex, Kajita & al., 2013), possibly resulting in a reticulate pattern of species evolution.

1.5.4 *Mezoneuron*

Mezoneuron also has been viewed as distinct from *Caesalpinia* s.l. based on its characteristic dorsally winged, usually thin, oblong, chartaceous and indehiscent fruits, even though in some *Mezoneuron* species the fruit is discoid in shape and coriaceous to sub-woody. The indehiscent, dorsally winged fruit typical of most *Mezoneuron* species provides a potential morphological synapomorphy for this clade. While *Mezoneuron* is usually considered to have wind-dispersed fruits it is also capable of dispersal by water (Lewis, 1998), which might explain its wide distribution from Africa and Madagascar, across the Indian subcontinent into Indonesia and Polynesia. Furthermore, fossils unequivocally assigned to *Mezoneuron* by Herendeen & Dilcher (1991) are known from North America, indicating that there has been a significant shift in the range of this genus. As for *Guilandina*, *Mezoneuron* has been variously recognised as a separate genus (Brenan, 1967; Verdcourt, 1979; Lock, 1989) or as a subgenus or section of *Caesalpinia* (Hattink, 1974; Vidal & Hul Thol, 1976; Herendeen & Zarucchi, 1990; Herendeen & Dilcher, 1991). The monophyly of *Mezoneuron* is supported by our results (Fig. 1.2A, BS: 72%, PP: 1.0), with a sister relationship to the *Pterolobium* clade (albeit lacking support) that was also found in other studies (Bruneau & al., 2008; Manzanilla & Bruneau, 2012; Nores & al., 2012).

1.5.5 *Caesalpinia* sensu stricto: two new clades

Caesalpinia s.s. as it was defined by Lewis (2005), is clearly polyphyletic with three distinct clades revealed in our study (Fig. 1.2A, B). This is perhaps not too surprising given the great morphological diversity and wide geographical distribution of the approximately 25 species placed in *Caesalpinia* s.s. by Lewis (2005). The species of the three clades together occupy much of the Succulent Biome as defined by Schrire & al. (2005). The type species, *C. brasiliensis* L., is placed in a group of Neotropical species, here re-circumscribed as a less speciose *Caesalpinia* s.s. (Fig. 1.2B). This clade includes the Caribbean species *Caesalpinia barahonensis* and *Caesalpinia bahamensis* (the latter known to be bat-pollinated; Koch & al., 2004), the widespread Guatemalan and Mexican (Sonora) species *Caesalpinia pulcherrima* (widely cultivated as an ornamental throughout the tropics and known to be butterfly-pollinated, Cruden & Hermann-Parker, 1979), and the northern Andean species *Caesalpinia cassioides* from the dry valleys of Colombia, Ecuador and Peru. All these species are armed (except for some cultivated forms of *C. pulcherrima*), eglandular shrubs, that have explosively dehiscent pods with twisting valves, similar to those found in the Poincianella-Erythrostemon Group.

A separate clade of species previously attributed to *Caesalpinia* s.s. (sensu Lewis, 2005), here informally designated as the C. trothae clade (Figs. 1.2A & 1.3), is made up of strictly African species that are found in dry forests and thickets from the Horn of Africa, through the arid ‘corridor’ that crosses Tanzania, Botswana, Namibia and Mozambique, to South Africa. While this clade has not previously been identified in phylogenetic analyses due to sparse taxon sampling, previous authors have noted the morphological similarity of the species in this assemblage, all spiny, multi-branched shrubs with reddish-pink flowers. For example, Brenan (1963) commented that *C. trothae*, *Caesalpinia glandulosopedicellata* and *Caesalpinia rubra* shared similar features and were probably related. Brummitt & al. (2007) also remarked that *Caesalphinia rostrata*, a South African endemic, not sampled here, showed affinities with *C. rubra* and *C. trothae*, including gland-dotted leaflets, similar bracts and anvil-shaped pods with an acuminate tip, characters which might provide synapomorphies for this clade.

The third robustly supported clade arising from the former *Caesalpinia* s.s. of Lewis (2005), here informally designated as the C. erianthera clade (Fig. 1.2B, BS: 96%, PP: 1.0), includes species distributed across the Caribbean, Central America and South America, to Madagascar, Somalia and the Arabian Peninsula. Both Simpson & al. (2003) and Nores & al. (2012) found a similar clade based on their *trnL–trnF* phylogenies, which included the same species except for *Caesalpinia buchii* and *C. erianthera*. However, with only sparse sampling of *Caesalpinia* s.s. sensu Lewis (2005) in their phylogenies, they could not confidently assert that this was a potentially new generic group. While this clade has not yet been characterised indepth, we note that all members are eglandular, spiny shrubs.

1.5.6 The Poincianella-Erythrostemon group: three different lineages

Together, the genera *Poincianella* and *Erythrostemon* comprise 47 species (Lewis, 1998), although two species, *Caesalpinia aphylla* Phil. and *Caesalpinia pumilio* Griseb., have since been transferred to *Hoffmannseggia* (Lewis & Sotuyo, 2010; Simpson et al., 2004, respectively). The genera *Poincianella* and *Erythrostemon* were revised by Lewis (1998) as a unit because of the difficulties of distinguishing between them morphologically. Our results suggest that *Erythrostemon* and *Poincianella* together form a polyphyletic assemblage as found by Nores & al. (2012) and Simpson & al. (2003), consisting of three distinct lineages (Figs. 1.2 & 1.3): a core Poincianella-Erythrostemon (P-E) clade (Fig. 1.2D, BS: 96%, PP: 1.0), the C. trichocarpa clade (Fig. 1.2C, BS: 98%, PP: 1.0) that is sister to *Pomaria*, and a third weakly supported clade composed of the two species of *Cenostigma* together with a subset of *Poincianella* species previously referred to as the Poincianella B group (Fig. 1.2C; Lewis & Schrire, 1995), with a centre of species diversity in South America, but also spanning across Central America and the Caribbean.

1.5.6.1 The core Poincianella-Erythrostemon (P-E) clade

The type species of *Erythrostemon* (*Erythrostemon gilliesii* Klotzsch) and *Poincianella* (*Poincianella mexicana* (A. Gray) Britton & Rose) are both placed in the large core P-E clade.

Within this core P-E clade, *Erythrostemon* is supported as monophyletic, albeit with weak to moderate support, and relationships amongst species are unresolved. Except for *Caesalpinia caudata* from North America and *Caesalpinia calycina* from Brazil, species of *Erythrostemon* are all found in South America, with a centre of diversity in Bolivia and Argentina, and are thus geographically separated from the rest of the core P-E group species, which are restricted to Mexico and Central America (Lewis, 1998). The distinction between *Erythrostemon* and *Poincianella* in this core P-E clade is further complicated by the unresolved placement of *Caesalpinia placida* from southern Baja California, which is morphologically more similar to species from the Erythrostemon clade, but geographically is much closer to other species of the Poincianella Group.

The P-E clade recovered here forms a group of unarmed shrubs and small to medium size trees (generally 3 to 10 metres in height), with fruits with dehiscent, twisting valves. Within the Caesalpinia Group, there is currently no known defining synapomorphy for this clade. For example, a prevalent feature of the P-E clade is the presence of glandtipped trichomes in inflorescences, but this is also found in *Pomaria*, Poincianella B, the C. trichocarpa clade and certain species of *Hoffmannseggia*. Furthermore, no obvious morphological synapomorphies are known that distinguish the Erythrostemon clade from the rest of this core P-E clade, due to the variable and highly homoplasious nature of morphological characters within each genus (Lewis, 1998). As an example, most species of *Erythrostemon* have black glands sunken into the crenulate depressions of leaflet margins (Lewis, 1998), but certain species (*Caesalpinia exilifolia, Caesalpinia coluteifolia* and *Caesalpinia angulata*) have eglandular leaflets. In the core P-E clade, species traditionally assigned to *Poincianella* have either eglandular leaflets or a submarginal ring of glands on the lower leaflet surfaces (*C. placida*, has the more typical *Erythrostemon* leaflet gland pattern but as indicated above occupies an unresolved position within the core P-E clade). Pollination syndromes in the P-E group also show a wide range of variation. For example, species traditionally placed in *Erythrostemon* are bee-pollinated, except *E. gilliesii* which is hawk moth-pollinated (Coccuci & al., 1992) and *Caesalpinia coulterioides* which has tubular flowers suggestive of hummingbird pollination. Members of *Poincianella* placed within the core P-E group encompass yellow-flowered species (often the standard petal inner surface blotched or network veined orange–red) thought to be principally pollinated by large solitary bees (e.g., of the genus *Xylocopa*), species with pendulous racemes of small pink flowers pollinated by territorial bees of the genus *Centris* (e.g. *Caesalpinia hintonii, Caesalpinia epifanioi, Caesalpinia laxa, Caesalpinia macvaughii, Caesalpinia melanadenia*), and orange, red or red and yellow flowered species, some with the standard petal to some degree laterally compressed, pollinated, at least in part, by hummingbirds (e.g. *Caesalpinia coccinea, Caesalpinia exostemma* and *Caesalpinia hughesii*). In most respects the core P-E clade forms a morphologically and ecologically coherent group of shrubs and small treelets of seasonally dry tropical forests with a bicentric amphitropical distribution restricted to the Neotropics. Based on current evidence we see no phylogenetic or morphological basis for separating *Erythrostemon* as a distinct genus from *Poincianella* in the core P-E group, though perhaps a study revisiting the morphology of this group and providing stronger resolution for the molecular phylogenies is needed before we can affirm that the P-E group should be treated as a single genus.

1.5.6.2 C. trichocarpa clade: a small group of Andean species

The second lineage of the polyphyletic Poincianella-Erythrostemon Groups, sensu Lewis (1998), here informally designated as the C. trichocarpa clade (Fig. 1.2C), occurs as sister to the genus *Pomaria* in our Bayesian analysis. This robustly supported clade comprises four to five species of suffrutescent to medium-sized shrubs restricted to midelevation seasonally dry inter-Andean valleys in Ecuador, Peru, Bolivia and Northwest Argentina. Although there are no obvious morphological synapomorphies for this group, species of this smaller clade have dark glands in depressions of the leaflet margin typical of the Erythrostemon clade and they have short stipitate glandular trichomes similar to those seen in *Pomaria* and in the P-E clade. However, *Pomaria* has a set of diagnostic synapomorphies including lateral (not terminal) stigmas, anthers nestled within a cucullate lower sepal, and orange glandular dots (drying dark red or black) on leaflets, calyces and fruits, that are not shared with the C. trichocarpa clade.

1.5.6.3 Poincianella B (sensu Lewis & Schrire, 1995) and *Cenostigma*

The Poincianella B clade (Fig. 1.2C) was first uncovered by Lewis & Schrire (1995), and also noted in the phylogenies of Simpson & al. (2003) and Nores & al. (2012) as a strongly supported clade composed of two species: *Caesalpinia eriostachys* and *C. pluviosa*. The relationship between species of Poincianella B (sensu Lewis & Schrire, 1995) and the two species of *Cenostigma* (Fig. 1.2C) is very weakly supported in this analysis, but differs from previous studies which placed *Cenostigma* as a genus outside of the Caesalpinia Group (Simpson & al., 2003; Nores & al., 2012). By sampling more than one specimen of each of the two species of *Cenostigma*, our study firmly establishes placement of the genus within the Caesalpinia Group, as also found by Manzanilla & Bruneau (2012; but in their study *Cenostigma* occurs in the Mezoneuron clade). Furthermore, *Cenostigma* shares with Poincianella B key morphological and anatomical features, which supports their position together in a clade distinct from both the core P-E and the C. trichocarpa clades.

A number of key characters distinguish Poincianella B from the rest of *Poincianella* in the core P-E group. A survey of the wood anatomy of 19 species of *Poincianella* s.l. revealed that *Caesalpinia gaumeri*, *C. eriostachys*, *Poincianella pyramidalis*, and *Poincianella pluviosa* (all Poincianella B species) differ from the other *Poincianella* species in having regularly storied rays and axial parenchyma (Gasson & al., 2009). Lewis (1998) noted that *C. eriostachys*, *C. gaumeri* and all of the Brazilian species of the clade share a distinct stigma with a subterminal bulbous chamber narrowing to a papillate-fringed pore that is distinct within the Poincianella-Erythrostemon group sensu Lewis (1998). de Queiroz (2009) in his study of the legumes of the caatinga vegetation of northeastern Brazil also used the presence of alternate to sub-opposite leaflets to distinguish *Poincianella* from other genera in *Caesalpinia* s.l. First reported by Lewis (1998), leaflet arrangement can be extremely variable within species and even on individual plants, with both alternate and opposite leaflets occurring in some species (e.g. in *P. pluviosa*, and in *Caesalpinia marginata*, unusual in the group in having singly pinnate, not bipinnate, leaves). Although not sampled here, morphological evidence suggests that the Caribbean species, *Caesalpinia glandulosa*, *C. myabensis*, *C. pellucida* and *C. pinnata*, probably belong in the Poincianella B group (Lewis, 1998; Gasson & al., 2009).

Perhaps the most important distinguishing features of the Poincianella B group are its unique glandular structures and indumentum, which are not found in the core Poincianella-Erythrostemon clade, but which are present in the genus *Cenostigma*. These include internal secretory cavities, which consist of resin ducts present in the lamina of leaflets and in inflorescences (Lersten & Curtis, 1994; Rudall & al., 1994). Some species of Poincianella B (*P. pluviosa* and *C. eriostachys*, Lewis, 1998) also have an indumentum of stellate hairs on leaflets and inflorescence rachis. This character is restricted elsewhere in tribe Caesalpinieae to the genus *Cenostigma*, and the more distantly related genus *Dimorphandra* (Lersten & Curtis, 1996), and needs to be carefully re-assessed in other members of Poincianella B. *P. pluviosa* and *C. eriostachys* also share with *Cenostigma* the development of a flutted trunk in mature individuals, a feature also seen in species of *Haematoxylum*. Finally, Poincianella B species and *Cenostigma* have fruits with conspicuously thickened sutures, a character not observed in the P-E clade. While our results do not resolve the relationships of *Cenostigma*, certain morphological features within the Poincianella B + *Cenostigma* clade support the Bayesian and parsimony topologies recovered in our analyses. More exhaustive morphological studies and more informative loci will need to be sampled before we can properly assess the degree to which the Poincianella B clade is related to *Cenostigma* and whether the two should be united under one generic name.

1.5.6.4 *Caesalpinia echinata*

C. echinata is the only species tentatively placed in the P-E group by Lewis (1998) that did not group closely with any of the three segregate clades identified in this study, i.e. the core P-E group, the Poincianella B clade, or the C. trichocarpa clade, but is instead unresolved within a large and poorly-supported polytomy (Fig. 1.2B). The taxonomic treatment of this species has long been problematic within *Caesalpinia* s.l., as it possesses a unique combination of morphological characters that are individually encountered in other genera of *Caesalpinia* s.l. and indeed across the larger Caesalpinia Group as a whole. This species is usually a large tree with upwardly curved thorns (arising from woody protuberances) arming the trunks and main branches. It has wood with a rich red-dye (not unlike that of species of *Haematoxylum* and *Caesalpinia sappan*, the latter an Asian species), and its floral morphology is similar to that of the Poincianella B group. It also has prickly pods superficially similar to those of *Guilandina*, although its seeds are laterally compressed and not globose as in *Guilandina*. Lewis (1998) placed *C. echinata* within his P-E group based on similarities in floral morphology, and the presence of red subepidermal glands, which were assumed to be homologous to the internal secretory cavities of the Poincianella B group. However, the species was not included in Lersten & Curtis' (1994, 1996) surveys of leaflet secretory structures in the tribe Caesalpinieae, and the glands of *C. echinata* have not been studied in detail. Wood anatomy also suggests that *C. echinata* may not belong in *Poincianella* in its broadest circumscription (Gasson & al., 2009). In addition, the different accessions of *C. echinata* sampled did not form a monophyletic group, perhaps reflecting wellknown intraspecific variation. Population genetics studies using RAPDs (Cardoso & al., 1998), chloroplast microsatellite markers (Lira & al., 2003) and AFLPs (Cardoso & al., 2005) have shown that there is significance among population variation between three morphological variants of *C. echinata* that are distinct in leaflet size, pinnation, and colour of the heartwood, and which occur in allopatric localities along the Brazilian coast (Lewis, 1998; Lima & al., 2002).

1.5.7 Unassigned Old World taxa: new genera?

Our analysis sheds new light on the affinities of some of the Old World taxa not previously sampled in phylogenetic studies and left unassigned to genera in Lewis's (2005) generic system for the Caesalpinia Group. These taxa are placed in three newly recognised clades, the C. decapetala clade, *Caesalpinia* sect. *Nugaria*, and *Caesalpinia* sect. *Cinclidocarpus* clades (Fig. 1.2A). These clades correspond in part to Vidal & Hul Thol's (1976) infrageneric system for Asian *Caesalpinia* that includes sections *Sappania*, *Cinclidocarpus* and *Nugaria*, originally proposed by de Candolle (1825) and Bentham (1865). We discuss the composition, status and affinities of these clades and how they might be treated taxonomically.

1.5.7.1 C. decapetala clade (section *Sappania* DC.)

Moderate support (Fig. 1.2A, BS: 74%, PP: 1.0) was found for the monophyletic C. decapetala clade, comprising the three Asian species *C. decapetala*, *C. parviflora* and *C. oppositifolia*. This group is likely also to include *C. sappan* and *C. godefroyana*, which although not sampled here, share similar geography and morphology (Hattink, 1974; Vidal & Hul Thol, 1976). Vidal & Hul Thol (1976) also included *C. mimosoides*, *Caesalpinia aestivalis* and *Caesalpinia caesia* in *Caesalpinia* section *Sappania*, but we exclude them from this clade. *C. aestivalis* is now known to be a synonym of *Pterolobium punctatum* and *C. caesia* is better placed in section *Nugaria* based on fruit morphology. *C. mimosoides* remains unresolved in our molecular analyses and in contrast to the rest of the species in the C. decapetala clade, *C. mimosoides* lacks idioblasts (Lersten & Curtis, 1994). *C. mimosoides* also has other distinctive features, such as straight rigid, needle-like trichomes and a vesicular, gland-covered fruit (Hattink, 1974), whereas the remaining species of the C. decapetala clade have oblong, laterally compressed, dehiscent pods with a sharp beak.

1.5.7.2 Does *Caesalpinia* sect. *Nugaria* represent a distinct genus, sister to *Pterolobium*?

The second clade of previously unassigned Asian taxa comprises C. crista, Caesalpinia vernalis and the type species of the genus *Pterolobium*, *P. stellatum* (Fig. 1.2A, BS: 79%, PP: 1.0). *Pterolobium*, as traditionally circumscribed, is a distinctive genus of 11 species, all of them scrambling shrubs and lianas with winged, samaroid pods (Vidal & Hul Thol, 1974). *Pterolobium* was placed by Pohill & Vidal (1981) in their Caesalpinia Group based on floral and vegetative characters. Despite the absence of a wing, the one-seeded and discoid to subelliptic fruits of *C. vernalis* and *C. crista* resemble those of *Pterolobium* (Ruth Clark, Royal Botanic Gardens, Kew, unpublished data). *C. vernalis* and *C. crista* were placed in Caesalpinia sect. *Nugaria* DC. by Vidal & Hul Thol (1976), a group of eight species with non-samaroid fruit. It is interesting to note that some of the species of this section have nonsamaroid fruits with a small wing (*Caesalpinia sinensis* and *C. caesia*) or a narrow keel on one side of the pod (*Caesalpinia magnifoliolata*). These are possibly an intermediate form between the samaroid pods of *Pterolobium* and the wingless fruits of *Caesalpinia* section *Nugaria*. More complete taxon sampling of both *Pterolobium* and *Caesalpinia* section *Nugaria* is needed to verify the generic status of these two groups

1.5.7.3 *Caesalpinia* sect. *Cinclidocarpus* (based on *Cinclidocarpus* Zollinger)

M. spicata and *C. welwitschiana*, two unassigned Asian species that did not group with the other Asian clades (i.e., the *Mezoneuron* + C. decapetala + *Pterolobium* + *Caesalpinia* section *Nugaria* clade), form an unsupported sister group in our phylogenetic analyses (Fig. 1.2A). *M. spicata* (synonym *Wagatea spicata* Dalzell), a liana from the Indian subcontinent, has long been considered a distinct genus in the Caesalpinia Group based on its densely flowered spicate inflorescences of flowers that have a showy red calyx with the sepals fused into a small tube at the base. *C. welwitschiana* is a scrambling liana from Central Africa previously referred to *Mezoneuron*, but which Brenan (1963) replaced into *Caesalpinia* because its fruit is similar to that of the Asian species *Caesalpinia tortuosa* and *Caesalpinia digyna*, neither of which were sampled in our study. Vidal & Hul Thol (1976) placed the latter two species in *Caesalpinia* section *Cinclidocarpus*, distinguishing them from section Sappania based on their indehiscent fruits. Closer morphological examination of these two species suggests a similar fruit type to that of *M. spicata* and *C. welwitschiana*. Descriptions of these four species all mention that they have straight, indehiscent, oblong to elliptic, somewhat laterally compressed fruits that are constricted between the seeds (subtorulose), ending with a small beak. They all have fruits with thickened sutures, and an exocarp and endocarp that are strongly adnate when dried (Brenan, 1967; Hattink, 1974; Brummitt & al., 2007). Inclusion of *C. digyna* and *C. tortuosa* in the molecular analysis is needed to test the apparently close relationship among these four species.

1.6 Conclusion

The greatest strength of the analyses presented here is the significantly expanded taxon sampling compared with previous studies. Our analyses have revealed a number of new distinct clades that merit consideration as new genera, and provide the most comprehensive hypothesis of phylogenetic relationships for the group to date. Conversely, reliance on a single plastid locus means that, while we find moderate or strong support for individual clades, our phylogeny lacks resolution and support across most of the backbone of the tree, such that the branching order and relationships among these major clades remain obscure. Our analyses clearly indicate that

Caesalpinia s.l. is non-monophyletic, and that five of the reinstated genera proposed by Lewis (2005), *Tara, Coulteria, Libidibia, Guilandina*, and *Mezoneuron*, form well-supported clades with good diagnostic morphological characters. However, our results also suggest that some of the other genera segregated and reinstated by Lewis (1998, 2005) are non-monophyletic and will probably need to be further subdivided. The Poincianella-Erythrostemon Group recognised by Lewis (1998, 2005), and *Caesalpinia* s.s. (sensu Lewis, 2005), are two such groups which, based on our analyses, are non-monophyletic. While it would be premature to outline a complete generic system for the Caesalpinia Group at this stage, we suggest that the *C. trothae*, *C. erianthera*, and *C. trichocarpa* clades merit recognition as new genera. Better phylogenetic resolution and more morphological studies are needed to clearly assess if the core P-E clade should be treated as a single genus, and whether species of the Poincianella B group should be transferred to *Cenostigma*. The remaining issues of generic delimitation will require both the inclusion of additional Asian taxa in the analysis, and generation of additional sequence data to increase resolution and support in critical parts of the tree.

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1.8 Authors contribution

EG, AB, CEH and GPL were involved in study conception and design; EG, AB, CEH, GPL, JSS collected and provided herbarium and field samples for analysis; EG and JSS generated the data, which EG analysed and interpreted; EG drafted the manuscript, and critical revision was provided by AB, CEH, JSS and GPL.

Figure 1.1 Summary phylogeny of the Caesalpinia Group, based on the parsimony strict consensus tree. Clades coloured in black contain only members of *Caesalpinia* s.l. Clades in white represent genera that are part of the Caesalpinia Group, but not *Caesalpinia* s.l. Size of triangles reflects size of clades and sampling efforts.

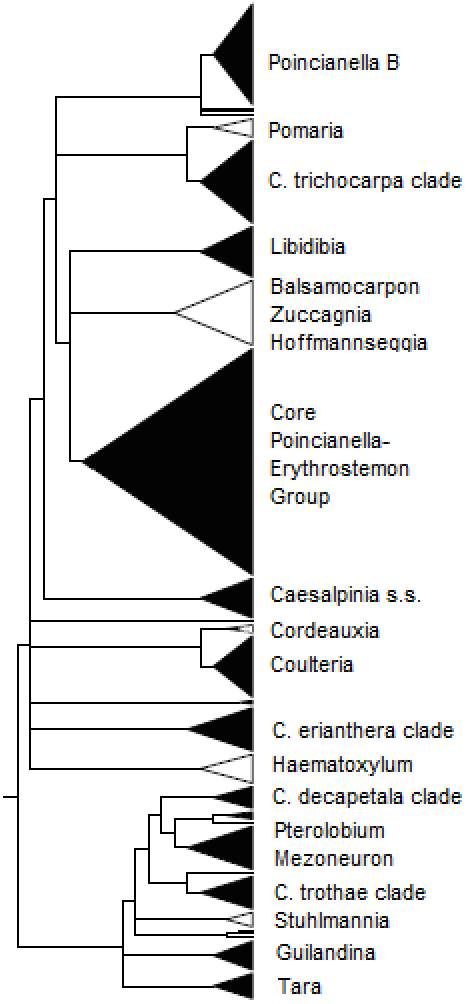


Figure 1.2 A–D Phylogeny of the informal Caesalpinia Group. Strict consensus of 100,000 equally parsimonious trees based on rps16 plastid sequences. Bootstrap support is shown in bold above branches, and posterior probability valuesare shown italicized, below the branch. Values below 50% or 0.5 are not shown, and are indicatedby two dashed lines (--).

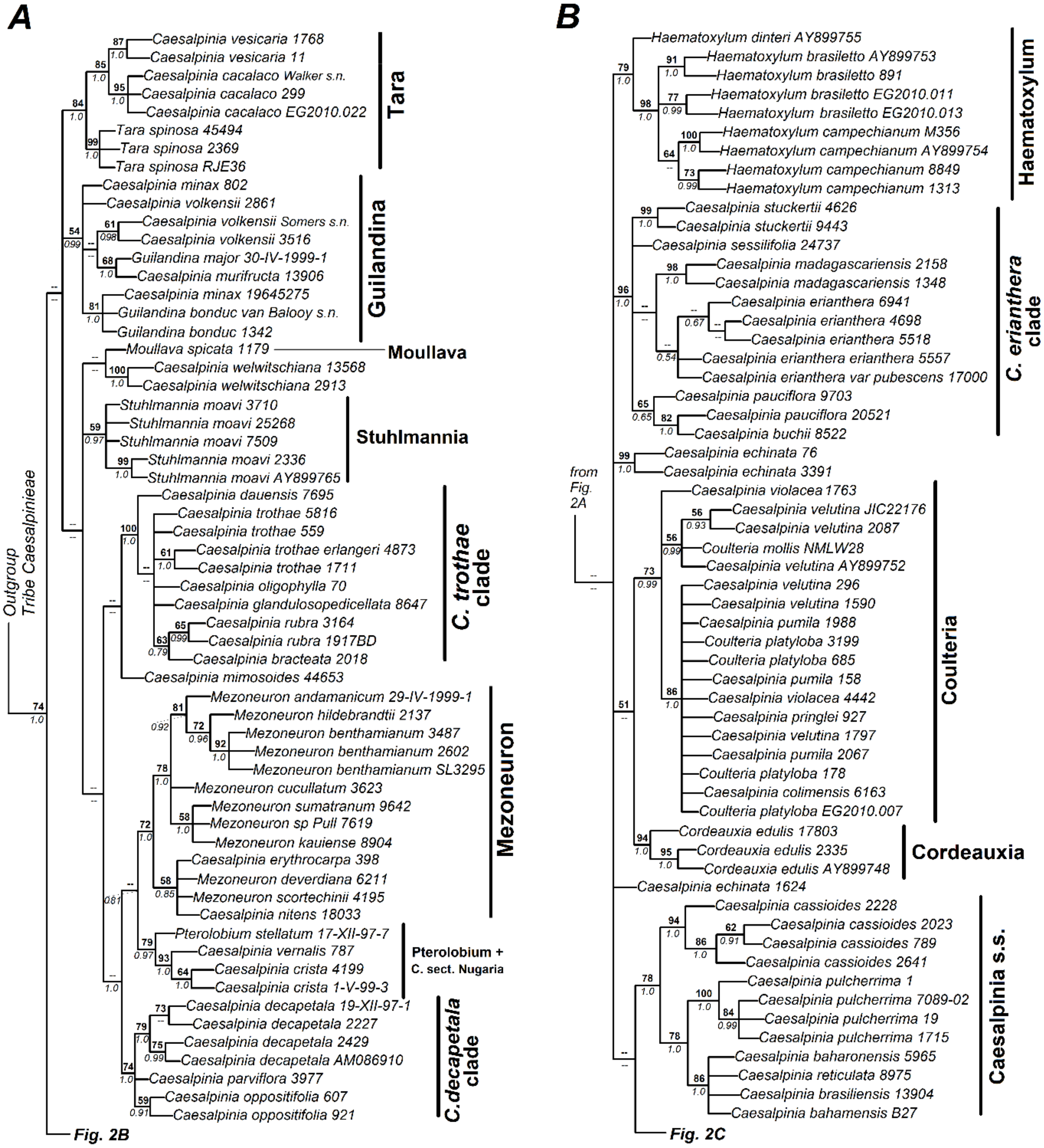


Figure 1.2 (continued)

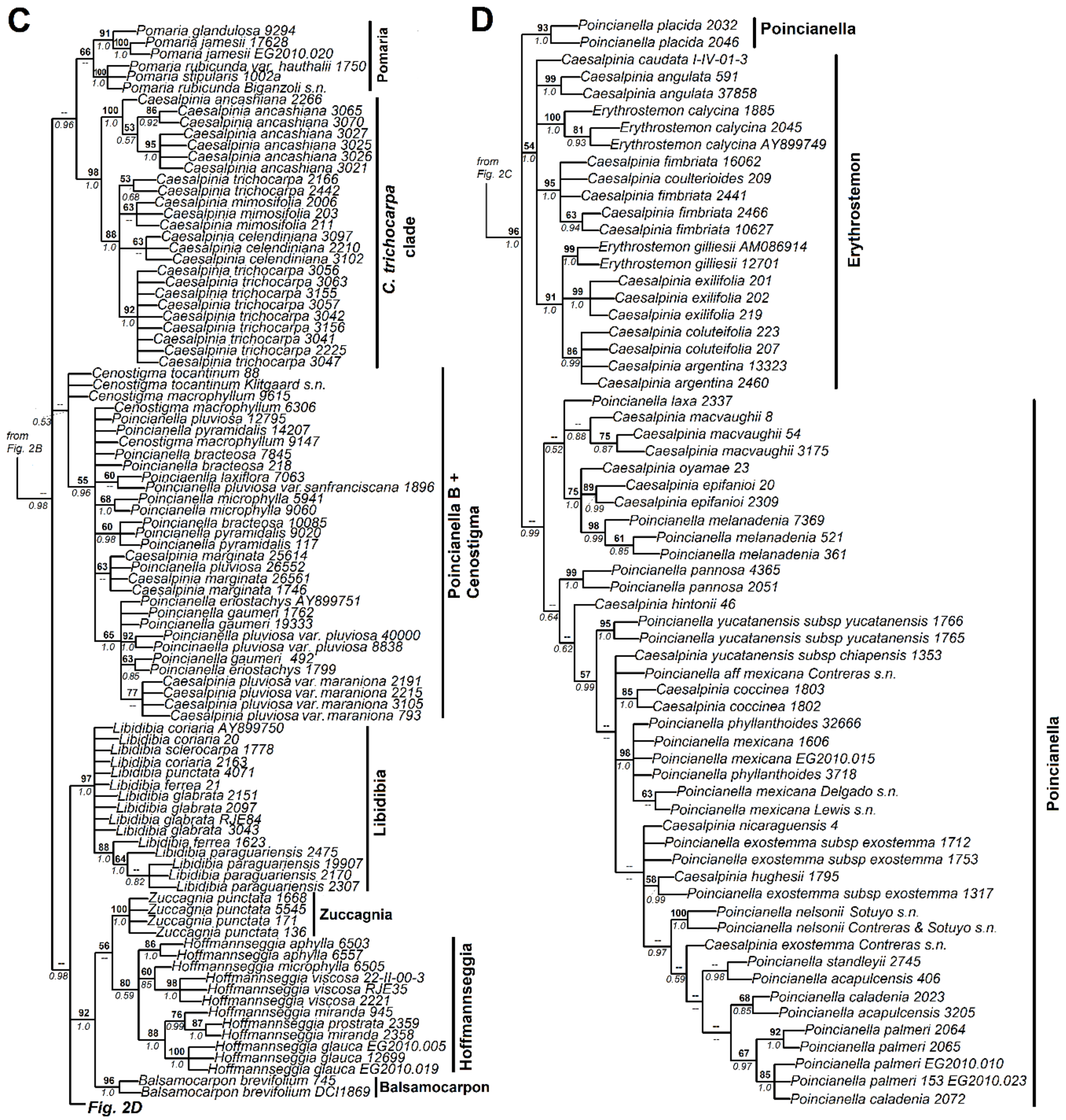
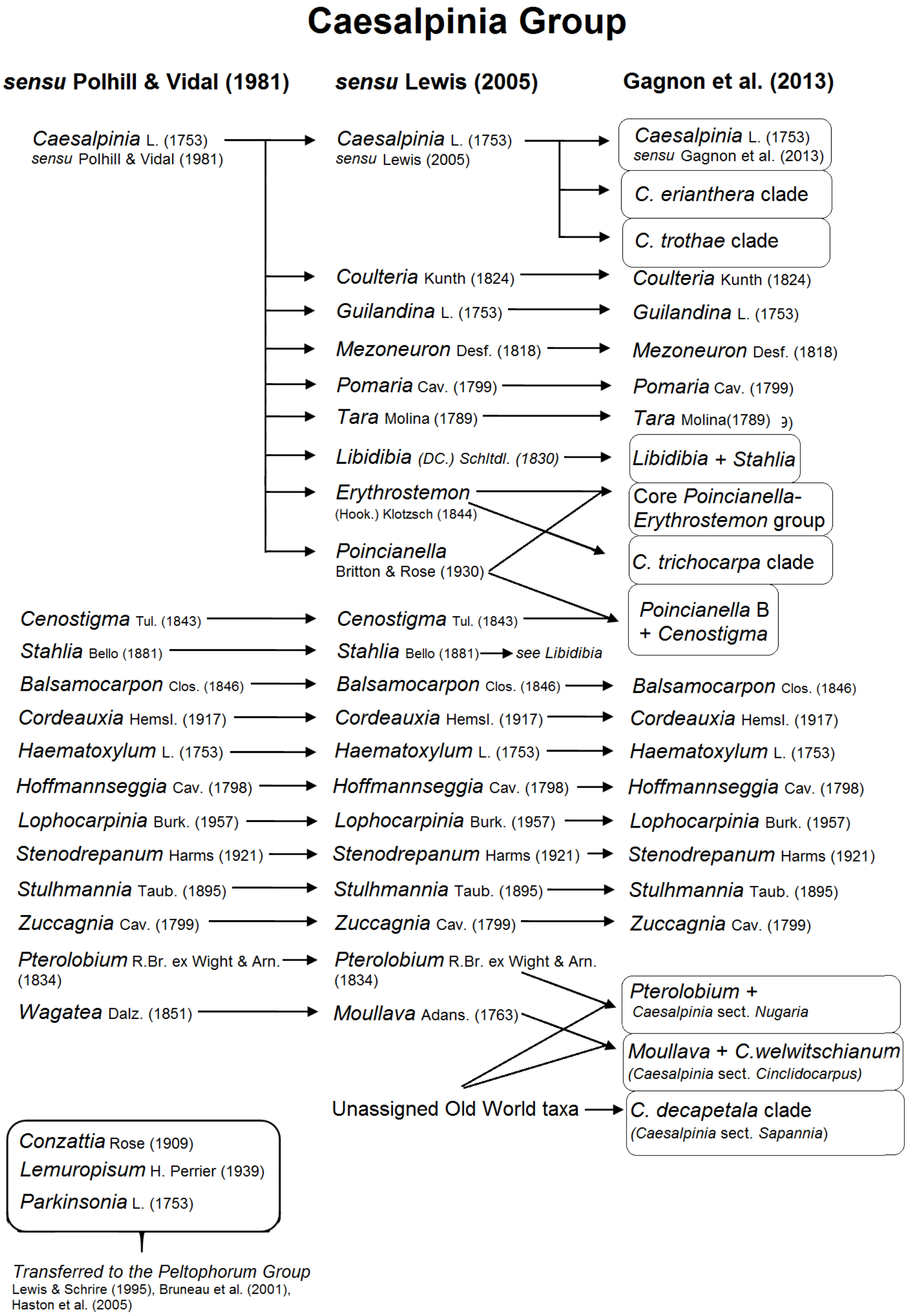


Figure 1.3 Comparison of generic classificationsof the Caesalpinia Group proposed by Polhill & Vidal (1981), Lewis (2005), and this study.



Chapitre 2: A new generic system for the pantropical Caesalpinia Group (Leguminosae)

Edeline Gagnon[1], Colin E. Hughes[2], Luciano Paganucci de Queiroz[3], Anne Bruneau[1], and Gwilym P. Lewis[4]

1. Institut de recherche en biologie végétale and Département de sciences biologiques, Université de Montréal, H1X 2B2, Montréal, Canada;
2. Institute of Systematic Botany, University of Zürich, 8008, Zürich, Switzerland;
3. Universidade Estadual de Feira de Santana, BR 116, Km 03, Campus Universitário, Feira de Santana 44031-460, Bahia, Brasil;
5. Comparative Plant and Fungal Biology Department, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, United Kingdom;

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(Modifié pour les besoins de la présente thèse)

2.1 Résumé/ Abstract

Résumé

Malgré qu'il soit le deuxième plus grand clade de la tribue des Caesalpinieae, les délimitations génériques au sein du groupe Caesalpinia demeurent incertaines. Ceci est en partie dû à un échantillonnage taxonomique insuffisant et au manque de résolution dans les arbres des études phylogénétiques précédentes. Afin de surmonter cette faiblesse, nous présentons ici de nouvelles analyses phylogénétiques réalisées à partir de cinq marqueurs génétiques chloroplastiques et un marqueur ribosomal nucléaire, tout en incluant 172 des 205 espèces connues (84%) du groupe Caesalpinia. Nos résultats vont dans le même sens que les conclusions d'études précédentes, lesquelles suggéraient que la classification actuelle du groupe Caesalpinia en 21 genres ne reflètent pas les relatons phylogénétiques entre espèces. Plusieurs genres sont non-monophylétiques, tels que *Poincianella, Erythrostemon,* et *Caesalpinia* sensu stricto. Par ailleurs, plusieurs espèces asiatiques et africaines dont l'affiliation générique était incertaine se retrouvent au sein de groupes caractérisés par des synapomorphies, et méritent donc d'être élèvés au rang de genre. L'échantillonnage taxonomique exhaustif de cette étude permet également d'identifier trois espèces qui ne sont pas imbriquées dans aucun des clades principaux de notre phylogénie, suggérant qu'il s'agit de nouveaux genres monospécifiques. Selon ces résultats, une nouvelle classification revisée du groupe Caesalpinia est présentée, dans laquelle un total de 26 genres sont reconnus. Entre autre, deux genres sont ré-instaurés (*Biancaea* Tod. et *Denisophytum* Vig.), quatre nouveaux genres sont décrits (*Gelrebia*, *Paubrasilia*, *Hererolandia* et *Hultholia*), et le transfert nomenclatural des espèces aux bons genres est effectué quand la taxonomie des espèces est suffisamment solide pour le permettre.

Mots-clés: *Caesalpinia*, clade Mimosoideae-Caesalpinieae-Cassieae, Leguminosae, Fabaceae, délimitation générique.

Abstract

The Caesalpinia Group is the second largest clades in tribe Caesalpinieae (Leguminosae), but its taxonomy is still uncertain as generic delimitations within this clade remains in a state of flux. This is due in part to incomplete taxon sampling and lack of resolution in previous phylogenetic studies of Caesalpinieae. We present new phylogenetic analyses based on five plastid and one nuclear ribosomal marker, with dense taxon sampling including 172 of the estimated 205 recognized species (84%) in the Caesalpinia Group. Our analyses confirm the preliminary results of previous studies, which suggested that the current classification of the Caesalpinia Group into 21 genera needs to be revised. Several genera are non-monophyletic, including *Poincianella*, *Erythrostemon* and *Caesalpinia* sensu stricto. In addition, previously unclassified Asian species segregate into clades that are morphologically diagnosable and merit elevation to generic rank. The completeness of our taxonomic sampling also allows us to identify three species that do not nest in any of the main clades in our phylogeny and these are recognized as new monospecific genera. We present a revised classification of the Caesalpinia Group that recognises 26 genera, with reinstatement of two genera (*Biancaea* Tod., *Denisophytum* Vig.), description of four new ones (*Gelrebia*, *Paubrasilia*, *Hererolandia* and *Hultholia*), and the nomenclatural transfer of species to their correct genera.

Keywords: *Caesalpinia*, Mimosoideae-Caesalpinieae-Cassieae clade, Leguminosae, Fabaceae, generic delimitation

2.2 Introduction

In the Leguminosae, as in angiosperm systematics more generally, delimitation of genera remains in a state of considerable flux (LPWG, 2013), in large part because of the lack of well-sampled phylogenies at the species level. While all but 11% of the 751 currently recognised genera have been included in molecular phylogenetic studies (LPWG, 2013), less than half of the ca. 19,500 species (7,482) of Legumes were represented in GenBank (Phylota (Sanderson & al., 2008), release 194 (February 2013). Phylogenetic analyses of Legume groups with increased taxonomic sampling, published in the past three decades, have revealed the non-monophyly of numerous genera previously delimited using morphology alone (e.g. *Acacia* s.l. (see Murphy, 2008 for a review of phylogenetic studies and the classification of this group, and the more recent publicatons Bouchenak-Khelladi & al., 2010; Miller & Seigler, 2012), *Piptadenia* (Jobson & Luckow 2007), *Monopetalanthus* (Wieringa 1999), *Hymenostegia* s.l. (Mackinder & al., 2013; Mackinder & Wieringa 2013; Wieringa et al. 2013), *Vigna* s.l. (Delgado-Salinas & al., 2011), *Lonchocarpus s.l.* (Silva & al., 2012), *Poecilanthe* (Meireles et al. 2014), *Derris* (Sirichamorn et al. 2014), *Otholobium* (Egan & Crandall 2008; Dludlu & al. 2013)). Furthermore, many groups remain in which non-monophyly of genera is known, but where phylogenies with increased molecular and taxonomic sampling are needed to accurately delimit genera (e.g. *Bauhinia*, *Cynometra*, *Maniltoa*, *Millettia, Albizia, Archidendron, Leucochloron, Entada,* etc.; for more details, see LPWG, 2013 and references therein)

Generic delimitation can be complicated by the lack of fixed guidelines, with different criteria and practices used by botanists to recognize genera. Most taxonomists agree that "good" genera are stable and predictive. By predictive, it is meant that they are clearly characterised enough to permit the identification and classification of newly discovered species. By stable, it is meant that names of species will not be subject to change; most taxonomist agree that in a Linnean classification system, this is best achieved by recognizing groups of species that are strongly supported as monophyletic, and that they are delimited in such a way that they are morphologicaly diagnosable, and that future new combinations in other genera will be unnecessary. Nevertheless, unlike for species delimitation, few protocols, guidelines or widely accepted criteria exist to aid generic delimitation (Humphreys & Linder, 2009; but see Garnock-

Jones, 2014 and Vences & al., 2013). Reciprocal illumination from different datasets, such as molecular phylogenies and morphological data, is used to identify clades which are defined by diagnostic morphological synapomorphies or sets of diagnostic characters. However, potential conflicts between these two data types mean that this is not necessarily straightforward. Debates persist around issues such as whether or not paraphyletic genera should be recognized, whether smaller or more widely circumscribed genera should be favoured, the importance of avoiding unnecessary nomenclatural disruption especially for widely-known and economically important taxa, and the importance of building classifications that both reflect evolutionary relationships and are at the same time useful and widely accepted by users (Diggs & Liscomb 2002).

The Caesalpinia Group is a good example of a group where generic delimitation has remained problematic due to lack of adequate taxonomic sampling in previous morphological and molecular studies. The group is placed in the Mimosoideae-Cassieae-Caesalpinieae, MCC clade (sensu Doyle, 2012; see also LPWG, 2013), forming one of the informal groups of tribe Caesalpinieae in subfamily Caesalpinioideae. The Caesalpinia Group comprises ca. 205 species currently classified in 21 genera (Lewis, 2005). Doubts persist about the status and monophyly of these 21 genera largely due to variation in the way the genus *Caesalpinia* has been cricumscribed. *Caesalpinia* L. in its broadest circumscription comprises ca. 150 species but these have had a tumultuous taxonomic and nomenclatural history, having been variously placed in up to 30 different genera since the description of *Caesalpinia* in 1753. These changing generic concepts illustrate the difficulties in establishing a stable classification of the group. The proliferation of generic names associated with *Caesalpinia* s.l. is due in part to the wide pantropical geographic distribution of the group spanning five continents, with many narrowly restricted endemic taxa, making it difficult to assemble representative material to achieve adequate taxon sampling for systematics, and especially in molecular phylogenetic studies. Several morphological and phylogenetic cladistics analyses (Lewis & Schrire, 1995) have attempted to elucidate generic delimitations within the Caesalpinia Group, including studies on floral development and ontogeny (Kantz & Tucker, 1994; Kantz, 1996), phytochemistry (Kite & Lewis, 1994), wood anatomy (Gasson & al., 2009), and leaf anatomy and secretory structures (Lersten & Curtis, 1995, 1996; Herendeen & al., 2003; Rudall & al., 1994). However, none of these studies achieved the sort of comprehensive taxon sampling needed to fully understand and synthesize the morphological diversity of the group. Furthermore, many morphological characters are highly homplastic, including conspicuous floral traits related to pollination syndromes, and some of the most robustly supported clades in molecular phylogenies of the group apparently lack any obvious diagnostic morphological synapomorphies (Gagnon & al., 2013, 2015, chapter 1 and 4).

Here we present a densely sampled and well-resolved molecular phylogeny of the Caesalpinia Group including the genus *Caesalpinia* s.l., to provide an explicit phylogenetic hypothesis as the basis for establishing a new generic system for this clade. All previous molecular and morphological phylogenies of the Caesalpinia Group (Lewis & Schrire, 1995; Simpson & Miao, 1997; Simpson & al., 2003; Haston & al., 2005; Bruneau & al., 2008; Mazanilla & Bruneau, 2012; Nores & al., 2012) have lacked sufficient taxon sampling and/or support to establish a comprehensive new classification. Other studies have focused on particular genera or clades, such as *Hoffmannseggia* Cav. (Simpson & al., 2004, 2005), *Pomaria* Cav. (Simpson & al., 2006), and *Arquita* Gagnon, G.P.Lewis & C.E.Hughes (Gagnon & al., 2015, chapter 4). Recently, Gagnon & al. (2013) produced a new phylogeny based on an informative plastid marker (*rps16*) and included the most extensive taxon sampling of the Caesalpinia Group to date (120 of ca. 205 species, or 58% of the group). The Gagnon & al. (2013, chapter 1) study suggested that a total of 23 genera could be recognized in the Caesalpinia Group, due to the polyphyly of two previously segregated genera and the grouping of lineages corresponding to sections of *Caesalpinia* described by Bentham (Fig. 2.1). However, stronger phylogenetic resolution and branch support were needed to confidently propose a new generic classification system. The Gagnon & al. (2013, chapter 1) phylogeny also lacked several critical taxa (notably *Lophocarpinia* Burkart, *Stahlia* Bello, *Stenodrepanum* Harms, *C. pearsonii* L.Bolus and *C. glandulosa* Bertero ex DC.), needed to adequately represent the morphological diversity and geographical range of the Caesalpinia Group.

The objectives of this study are to resolve the phylogenetic relationships within the Caesalpinia Group and propose a new generic classification. In order to achieve greater phylogenetic resolution, this new phylogeny is based upon increased gene sampling, using one nuclear ribosomal and five plastid markers as well as increased taxon sampling compared to the previous study (Gagnon & al. 2013, chapter 1). The sampling employed here encompasses the full morphological diversity of the group and almost the entire geographical range of the Caesalpinia Group. Specifically, we use this new phylogenetic analysis to propose a new generic classification and associated taxonomic synposis of the Caesalpinia Group, in which we recognise 26 clades at generic rank, provide new or emended generic descriptions, a key to genera and, where no further ambiguity as to species placement exists, the necessary new combinations for species as required.

2.3 Material and Methods

2.3.1 Molecular methods

Samples were obtained from herbarium specimens and field-collected silica-dried leaves from wild and cultivated plants. When possible, multiple individuals per species from different localities were sampled. In addition, sequences were downloaded from GenBank, including from the following studies: Bruneau & al. (2001, 2008), Simpson & al. (2003, 2005, 2006), Haston & al. (2005), Marazzi & al. (2006), Marazzi & Sanderson (2010), Manzanilla & Bruneau (2012), Nores & al. (2012), Babineau & al. (2013), and Gagnon & al. (2013, 2015, chapter 1 et 4). These GenBank sequences enabled us to include all 21 genera belonging to the informal Caesalpinia Group (sensu Lewis, 2005), including *Lophocarpinia* and *Stenodrepanum* (Nores & al. 2012). We included the type species for all genera, with the exception of *Mezoneuron* Desf.

A total of 429 samples, representing 172 of an estimated total 205 species (83.9%) from the Caesalpinia Group including 131 species from the genus *Caesalpinia* s.l., are included in the analyses. Our taxonomic sampling, although not complete, very adequately represents the geographical range and morphological diversity of the group, with the important exception of about seven species distributed in mainland China for which no material was available for study. In addition, several species, whose phylogenetic and taxonomic positions were previously unclear, are analysed here for the first time, including *Caesalpinia digyna* Rottler*, C. tortuosa* Roxb., *C. pellucida* Vogel*, C.glandulosa,* and *C. pearsonii.*

Nine species were included as outgroup taxa to root the phylogenetic trees. These include representatives of the Umtiza grade (*Gymnocladus chinensis* Baill.*, Tetrapterocarpon geayii* Humbert), the Peltophorum Group (*Colvillea racemosa* Bojer*, Conzattia multiflora* (Robinson) Standl.) and the Cassieae clade (*Cassia javanica* L.*, Pterogyne nitens* Tul.*, Senna alata* (L.) Roxb.*, Senna covesii* (A.Gray) H.S.Irwin & Barneby*, Senna spectabilis* (DC.) H.S.Irwin & Barneby), all of which occur within the more inclusive MCC clade. Locality details and information about herbarium vouchers all accessions are listed in Annex 1.

Three protocols were used to extract DNA: (1) a modified CTAB protocol (Joly & Bruneau, 2006); (2) QIAGEN DNeasy Plant Mini Kit (Mississauga, ON, Canada); or (3) a 4% MATAB protocol (Ky & al., 2000). Six genetic markers were amplified, including the 5.8S subunit and flanking internal transcribed spacers, ITS1 and ITS2 of the ribosomal DNA, and five plastid loci: *rps16,* the *trnD-trnT* intergenic spacer, *ycf6-psbM,* the *matK* gene and *3'-trnK* intron, and the *trnL-trnF* intron-spacer region. The first four markers were amplified using both standard and nested-PCR protocols, described in Gagnon & al. (2015, chapter 4). The *matK*-3'-*trnK* region was amplified using the primers trnK685F (Hu & al. 2000), trnK4La (Wojciechowski & al. 2004), trnK2R* and KC6 (Bruneau & al. 2008), according to the protocols described in Bruneau & al. (2008). Because of initially poor amplifications, we designed a new primer, matK-C6-Caesalpinia (GAA TGC TCG GAT AAT TGG TTT), which improved the amplification of the first section of this locus. The *trnL-trnF* intron-spacer region was amplified using the primers trnL-C, -D, -E and -F (Taberlet & al., 1991), using the same protocols as for the *rps16* locus (Gagnon & al. 2013, chapter 1), with annealing temperatures varying between 50 and 53 °C. While we attempted to amplify the first four loci for all available material, we selectively targeted samples for amplification for the *matK*-3'*trnK* and *trnL-trnF* region, due to the availability of a large number of sequences from previously published studies. For the most problematic samples, including those where we had sequencing problems due to mononucleotide repeats, we used a protocol with Phusion Hot Start II High-Fidelity DNA polymerase (Thermo Scientific, United States), as described by Gagnon et al. (2013, chapter 1), which yields more accurate and longer quality mononucleotide sequence reads (Fazekas & al., 2010).

PCR amplifications were sequenced by Genome Quebec (Montreal, Canada), with Big Dye Terminator 3.1 chemistry on an ABI 3730xl DNA Analyzer (Applied Biosystems, Carlsbad, CA, USA). The program Geneious (version 5.6-6.1.8, Biomatters, Auckland, New Zealand) was used to assemble chromatograms and to visually inspect the resulting contigs. All sequences were submitted to BLAST (Altschul & al., 1990) to verify for non-specific amplification, and eliminated if they did not match Leguminosae sequences in GenBank. All GenBank numbers for sequences produced in this study is listed in Annex 1.

2.3.2 Phylogenetic analyses

Sequences were aligned, inspected and manually adjusted with the software Geneious. Ambiguous portions of the alignments were identified visually, and corresponded mostly to variable mononucleotide and/or tandem repeats that were difficult to align. This resulted in the exclusion of 42 nucleotides for *ITS,* 92 for *rps16*, 146 for *trnD-trnT*, 157 for *ycf6-psbM,* 86 for *trnL-trnF* and 16 for *matK-3'trnK*. Gaps were coded using simple indel coding (Simmons & Ochoterena, 2000), implemented in SeqState 1.4.1 (Müller, 2005). Only non-autapomorphic indels were retained.

To reconstruct phylogenetic relationships, Maximum Likelihood (ML) analyses were initially carried out on each of the six loci individually, as well as on two other matrices, one where all five plastid loci were combined and a second matrix with all six loci to verify whether the phylogenies were informative, and to detect significant conflicts amongst the resulting topologies. Matrices were concatenated using the program Sequence Matrix (Vaidya et al. 2011). ML analyses were carried out with the software RaxML 8.0.0 (Stamatakis, 2014) on the CIPRES gateway v.3.3 (Miller & al., 2010). The analyses were conducted using the GTRGAMMA model for the DNA sequences and the BINCAT model for the indel partitions. Bootstrap support was assessed through 1000 non-parametric bootstrap replicates.

As topological conflicts were minimal, and we never found bootstrap support (above 60%) for conflicting relationships between the topologies of the resulting gene trees, we proceeded with a second series of phylogenetic analyses that combined the six loci in a concatenated matrix. Initially we analysed this six-locus matrix, keeping all accessions of a species as separate terminals, but this resulted in a matrix with large amounts of missing data because not all accessions had been sequenced for all six loci. In an effort to reduce missing data, multiple accessions of the same species were in some cases concatenated to maximize the number of loci represented for a species. We only combined different accessions of the same species if they occurred in the same clade in the preliminary RaxML analyses. If sequences from the same locus were available for two accessions, we visually checked to make sure there was no sequence variation in the overlapping section, and selected the longest sequence. This resulted in the combination of accessions for the following 16 species (see Annex 1): *Caesalpinia cacalaco* Humb. & Bonpl., *C. caladenia* Standl., *C. caudata* (A.Gray) E.M.Fisher, *C. colimensis* F.J.Herm., *C. epifanioi* J.L.Contr., *C. exilifolia* Griseb., *C. madagascariensis* (R.Vig.) Senesse, *C. melanadenia* (Rose) Standl., *C. mimosoides* Lam., *C. pringlei* (Britton & Rose) Standl., *C. sappan* L., *C. sessilifolia* S.Watson, *Libidibia sclerocarpa* (Standl.) Britton & Rose, *Haematoxylum brasiletto* H.Karst., *H. dinteri* Harms and *Tara spinosa* (Molina) Britton & Rose. In addition to concatenating sequences obtained from different accessions, the impacts of different levels of missing data were examined by creating a series of matrices that progressively excluded accessions with five, four, three, two and one missing loci, resulting in a total of six different matrices. Because the matrix containing sequences without any missing data lacked representatives from a number of genera and critical clades or species, a seventh matrix was generated (with 39 taxa) that added an accession from each of the missing critical taxa to maximize the taxonomic representation while minimizing the amount of missing data.

For these seven matrices, phylogenetic analyses were carried out using ML, maximum parsimony (MP) and Bayesian methods. For the ML analyses, we used RaxML (Stamatakis, 2014) as described above. For parsimony analyses, PAUP* (Swofford, 2003) was used with the two-step approach (Davis & al., 2004) as described in Gagnon et al. (2013, chapter 1), but saving in memory a maximum of 50,000 trees, and carrying out a total of 5,000 bootstrap replicates, with two trees retained per replicate. For the Bayesian analyses, which were conducted in

MrBayes 3.2 (Ronquist & al., 2012), Jmodeltest 2 (Darriba & al., 2012) was used to estimate the best evolutionary model for each DNA locus separately. Based on the Akaike Criterion, the best models selected were GTR + I + G for *ITS*, GTR + G for *rps16,* TPM1uf+ I + G for *trnD-trnT*, and TVM + I + G for *trnL-trnF* and *matK,* and TVM + G for *ycf6-psbM*. We specified the GTR+I+G and GTR+G model for the *ITS* and *rps16* regions, but because it is not possible to specify the exact models for the four other gene regions in MrBayes v.3.2, we used the reversible-jump MCMC option, which allows sampling of different schemes of nucleotide substitution as part of the MCMC run (nst=mixed). The F81 model was specified for all partitions corresponding to indel characters. The analyses were run on a high performance computer cluster (Calcul Québec, Université de Montréal, Canada) with two parallel runs of eight Markov Chain Monte Carlo (MCMC) chains each, four swaps per swapping cycle, and trees sampled every 1000 generations. The stop criterion was set to an average standard deviation of split frequencies that dropped to below the critical value of 0.01. We observed results with Tracer v.1.6 (Rambaut & al., 2009) ensuring that effective sample sizes were above 200 and that chains mixed appropriately; if not, we continued to run the MCMC analysis until these criteria were met. The “burn-in” fraction for all analyses was set to 10%.

2.4 Results

The number of accessions sequenced for each locus, as well as their aligned lengths, the number of indels coded and retained, and the percentages of parsimony informative characters are indicated in Table 2.1. Of the six loci, ITS had the highest percentage of parsimony-informative characters (61.7%), followed by *ycf6-psbM*, *rps16*, *trnD-trnT*, *trnL-trnC*, and *matK-3'trnK*. The concatenated six-locus matrix (aligned length = 8803) included 429 accessions, which decreased to 408 when accessions were combined for the 16 species mentioned above. Table 2.2 summarizes the number of accessions and species per loci, the percentage of missing data, the number of trees, tree length, CI and RI obtained in the MP analyses for the series of seven matrices with successively lower numbers of taxa with missing loci. The Bayesian

Table 2.1 Character data for the six loci analysed, with the number of accessions for each matrix, aligned length (ambiguous regions included), number of indels scored, % of parsimony informative characters and critical missing genera and taxa.

Locus	**Number of accessions**	**Aligned length** (ambiguous regions included)	**Number of indels retained**	**% parsimony informative characters**	**Missing genera and critical taxa**
ITS	251	820	113	550/891 = 61,7%	*C. mimosoides* *Lophocarpinia* *Stenodrepanum* *Stahlia*
rps16	298	1081	45	311/1034 = 30,08%	*Lophocarpinia* *Stenodrepanum*
trnD-trnT	235	1921	108	513/1883 = 27,24%	*Lophocarpinia* *Stenodrepanum*
ycf6-psbM	193	1795	141	540/1779 = 30,35%	*Lophocarpinia* *Stenodrepanum*
trnL-trnF	171	1347	65	307/1326 =23,15%	None
matK-3'trnK	89	1839	20	308/1843 = 16,71%	*C. mimosoides*

analyses for the seven combined data matrices with differing levels of missing data ran between 2 million and 30 million generations, depending on the size of the matrix.

With the exception of the least informative (*trnL-trnF*) gene tree the Caesalpinia Group is monophyletic in all other analyses, generally with strong bootstrap or PP support (Tables 2.3 & 2.4). The 23 major clades hypothesized from the *rps16* phylogeny of Gagnon et al. (2013, chapter 1) generally are recovered in the ML topology for each individual locus. However, three species, *C. echinata* Lam., *C. pearsonii,* and *C. mimosoides*, were placed outside these 23 clades, resulting in a total of 27 lineages that potentially could be recognised at the generic level.

All of the 27 lineages were recovered in the MP, ML, and Bayesian analyses, with varying degrees of support in each analysis, which increased when all six loci were combined and the amount of missing data was reduced (Tables 2.3 & 2.4). In five of the six individual locus analyses (all except *ycf6-psbM*) the genera *Mezoneuron*, *Moullava*, *Caesalpinia* s.s., *Coulteria, Pterolobium* and *Haematoxylum* were not supported as monophyletic, and the multiple accessions of both *Caesalpinia echinata* and *Stuhlmannia* did not cluster into monophyletic groups. However, all but two of these genera were consistently recovered as monophyletic with robust support in all of the combined analyses (MP, ML and Bayesian). The two exceptions were the genera *Haematoxylum* and *Pterolobium.* In the MP and ML analyses, *Haematoxylum* had *Lophocarpinia* (when this taxon was represented in the matrix) nested within it, but in the Bayesian analyses *Lophocarpinia* occurred as sister to *Haematoxylum*. The *Pterolobium* clade was strongly supported only in the individual *ycf6-psbM* ML analysis. In all other analyses, it was recovered non-monophyletic, with *C. crista* nested within it, or was recovered as monophyletic with poor to moderate support.

While interclade relationships were generally weakly supported or unsupported in the individual gene trees, support values increased in the analyses of the combined matrices. In the combined ML and Bayesian analyses, the same topology was recovered in all analyses regardless of the amount of missing data or number of missing genera/critical species (with the exception of the Bayesian 312-accession analysis (Fig. 2.3)), where the only difference is in the placement of *Cordeauxia* + *Stuhlmannia*, which occurs as a polytomy at the base of the Caesalpinia Group). The topology recovered shows two main Caesalpinia Group clades (Fig. 2.2). One large clade includes the *Cordeauxia* + *Stuhlmannia* pair (clade A) as sister to the *Cenostigma*-Poincianella B clade, and these two clades together are sister to a clade (clade B) consisting of *Stahlia* + *Libidibia*, *Balsamocarpon* + *Zuccagnia* + *Stenodrepanum* + *Hoffmannseggia* (clade D), and the core P-E group + *Pomaria* + *Arquita* (clade C). The second major clade includes *C. pearsonii*, sister to a clade that includes *Lophocarpinia* + *Haematoxylum*

Table 2.2 Statistics for the seven combined matrices, with the number of accessions, number of ingroup and outgroup species, % missing data, and missing genera/critical taxa. The results of the parsimony analyses are indicated, with the number of trees retained, the length of the shortest trees (length), consistency index (CI), and retention index (RI).

	All sequences	**2 loci +**	**3 loci +**	**4 loci +**	**5 loci +**	**All 6 loci +**	**No missing genera**
Accessions	408	312	223	175	76	30	39
Nb. of Caesalpinia Group species	171/~205	163/~205	128/~205	103/~205	55/~205	26/~205	35/~205
Nb. *Caesalpinia* s.l. species	130/~155	123/~155	106/~155	84/~155	44/~155	20/~155	23/~155
Outgroup species	9	9	9	9	8	4	4
Missing genera/critical taxa	None	None	*2:* *Lophocarpinia* *Stenodrepanum*	*2:* *Lophocarpinia* *Stenodrepanum*	*3:* *Lophocarpinia* *Stenodrepanum* *C.mimosoides*	*8:* *C.mimosoides* *Cenostigma* *Guilandina* *Moullava* *Lophocarpinia* *Pterolobium* *Stahlia* *Stenodrepanum*	None
% missing data	61.35%	52.70%	42.64%	37.69%	27.89%	23.4%	29.6%
Nb trees found	50,000	50,000	50,000	50,000	7	2	2
Length	12,212	11,986	10,909	10,101	7,615	4,715	5405
CI	0.4320	0.445	0.4508	0.4708	0.5292	0.6244	0.5991
RI	0.8141	0.8094	0.7891	0.7763	0.6567	0.4862	0.4806

Table 2.3 Bootstrap support from the ML analyses of the six individual loci and the combined datasets, for various proposed genera from Gagnon et al. (2013, chapter 1).

	Maximum likelihood											
	ITS	***matK***	***rps16***	***trnD-trnT***	***trnL-trnC***	***ycf6-psbm***	**All**	**2+**	**3+**	**4+**	**5+**	**6 loci**
Nb sequences	251	89	298	235	171	193	408	312	223	175	76	30
Clades												
Caesalpinia Group	**96**	79	80	**94**	39	**95**	79	**100**	**100**	**100**	**100**	**100**
Haematoxylum	**98**	*	**91**	72	**N-M**	50	N-M	N-M	**100**	**100**	**100**	*
Tara	82	66	83	**99**	70	64	**98**	**100**	**100**	**100**	**100**	**100**
Coulteria	**100**	N-M	59	**100**	83	**94**	69	**100**	**100**	**100**	**100**	*
Caesalpinia s.s.	32	N-M	N-M	**95**	68	68	**96**	**96**	**100**	**100**	**100**	*
C. erianthera clade	**100**	*	**96**	**99**	**97**	**97**	**100**	**100**	**100**	**100**	**100**	*
C. trothae clade	**100**	**100**	**100**	**100**	**99**	**100**	**100**	**100**	**100**	**100**	**100**	*
Guilandina	**100**	60	63	**91**	82	**100**	**91**	**100**	**100**	**100**	*	--
Mezoneuron	N-M	57	84	41	N-M	**94**	**95**	**100**	**100**	**100**	**100**	**100**
Moullava	**99**	**95**	N-M	69	*	*	**90**	**99**	**100**	**97**	*	--
C. crista clade	*	*	**92**	*	*	*	N-M	*	*	*	*	*
Pterolobium	42	*	57	39	*	**100**	N-M	68	47	*	*	--
C. decapetala clade	68	78	70	33	*	80	**94**	**100**	**100**	**99**	*	*
Cenostigma + Poincianella B	**99**	**92**	51	72	46 **	**94**	54	**100**	**100**	**100**	**100**	--
Arquita	**100**	**100**	**92**	68	**95**	**100**	**100**	**100**	**100**	**100**	**100**	**100**
Pomaria	**100**	*	71	**100**	**92**	**99**	**100**	**100**	**100**	**100**	*	*
Core P-E group	**100**	52	**97**	64	**100**	**100**	86	**100**	**100**	**100**	**100**	**100**
Stahlia + *Libidibia*	**100†**	57	85	78	61	85	83	**100**	**100**	**100**	**100**	*,†
Hoffmannseggia	**100**	*	**90**	84	84	**97**	**97**	**96**	**100**	**100**	*	*
Monospecific genera												
Cordeauxia	*	*	**95**	*	32	*	77	**95**	*	*	*	*
Stuhlmannia	N-M	*	N-M	84	N-M	78	36	68	**96**	**94**	*	*
C. echinata	**100**	N-M	N-M	N-M	79	30	71	83	**100**	**99**	**100**	*
C. pearsonii	**100**	**100**	**100**	**100**	*	**100**	**100**	**100**	**100**	**100**	**100**	*
Lophocarpinia	--	*	--	--	*	--	*	*	--	--	--	--
Stenodrepanum	--	*	--	--	**100**	--	**100**	*	--	--	--	--
C. mimosoides	--	--	**100**	**100**	*	**100**	*	*	*	*	--	--
Balsamocarpon	**100**	**98**	**97**	**95**	**100**	**97**	**98**	**100**	**100**	**100**	*	*
Zuccagnia	**100**	**100**	**100**	**100**	**95**	**100**	**100**	**100**	**100**	**100**	**100**	*

Legend

-- Not represented in the matrix

* Impossible to evaluate monophyly: only one accession or species included in the matrix

N-M: Non-monophyletic

** *Cenostigma* not included.

† *Stahlia* not included

(clade E), these together sister to the remaining clades of *C. echinata*, *Caesalpinia* s.s., *Tara* + *Coulteria* + *C. erianthera* clade (clade F), and the group containing the *C. trothae* clade and all the lineages of Asian lianas (*C. mimosoides* + *Guilandina* + *Moullava* + the *C. decapetala* clade + the *C. crista* clade + *Pterolobium* + *Mezoneuron*) (clade G).

Although many of the same clades were recovered in the parsimony analysis (i.e., clades A-G of Fig. 2.2), differences were noted in the relationships of the early diverging lineages. However, bootstrap support for the alternative topology of these early diverging branches was always under 50% (results not shown). The positions of certain taxa also varied amongst the three analytical methods, but generally these differences were found for relationships with relatively low branch support (branches with low support on Fig. 2.2). For example, while *C. echinata* was always recovered as sister to *Caesalpinia* s.s. in the ML analyses (bootstrap below 50%), in the Bayesian analyses it sometimes was sister to *Caesalpinia* s.s. (PP between 64 and 97) or sister to clade F (in the 76-, 39- and 30-accession matrices with less missing data, and in parsimony analyses it always was sister to clade G (bootstrap below 50%). As noted above, the relative positions of *Lophocarpinia* and *Haematoxylum* also varied in the Bayesian analysis relative to the parsimony and ML analyses. The relationships between the *C. trothae* clade, *C. mimosoides* and *Guilandina* were also variable but again generally with low branch support in all three types of analyses. The positions of *C. placida* and *C. glandulosa* within the core P-E clade were also variable, recovered either as sister to a Central American lineage or to a South American lineage in different analyses. Finally, the position of *Stenodrepanum* as sister to *Hoffmannseggia,* was consistent across all analyses, but always with low branch support (e.g. Fig. 2.3).

2.5 Discussion

The increased sampling of genes and taxa in the phylogenies presented here confirms the preliminary findings of Gagnon & al. (2013, chapter 1) that the current generic classification of the Caesalpinia Group needs to be revised. While proposing a new classification for *Caesalpinia* s.l., Lewis (2005) suggested throughout his treatment that molecular phylogenies with increased taxon sampling were needed to accurately test the monophyly of the genera he was reinstating, including a group of 12-15 Asian species that could not be placed in any of the proposed segregates. Of the 21 genera proposed by Lewis (2005; Fig. 2.3), it is now clear that certain lineages, such as the *Poincianella-Erythrostemon* Group and *Caesalpinia* s.s., are polyphyletic. Our analyses also reveal new groupings for the Asian species that do not correspond to any of the genera in the Lewis (2005) classification system. In addition, three species (*C. echinata*, *C. mimosoides* and *C. pearsonii*) do not nest within clades corresponding to any of the genera proposed by Lewis (2005) or Gagnon & al. (2013, chapter 1). Based upon our comprehensively sampled phylogeny of the Caesalpinia Group, we propose here a total of 27 genera corresponding to clades, several of which need new descriptions.

These 27 genera are supported as monophyletic with robust support in all analyses of the combined data matrices, regardless of the amount of missing data in the matrix. Combining all six loci together also increased support for intergeneric relationships compared to previous analyses (Simpson & al., 2003; Gagnon & al. 2013, chapter 1). For example, we find the same interclade relationships, but with greater support, as those reported by Nores & al. (2012) in their parsimony analysis of two plastid markers (*trnL-trnF* and *matK-3'trnK*) and 40 morphological characters for 23 representatives of the Caesalpinia Group, except in the placement of *Cenostigma,* which they found to occur outside the Caesalpinia Group. This increased support for interclade relationships reinforces the previous suggestions for the non-monophyly of the *Poincianella-Erythrostemon* Group and of *Caesalpinia* s.s., allowing for a more confident assessment of homology and interpretation of morphological character evolution within the Caesalpinia Group. A similar supermatrix approach has been shown in other groups, both in empirical and simulation studies, to help recover robust phylogenetic relationships,

Table 2.4 Bootstrap support and Posterior probabilities from the parsimony and Bayesian analyses of the combined datasets, for various proposed genera from Gagnon et al. (2013, chapter 1).

	Parsimony						**Bayesian**					
	All	**2+**	**3+**	**4+**	**5+**	**6 loci**	**All**	**2+**	**3+**	**4+**	**5+**	**6 loci**
Nb sequences	408	312	223	175	76	30	408	312	223	175	76	30
Clades												
Caesalpinia Group	79	**100**	**100**	**100**	**100**	**100**	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**
Haematoxylum	N-M	N-M	**100**	**100**	**100**	*	0.55	0.63	**1.0**	**1.0**	**1.0**	*
Tara	**96**	**100**	**100**	**100**	**97**	**96**	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**
Coulteria	N-M	**100**	**100**	**100**	**100**	*	**0.99**	**1.0**	**1.0**	**1.0**	**1.0**	*
Caesalpinia s.s.	88	**93**	**96**	**97**	**98**	*	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**	*
C. erianthera clade	**97**	**100**	**100**	**100**	**100**	*	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**	*
C. trothae clade	**95**	**100**	**100**	**100**	**100**	*	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**	*
Guilandina	72	**100**	**100**	**100**	*	--	**1.0**	**1.0**	**1.0**	**1.0**	*	--
Mezoneuron	**93**	**100**	**100**	**100**	**100**	**100**	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**
Moullava	57	**98**	**99**	**97**	*	--	**0.98**	**1.0**	**1.0**	**1.0**	*	--
C. crista clade	N-M	*	*	*	*	*	**0.96**	*	*	*	*	*
Pterolobium	N-M	N-M	N-M	*	*	--	0.77	0.87	0.76	*	*	--
C. decapetala clade	85	**96**	**93**	**80**	*	*	**1.0**	**1.0**	**1.0**	**1.0**	*	*
Cenostigma + Poincianella B	76	**99**	**100**	**100**	**100**	--	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**	--
Arquita	**100**	**100**	**100**	**100**	**100**	**100**	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**
Pomaria	**98**	**100**	**100**	**100**	*	*	**1.0**	**1.0**	**1.0**	**1.0**	*	*
Core P-E group	56	**100**	**100**	**100**	**100**	**100**	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**
Stahlia + *Libidibia*	68	**99**	**100**	**100**	**99**	*,†	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**	*,†
Hoffmannseggia	80	87	85	**100**	*	*	**1.0**	**1.0**	**1.0**	**1.0**	*	*
Monospecific genera												
Cordeauxia	64	**92**	*	*	*	*	**1.0**	**1.0**	*	*	*	*
Stuhlmannia	N-M	N-M	**92**	**92**	*	*	0.77	0.82	**1.0**	**1.0**	*	*
C. echinata	62	83	**98**	**96**	**100**	*	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**	*
C. pearsonii	**100**	**100**	**100**	**100**	**100**	*	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**	*

Lophocarpinia	*	*	--	--	--	--	*	*	--	--	--	--
Stenodrepanum	**97**	*	--	--	--	--	**1.0**	*	--	--	--	--
C. mimosoides	*	*	*	*	--	--	*	*	*	*	--	--
Balsamocarpon	**99**	**100**	**100**	**100**	*	*	**1.0**	**1.0**	**1.0**	**1.0**	*	*
Zuccagnia	**93**	**99**	**100**	**100**	**100**	*	**1.0**	**1.0**	**1.0**	**1.0**	**1.0**	*

Legend:

-- Not represented in the matrix

* Impossible to evaluate monophyly: only one accession or species included in the matrix

N-M: Non-monophyletic

† Stahlia not included

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despite sometimes large amounts of missing data (Wiens, 2003, 2006; Phillipe & al. 2004; Pyron & al. 2011; Johnson & al. 2012; Hinchliff & Roalson, 2013).

2.5.1 Implications for the classification of the Caesalpinia Group and *Caesalpinia* s.l.

In their description of the Caesalpinia Group, Polhill & Vidal (1981) suggested that this was one of the most distinctive of the nine informal generic groups in tribe Caesalpinieae, based on several morphological characters, notably the presence of a lower cucullate sepal on the calyx. Although they had included the genera *Conzattia, Lemuropisum* and *Parkinsonia*, these were subsequently found to belong to the Peltophorum Group (Haston & al., 2005). We find here that the Caesalpinia Group, as described by Lewis (2005), is a robustly supported clade, and that most of the 13 genera outside *Caesalpinia* s.l., with the exceptions of *Cenostigma* and *Moullava*, form robustly supported monophyletic groups. Of the original eight genera re-instated by Lewis (2005), five constitute robust monophyletic groups, including the segregates *Tara, Coulteria, Guilandina, Mezoneuron,* and *Libidibia*. These five genera are well defined by morphological synapomorphies, as discussed in Gagnon et al. (2013, chapter 1). In the case of *Libidibia,* however, we suggest that it shares many similarities with the monotypic genus *Stahlia* from the Caribbean. Despite having a somewhat fleshy red fruit and singly pinnate leaves, the pods of *Stahlia* are indehiscent and most similar to those of *L. sclerocarpa* and other South

American species of *Libidibia,* whereas all other sister groups and closely related genera have dehiscent pods. Furthermore, the dark punctate gland dots on the undersurface of the leaflets, which are distinctively aligned parallel to the midvein, and are typical of *Stahlia*, are also found in certain species of *Libidibia*, including *L. coriaria* and *L. ferrea* (Simpson & al. 2003; Nores & al. 2012; Gagnon & al., 2013, chapter 1). Given these morphological similarities and their robustly supported sister group relationship, we conclude that there is no justification for keeping *Stahlia* and *Libidbia* as separate genera. In addition, our phylogenies suggest that the character traditionally used to segregate the two genera, pinnate vs. bipinnate leaves (Pohill & Vidal*,* 1981), is homplastic. Other examples are known of clades containing species with both pinnate and bipinnate leaves, such as in the *Cenostigma* + Poincianella B group, and in *Stuhlmannia*, and in some species, the two states occur on the same individual (e.g. *Haematoxylum*).

The remaining three genera reinstated by Lewis (2005), *Poincianella*, *Erythrostemon* and *Caesalpinia* s.s.*,* are non-monophyletic, as found previously (Gagnon & al. 2013, chapter 1), but here with sufficiently supported interclade relationships to confidently propose new generic delimitations. Although the genera *Poincianella* and *Erythrostemon* were thought to form together a clade of closely related species (Lewis, 1998), here we find a distinct subgroup of *Poincianella* species that clusters with *Cenostigma.* These species correspond to the Poincianella B group of Lewis & Schrire (1995) who, in their morphological cladistic analysis of the Caesalpinia Group, also found these species to be related to *Cenostigma.* These Poincianella B species differ from the remaining *Poincianella* and *Erythrostemon* species in their wood anatomy (Gasson & al., 2009) and in an alternate to subopposite leaflet arrangement (de Queiroz, 2009). While *Cenostigma* was considered as a distinct genus, in part due to its pinnate leaves, two species of the Poincianella B clade also have pinnate leaves (*C. marginata* and *C. pinnata*), and more importantly, several species of *Poincianella* B have internal secretory cavities in the leaflet lamina and inflorescences (Lersten & Curtis, 1994; Rudall & al., 1994), as well as stellate indumentum on the stems, leaves and/or inflorescences. The latter two characters are diagnostic of *Cenostigma,* but are completely lacking in the core Poincianella-Erythrostemon group. In addition, Poincianella B and *Cenostigma* share pods with conspicuously thickened margins, a character not found in the other species of the Poincianella-

Erythrostemon Group. Poincianella B and *Cenostigma* illustrate yet another case where morphological homoplasy (e.g., pinnation of leaves, alternate to subopposite leaflets, the presence/absence of stipitate glands, stellate indumentum), have obscured our understanding of groups resulting in non-monophyletic genera. Given the strong support for monophyly of this group, and the combination of diagnostic morphological characters, we suggest expanding *Cenostigma* to include these species formerly associated with the Poincianella-Erythrostemon Group.

The remaining species of the former *Poincianella* and *Erythrostemon* form two large clades: an Andean clade of five species, which is sister to *Pomaria*, and a second lineage containing the type specimens of both *Poincianella* and *Erythrostemon*. The Andean clade of five species has recently been recognized as the new genus *Arquita,* based on a combination of morphological, ecological and geographical characters (Gagnon & al., 2015, chapter 4). In the other lineage, the two monophyletic groups that contain the type specimens, *Erythrostemon gilliesii* and *Poincianella mexicana*, could be recognised as distinct genera. However, the unresolved relationships of *C. glandulosa* and *C. placida* at the base of this large clade (Fig. 2.3C) could imply the need to recognize two additional genera to account for these species. The alternative is to treat the whole Poincianella-Erythrostemon clade as a single genus. As previously discussed (Gagnon & al. 2013, chapter 1), this combined Poincianella-Erythrostemon lineage forms a morphologically and ecologically coherent group of shrubs and small treelets in seasonally dry tropical forests with a bicentric amphitropical distribution, restricted to the Neotropics. Although there are currently more species under the name *Poincianella* Britton & Rose (1930), *Erythrostemon* Klotzsch (1844) takes precedence because it is an older name. Maintaining *Poincianella* could also lead to confusion, because a number of species that have been classified under this name (the Poincianella B group), are now known to be related to the genus *Cenostigma*.

Caesalpinia s.s. is also non-monophyletic and is made up of three independent lineages. The most distinctive of these – the *C. trothae* clade – is clearly not closely related to the remaining *Caesalpinia* s.s. species. This clade consists of African species found in dry forests and thickets from the Horn of Africa, across Tanzania, Botswana, Mozambique, and South

Africa to Namibia. This clade is characterised by a number of diagnostic morphological synapomorphies: they are spiny, multi-branched shrubs with racemes of reddish-pink to whitish-pink flowers; they have distinct pyriform pods, with large, rounded, oblique bases and an acute apex; the bracts have an aristate tip; the leaflets have translucent dots on the lower surface. Species limits within this clade need to be closely re-examined. For example, Brenan (1963, 1967) remarked that the rostrate appendage on the calyx, which distinguishes *C. rostrata*, is also found on some specimens of *C. rubra*. Despite uncertainty about the number of species in this clade, it is clearly phylogenetically, morphologically and geographically distinct meriting recognition as a distinct new genus, here named *Gelrebia*, from the Somali vernacular name for *Caesalpinia trothae* which means camel trap and evidently alludes to the plants highly thorny and impenetrable habit.

For the other two clades from the former *Caesalpinia* s.s., there are no obvious diagnostic morphological synapomorphies. Both clades consist of shrubs or small treelets that are eglandular and generally spiny (except for one species in each clade), and have explosively dehiscent pods with twisting valves. The type species of *Caesalpinia s.s.*, *Caesalpinia brasiliensis*, falls within a clade containing from 1 to 5 species of Caribbean species pollinated by bats, the Central American species *C. pulcherrima* pollinated by butterflies*,* the northern Andean scarlet-flowered species *C. cassioides* with red, laterally-compressed, tubular corollas, likely pollinated by birds, and *C. nipensis,* endemic to the Sierra de Nipe in Cuba, which has a flower morphology and yellow corolla suggestive of bee pollination. The other group, the *C. erianthera* clade, contains only yellow-flowered species, that are found in Madasgascar (*C. madagascariensis*), Ethiopia, Somalia and the Arabian Peninsula (*C. erianthera*), South America (*C. stuckertii*), Mexico (*C. sessilifolia*), and the Caribbean (*C. buchii, C. pauciflora* and *C. rosei*). The *C. erianthera* clade is quite distinct from its sister clade, the combined *Tara* + *Coulteria* clade, which is characterized by distinctive lower cucullate-fimbriate sepals and pods that are both thick and indehiscent (*Tara*), or thin, chartaceous and indehiscent to tardily dehiscent (*Coulteria*). It is clear that the *C. erianthera* clade is more closely related to the combined *Tara* + *Coulteria* clade than it is to the more narrowly circumscribed *Caesalpinia s.s.* clade, such that both clades can no longer be retained within a more inclusive *Caesalpinia s.s.*, and that the *C. erianthera* needs to be recognized as a distinct genus. Within the *C. erianthera* clade, *C. madagascariensis*, endemic to Madagascar, was formerly recognised as the monospecific genus *Denisophytum*. *Denisophytum* is reinstated here with an emended circumscription that includes all species of the *C. erianthera* clade.

The majority of the rest of the unclassified Old World species fall into two main clades, including the *C. decapetala* clade, and a clade containing the monospecific genus *Moullava*, *Caesalpinia welwitschiana* and two species from *Caesalpinia* section *Cinclidocarpus*, which Gagnon & al. (2013, chapter 1) predicted would be closely related to *Moullava.* These two clades consist of lianas and scrambling shrubs, and are distinguished by their distinctive pods, which are different from the other closely related clades of lianas (Fig. 2.2, with liana taxa concentrated in clade G). In the *C. decapetala* clade, the pods are oblong and somewhat laterally compressed, dehiscent, and slightly enlarged and truncate towards the apex, terminating in a sharp beak. In the second clade, despite the uniquely distinctive spicate inflorescences of *Moullava spicata*, all four species have similar rounded, sub-torulose pods, with thickened margins, an exocarp and endocarp that are strongly adnate when dried, and that are indehiscent. It is apparent that both clades merit to be recognized at the generic level, which is achieved by emending the description of *Moullava* to include the description of three additional species, and by reinstating the genus *Biancaea* Todaro (1860), the second oldest legitimate name available for the first clade (see generic descriptions below for more details on the nomenclature of this clade).

2.5.2 Monospecific taxa

With near-complete taxon sampling, it is clear that three species, *Caesalpinia echinata, C. mimosoides* and *C. pearsonii,* do not nest within any of the well resolved clades of the Caesalpinia Group. All six loci were sequenced for these species, with the exception of ITS for *C. mimosoides.* It is perhaps no surprise that the taxonomic placements of these taxa have been problematic in the past because of their unique morphologies and character combinations, and all three species have pods quite unlike any other taxa in the Caesalpinia Group. For example, *C. mimosoides* is a liana found in India and Bangladesh to Thailand, Vietnam, Laos, Myanmar and South-West China, and is quite distinct from other Asian lianas because the stem, calyx and fruits are covered in glandular dots, and it has a distinct falcate, chartaceous, inflated pod. The robust, needle-like trichomes in *C. mimosoides* are also distinct from the more robust and strongly recurved spines in other Asian species of the Caesalpinia Group. These needle-like trichomes in *C. mimosoides* are also present on the inflorescence rachis and pedicels, whereas they are mostly absent from the inflorescences, or only occur sparsely at the base of the inflorescences of other Asian taxa. We propose the new generic name *Hultholia*, after the Cambodian taxonomist Dr. Salvamony Hul Thol, who revised the Asian species of *Caesalpinia* s.l. and the genus *Pterolobium* as part of her doctoral thesis (Vidal & Hul Thol, 1974; 1976; Hul Thol, 1976), and who has made significant contributions to the flora of Laos, Vietnam, and Cambodia.

Similarly, *C. pearsonii* differs from the rest of *Caesalpinia* s.l. primarily by its flattened, circular or semi-circular one-seeded pods, covered in patent red trichomes up to 6mm long. This rarely collected species, endemic to Namibia, has a poorly supported phylogenetic position, despite having sampled all six loci, and is possibly one of the earliest diverging lineages in the Caesalpinia Group. It is thus difficult to determine what is the closest relative to this species, but in the topology of the analyses presented here it shares some close (albeit unsupported) relationship with *Lophocarpinia* and *Haematoxylum,* and *C. pearsonii* is either recoverd as their sister lineage (Fig. 2.2) or as the earliest diverging lineage in Clade 2 (Fig. 2.3A). *Caesalpinia pearsonii* differs from *Lophocarpinia* and *Haematoxylum* by having reduced bipinnate leaves (one pinna pair plus a terminal pinna) rather than the pinnate or bipinnate leaves typical of these latter two genera. In addition, the secondary venation of leaflets of *C. pearsonii* are not visible, whereas in *Haematoxylum* the secondary veins are ascending, and form a sharp angle with the primary vein. Furthermore, the prickles on the stems of *C. pearsonii* are curved and deflexed, compared with the straight armature of *Haematoxylum,* which has spinescent branches. Recurved thorns also occur on the rachis of the inflorescence in *C. pearsonii*, a feature rarely found elsewhere in *Caesalpinia* s.l. Given the phylogenetic position of this taxon and given its morphological distinctiveness, we propose to include this species in a new genus called *Hererolandia*, which is a reference Bolus, who originally described this species as coming from "Hereroland" in Namibia.

The third unplaced taxon, *C. echinata*, also has an unusual morphology. The pods of this species can be thought of as intermediate between those of *Guilandina* and *Caesalpinia* s.s. The patent, sub-woody bristles on the pod valves are reminiscent of *Guilandina* pods, but the fruit is laterally compressed and lunate-falcate with valves that twist upon dehiscence, and the seeds are flattened, not unlike many species of *Caesalpinia* s.s. In contrast to *Caesalpinia* s.s and *Guilandina*, *C. echinata* has a reddish heartwood from which can be extracted a red dye (a quality also found in *C. sappan* and the genus *Haematoxylum*), and forms medium-sized to large trees with upcurved prickles arising from woody protuberances on the trunk and branches. The long-standing unresolved position of *C. echinata* might be due to conflicting phylogenetic relationships amongst analyses, depending on the morphotype sampled. For example, different accessions form a monophyletic species clade in the ITS and *ycf6-psbM* gene trees, but in the other plastid gene trees the multiple accessions of the species of *C. echinata* are paraphyletic or polyphyletic, and their phylogenetic placement in the trees lack posterior probability and bootstrap support. *Caesalpinia echinata* populations have been shown to be strongly differentiated genetically (Cardoso & al., 1998; Lira & al., 2003; Cardoso & al., 2005) and this could reflect known intraspecific morphological variants that occur at different localities along the Brazilian coast (Lewis, 1998; Lima & al., 2002), but which were not all sampled here. Denser sampling and detailed phylogeographical analyses are needed to assess whether morphotypes represent a continuum or a set of discrete units worthy of taxonomic recognition, but regardless, we consider that *C. echinata* should be recognised as a distinct genus based on the evidence presented here. We propose the genus name *Paubrasilia*, based on the common name Pau Brasil, the national tree of Brazil, which has a long history of association with the country.

2.5.3 Problematic relationships because of lack of information

Three areas of the phylogeny remain unclear and warrant further sampling before making taxonomic decisions. While we hypothesize, based on morphology, that nine species from mainland Asia group with *C. crista* and form a clade that is sister to *Pterolobium*, only two of the nine Asian species have been sampled and only four of the eleven *Pterolobium* species are included. We previously referred to this group of nine species as the *C. nuga* clade (Gagnon & al., 2013, chapter 1). If it is consistently resolved as monophyletic with greater taxon sampling, the oldest available generic name for the clade would be *Ticanto* Adanson (1763). It is notable that two of the species from mainland China (*C. caesia* and *C. sinense*) sometimes have a small wing on the fruit resulting in a fruit morphology that is intermediate between the typical samara of *Pterolobium* and the wingless pod of the *Ticanto* clade, suggesting that better sampling and further study are required.

The other problematic taxa are the monospecific genera *Lophocarpinia* and *Stenodrepanum*, two taxa that could potentially be sunk into other genera, but whose placements are currently only weakly supported in the phylogeny. As also found by Nores & al. (2012), *Lophocarpinia* is recovered as sister to *Haematoxylum* (Fig. 2.2), and despite the very distinctive fruit of *Lophocarpinia* (which is lamented and has coarsely serrate wings), Burkart (1944, 1952) proposed that *Lophocarpinia* could be synonymised under *Haematoxylum*, due to their similar vegetative morphology. These are likely indeed sister genera but support for this relationship remains weak, and under that hypothesis, the very distinctive fruits of *Lophocarpinia* could merit generic recognition. Similarly, *Stenodrepanum* and *Hoffmannseggia* are separable only by their fruits, which is more linear, cylindrical, and torulose in *Stenodrepanum*. The reason for the unsupported positions of *Lophocarpinia* and *Stenodrepanum* in our analyses may be because we only had *trnL-trnF* and *matK-3'trnK* sequences for these two taxa and these are the two least informative markers in our study. Sequencing additional loci should provide the support needed to confidently assess their phylogenetic relationships and generic status.

2.5.4 Conclusion and future prospects

Taxonomic classifications should be based on solid evidence from multiple sources, including morphology and well-sampled and resolved molecular phylogenies. Based on the current phylogeny 27 genera are recognized in the Caesalpinia Group. Better data and more complete taxon sampling are required before we can assess with confidence whether members of the 27th lineage, the *Ticanto* clade, here represented by *C. crista* and *C. vernalis*, are reciprocally monophyletic to the well-defined genus *Pterolobium*.

As part of this new generic system for the Caesalpinia Group, we present a key to the identification of genera, descriptions of new, reinstated or expanded genera, new nomenclatural combinations (where we are confident about species affinities and taxonomy, including for *Cenostigma*, *Erythrostemon*, *Libidibia*, *Tara*, *Moullava*) and lists of names associated with each genus, or references to recently published taxonomic accounts (*Arquita*, *Coulteria*, *Hoffmannseggia*, *Pomaria*, *Pterolobium*). *Guilandina* and *Mezoneuron* species names are not listed because they are taxonomically problematic and nomenclaturally complex and species delimitation within these genera requires further taxonomic work. Genera for which no changes are required are included in the key.

2.6 Taxonomic account of the genera of the Caesalpinia Group: key, diagnoses, descriptions, species, synonymy, types

Prior to publication, all types for the species name listed in these 27 groups will be identified, and we will include illustrations with line drawings and photos for each genus.

2.6.1 List of genera, in systematic order

1. *Hererolandia*
2. *Lophocarpinia*
3. *Haematoxylum*
4. *Paubrasilia*
5. *Caesalpinia*
6. *Denisophytum*
7. *Tara*
8. *Coulteria*
9. *Gelrebia*

10. *Hultholia*
11. *Guilandina*
12. *Moullava*
13. *Biancaea*
14. *Pterolobium*
15. *Mezoneuron*
16. *Cordeauxia*
17. *Stuhlmannia*
18. *Cenostigma*
19. *Libidibia*
20. *Balsamocarpon*
21. *Zuccagnia*
22. *Stenodrepanum*
23. *Hoffmannseggia*
24. *Arquita*
25. *Pomaria*
26. *Erythrostemon*
27. *Ticanto*

2.6.2 Key to genera

1a. Leaves pinnate: *2*

2a. Armed shrubs or trees, prickles scattered along the branches, or plant with short branches with modified spiny-tips

3a. Fruit segmented, and with 4 coarsely serrate wings

2. Lophocarpinia

3b. Fruit flat, membranous to papyraceous, oblong to elliptic, dehiscing along the middle of the valves

3. Haematoxylum

2b. Unarmed shrubs or trees: *4*

4a. Sepals persistent: *5*

5a. Fruit cylindrical, thick-walled, bright orange, resinous

20. Balsamocarpon

5b. Fruit small and gall-like and covered in long bristles

21. Zuccagnia

4b. Sepals caducous: *6*

6a. Fruit an oblanceolate to oblong-elliptic pod, sometimes oblique, with valves twisting upon dehiscence

7a. Fruit subligneous, lacking a crest; sepals valvate; stellate indumentum lacking; restricted to Africa and Madagascar

17. Stuhlmannia

7b. Fruit woody, with conspicuously thickened sutures, sometimes with a crest proximally on the adaxial side; sepals imbricate; stellate indumentum often present; restricted to the Neotopics

18. Cenostigma

6b. Fruit an ovoid or elliptic, not oblique, thickened, indehiscent pod: *8*

8a. Fruit elliptic, somewhat thick and fleshy, bright red, rounded at apex, 1 – 2-seeded; leaflets with black, sessile glands on the under-surface; seeds compressed-turgid; sepals imbricate; endemic to the Dominican Republic

19. Libidibia monosperma

8b. Fruit ovoid, apex beaked, 1 – 4-seeded; leaflets with red glands on the lower surface (best seen in fresh specimens); seeds ovoid; sepals valvate; endemic to NE Africa

16. Cordeauxia

1b. Leaves bipinnate: *9*

9a. Leaves with a single terminal pinna:

10a. Plant armed and eglandular; leaves with one pair of pinnae plus a single terminal pinna; fruit circular, clothed with long, patent trichomes, glabrous

1. Hererolandia

10b. Plant unarmed and eglandular, or with glandular trichomes, or black sessile glands; leaves with two to many pairs of pinnae plus a terminal pinna; fruits falcate to oblong-elliptic, lacking long patent trichomes, glabrous to pubescent, sometimes with a stellate indumentum; : *11*

11a. Sepals persistent: *12*

12a. Fruits cylindrical-torulose, slightly falcate

22. Stenodrepanum

12b. Fruits oblong to ovate, not torulose

23. Hoffmannseggia

11b. Sepals caducous: *13*

13a. Stipules linear, persistent; androecium and gynoecium cupped in the lower cucullate sepal; lower lateral petals forming a platform at right angles to the abaxial cucullate sepal; fruits with simple trichomes, glandular trichomes, and plumose and/or stellate trichomes.

25. Pomaria

13b. Stipules caducous; androecium and gynoecium not cupped in lower cucullate sepal; lateral petals not forming a platform at right angles to the abaxial cucullate sepal; fruits glabrous or with simple and/or glandular trichomes, but lacking stellate or plumose trichomes: *14*

14a. Fruits indehiscent; inflorescence a raceme or panicle, often corymbose; leaflets glabrescent, eglandular or with glandular dots parallel to the midvein

19. Libidibia

14b. Fruits dehiscent, often with twisting valves; inflorescence a raceme or panicle, sometimes pyramidal in shape; leaflets glabrescent or with a stellate indumentum, eglandular, with or without dark subepidermal glands, and/or with glandular dots sunken in the margins of the leaflets or parallel to the margin on the abaxial side: *15*

15a. Leaflets alternate, on occasion nearly opposite, with dark subepidermal glands (best seen with a x10 hand lens); stellate indumentum sometimes present on foliage and inflorescence rachis; fruit subligneous to woody, sutures thickened

18. Cenostigma

15b. Leaflets always opposite, without dark subepidermal glands; stellate indumentum never present on foliage or rachis; fruit coriaceous to subligneous, sutures not thickened: *16*

16a. Shrubs or small to medium-sized trees, or occasionally woody-based perennial herbs, (0.5–) 1 – 12 (–20) m tall; flowers yellow, red, pink or orange, sometimes laterally compressed; ovary eglandular or covered in gland-tipped trichomes, that are never dendritic; widespread across low-elevation SDTFs across Mexico, Central America, the Caribbean, and in Caatinga in Brazil, and in patches of dry forests, deserts, yungas-puna transition zones, and chaco-transition forests in Argentina, Bolivia, Chile and Paraguay;

26. Erythrostemon

16b. Small to medium-sized, often decumbent, shrubs, 0.3 – 2.5 m tall; flowers yellow, sometimes all five petals streaked with red markings, never laterally compressed; ovary covered in gland-tipped trichomes, which are sometimes dendritic; occuring on dry slopes of the Andes, mainly in dry inter-Andean valleys in Ecuador, Peru, Bolivia and Argentina;

24. Arquita

9b. Leaves with a terminal pinnae pair: *17*

17a. Plants unarmed: *18*

18a. Fruit thin, flat, oblong-elliptic to elliptic, membranaceous to papyraceous, indehiscent; margin of the lower cucullate sepal pectinate-glandular; flowers unisexual; leaflets eglandular

8. Coulteria

18b. Fruit an oblong-elliptic pod, elastically dehiscent with twisting valves; margin of the lower cucullate sepal entire; flowers bisexual; leaflets eglandular or with red glands: *19*

19a. Flowers nearly actinomorphic; trees, up to 25 tall; leaflets eglandular or with red glands; E Africa (Kenya and Tanzania), and N & NW Madagascar

17. Stuhlmannia

19b. Flowers clearly zygomorphic; shrubs or small trees, up to 5m tall; leaflets eglandular; Cuba or N Madagascar (known only from near Antsiranana): *20*

20a. Fruits laterally compressed; anthers glabrous; endemic to Cuba (near Moa, in the Sierra de Nipe)

5. Caesalpinia nipensis

20b. Fruits inflated and hollow; anthers pubescent; endemic to the northern tip of Madagascar (Orangea peninsula, near Antsiranana)

6. Denisophytum madagascariense

17b. Plants armed: *21*

21a. Trees or erect shrubs: *22*

22a. Fruits indehiscent; lower sepal with a pectinate-fimbriate margin

7. Tara

22b. Fruits dehiscent; lower sepal with an entire margin: *23*

23a. Fruits dehiscing along the middle of the valves, or parallel to the margin, valves not twisting after dehiscence

3. Haematoxylum

23b. Fruits dehiscing along the sutures, valves often twisting after dehiscence: *24*

24a. Fruits armed with woody spines, stems with upturned thorns arising from woody protuberances; flowers yellow, the standard with a conspicuous red blotch on the inner face

4. Paubrasilia

24b. Fruits unarmed, stems with straight to deflexed prickles; flowers yellow, white, pink, red or orange: *25*

25a. Flowers pink-purple to whitish pink; bracts with aristate apex; pods pyriform with rounded, oblique bases; leaflets sometimes with translucent dots on lower surface

9. Gelrebia

25b. Flowers yellow, red, orange or white; bracts lanceolate to linear with an acute to acuminate apex; pods oblong-elliptic, short-stipitate, with a cuneate base; leaflets eglandular: *26*

26a. Flowers orange, red, or white; Central America, the Caribbean and the Northern Andes (Peru to Colombia)

5. Caesalpinia

26b. Flowers yellow, sometimes with red markings on the standard (median petal); Somalia, Ethiopia, Argentina, Paraguay, Mexico, Florida and the Carribean;

6. Denisophytum

21b. Lianas or climbing or trailing shrubs: *27*

27a. Fruits with a wing: *28*

28a. Fruit a samara

14. Pterolobium

28b. Fruit not a samara: *29*

29a. Fruit with a longitudinal wing, 2 mm or more wide along the upper suture; chartaceous, coriaceous or ligneous; Africa and Madagascar and SE Asia across the Malaysian peninsula and archipelago to New Guinea, New Caledonia and Australia), one species endemic to Hawaii

15. Mezoneuron

29b. Fruits with a narrow wing, 2 mm wide or less; coriaceous or ligneous; Southern (principally mainland) China, Myanmar (Burma), N Laos and N Vietnam: *30*

30a. Fruits oblong-elliptic, 4 – 9-seeded

13. Biancaea decapetala

30b. Fruits rhomboid-circular to sub-elliptic, 1-(rarely 2) -seeded

***27. Ticanto** (C. caesia and C. sinense)*

27b. Fruits without a wing: *31*

31a. Plants with glands on the stems, leaf rachis, inflorescence, and fruits; needle-like trichomes on the inflorescence rachis and pedicels

10. Hultholia

31b. Plants eglandular; recurved prickles present on stems, sometimes also present at the base of the inflorescence rachis and pedicels: *32*

32a. Fruit oblong to oblong-elliptic: *33*

33a. Fruit indehiscent, oblong, somewhat fleshy, sub-torulose, with thickened sutures, with a regular width from the base towards the apex; exocarp and endocarp strongly adnate; seeds subglobose

12. Moullava

33b. Fruit dehiscent, oblong to oblong-elliptic, laterally compressed, coriaceous to subligneous, with a smooth, regular outer surface, the sutures not conspicuous, base often much narrower than the truncate apex; exocarp and endocarp separate easily; seeds flattened to ellipsoidal

13. Biancaea

32b. Fruit broadly elliptic to circular: *34.*

34a. Flowers unisexual, segregated in female and male racemes; fruits usually covered in spinescent bristles; seeds globose, with parallel fracture lines concentric with the small apical hilum

11. Guilandina

34b. Flowers bisexual, in racemes; fruits always glabrous; seeds laterally compressed, smooth, without fracture lines

27. Ticanto

2.6.3 Generic descriptions

1. ***Hererolandia*** E. Gagnon & G.P. Lewis, **gen. nov.**

Diagnosis: *Hererolandia* is phylogenetically closely related to *Lophocarpinia* (from Argentina and Paraguay), but differs in having curved, deflexed prickles scattered along the branches (vs. straight, conical spines, either scattered along the branches or at the tips of short, lateral branches), bipinnate leaves with one pair of pinnae and a single terminal pinna (vs. paripinnate leaves with 2 – 3 pairs of leaflets), and leaflets elliptic to oblong-elliptic (vs. leaflets obovate or elliptic-orbicular), with the main vein prominent but the secondary venation not visible (vs. the centric main vein and the secondary veins visible, the secondaries ascending, and forming a sharp angle with the primary vein). The most distinctive feature of *Hererolandia* is the thinly woody, laterally compressed, almost circular to strongly sickle-shaped pods, convered in robust trichomes up to 6 mm long, these usually 1-seeded (vs. a segmented, falcate fruit, with 4 coarsely serrate wings, and usually more than 1 seed).

Type species: *Hererolandia pearsonii* (L. Bolus) E. Gagnon & G.P. Lewis

Description: A **multi-stemmed shrub** up to 2 m, but usually less than a 1 m tall, armed with curved, deflexed, 7 mm long prickles scattered along the branches. **Bark** white or brown. Stems terete and slightly sinuous, with a fine silvery indumentum covering the young twigs, older stems glabrescent. **Stipules** not seen. **Leaves** alternate, bipinnate, with one pair of pinnae and a single terminal pinna, 7 – 17 mm long, sessile, sometimes borne on short woody brachyblasts, and subtended by a pair of prickles. **Leaflets** opposite, 4 – 9 pairs per pinna, eglandular, covered in a fine silvery pubescence, 5 – 6.5 x 2.5 – 3 mm, elliptic to oblong-elliptic, apex obtuse, with an acuminate tip, main vein prominent, secondary venation not visible. **Inflorescence** a short raceme of pedicellate, bisexual flowers, about 5 cm long, usually borne on brachyblasts, covered in a fine silvery pubescence, with prickles along the inflorescence rachis; bracts about 2 – 3 x 1.5 mm, ovate, apex acute, caducous. **Corolla** zygomorphic, yellow; **calyx** with a short hypanthium, and 5 free sepals, c. 3 – 5 mm long, covered in a fine white pubescence, sepals caducous, but hypanthium persistent as a ring around the stipe of the fruit; **petals** 5, free, c. 6 –

9 mm long, obovate, pubescent at base on inner surface. **Stamens** 10, free, up to 10 mm long, eglandular, pubescent on the lower half. **Ovary** pubescent; stigma a fringed chamber. **Fruit** a thinly woody, laterally compressed, almost circular to strongly sickle-shaped pod, c. 2 – 2.3 x 1 – 1.5 cm, with a fine pubescence and covered in robust trichomes up to 6 mm long, usually 1-seeded. **Seeds** laterally compressed, about 6 – 8 mm long.

Hererolandia pearsonii (L. Bolus) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia pearsonii L. Bolus, in Annals of the Bolus Herbarium 3: 4 (1920). Type: Namibia, Ababes, breccia banks of Tsondab River below farm, 29 December 1915, *Pearson* 9162 (holotype: BOL; isotypes: K!, GRA, NBG, PRE).

Geographic distribution: A monospecific genus endemic to Namibia, in the great Escarpment.

Habitat: semi-desert and desert areas, on stony, sandy soils.

Etymology: Semiarid Hereroland, a geographic region of eastern Namibia, is the type locality of *H. pearsonii*. The proud Herero people who inhabit the region are nomadic cattle herders and it is they and their region that are honoured in the name proposed for this monospecific genus that is endemic to a restricted area of Namibia.

References: Bolus (1920); Roux (2003); Curtis & Mannheimer (2005: 227).

2. *Lophocarpinia* Burkart, in Darwiniana 11: 256 (1957).

Type species: *Lophocarpinia aculeatifolia* (Burkart) Burkart (*Cenostigma? aculeatifolium* Burkart).

Description: **Shrub** 0.5 (–3) m tall, armed with straight, conical, 2 – 5 mm long spines, scattered along the branches; leaves and inflorescences crowded on brachyblasts; branches glabrous, reddish, sometimes modified into short, lateral, spine-tipped branchlets. **Stipules**

acuminate, caducous. **Leaves** alternate, paripinnate, 5 – 10 mm long, with 2 – 3 pairs of leaflets, obovate or elliptic-orbicular, 4 – 7 x 2 – 2.4 mm, finely pubescent, eglandular, with a small pair of spines at the insertions of the leaflets. **Inflorescences** short, corymbiform, pubescent racemes, each with 3 – 6 bisexual flowers; bracts small, caducous. **Corolla** zygomorphic, yellow to yellow-orange, 1 – 1.5 cm long; **calyx** with a turbinate, fleshy hypanthium, and 5 oblong, pubescent, caducous sepals, lower sepal cucullate and covering the other 4 sepals in bud, embracing the androecium and gynoecium at anthesis; **petals** 5, free, the median petal differentiated from the rest by a fleshy claw and wavy blade edges, pubescent. **Stamens** 10, free, filaments pubescent. **Ovary** glabrous; stigma apical, concave. **Fruit** segmented, falcate, with 4 coarsely serrate wings. **Seed**s ellipsoid to reniform, smooth.

Geographic distribution: A monospecific genus restricted to Argentina and Paraguay (possibly also occurring in Mato Gross do Sul, Brazil, pers. comm. H. C. de Lima).

Habitat: seasonally dry tropical to subtropical woodland, including Chaco forests.

Etymology: From *lopho-* (Greek: combed or crested) and *carpos* (Greek: fruit), the fruit has 4 crested wings, the ending -inia signifies a close relationship with *Caesalpinia*

Lophocarpinia aculeatifolia (Burkart) Burkart, in Darwiniana 11(2): 257 (1957).
Cenostigma ? aculeatifolium Burkart, in Darwiniana 6: 483, f. 2 – 3 (1944). Type: Paraguay, Chaco boreal, kilómetro 220 del sector López de Filippis, Oct. 1938, *T. Rojas* 8441 (holotype SI).

References: Burkart (1957); Ulibarri (2008); Nores & al. (2012).

3. *Haematoxylum* L., in Sp. Pl. 1: 384 (1753).

Type species: *Haematoxylum campechianum* L.

Haematoxylon L. (1764), orthographic variant.
Cymbosepalum Baker (1895).

Description: Multi-stemmed shrubs, up to 3 m, **to medium-sized or large trees** (from 3 – 15 m), armed both with straight conical spines (between 0.5 – 1.5 cm long), scattered along the younger branches, as well as with modified, short, lateral, spine-tipped branchlets, mature trees with conspicuously fluted trunks, shrubs often with ribbed branches, young stems reddish brown to grey, glabrous to pubescent, eglandular (or with stalked glands in *H. dinteri*). **Leaves** alternate, pinnate or bipinnate (both can be present on the same individual in some species), glabrous to pubescent, eglandular, 1 – 10 cm long; pinnate leaves with 2 – 6 pairs of leaflets, 2.5 – 35 x 3 – 30 mm, glabrous to slightly pubescent, eglandular; bipinnate leaves with 1 – 3 pairs of pinnae, each pinna with 3 – 5 pairs of leaflets, 5 – 11 x 2 – 4.5 mm. **Leaflets** in opposite pairs, obcordate to obovate, apex emarginate to obtuse, base cuneate to attenuate (occasionally obtuse), short-petiolulate; primary vein centric, secondary veins ascending, and forming a sharp angle with the primary vein. **Inflorescences** terminal or axillary racemes or panicles of pedicellate, bisexual flowers; rachis and pedicels unarmed, glabrous to pubescent, eglandular or glandular. **Corolla** actinomorphic to zygomorphic, yellow to pale yellow or white; **calyx** comprising a hypanthium and 5 free sepals, that are c. 6 – 7 mm long, glabrous to pubescent, eglandular or glandular, the lower sepal cucullate and slightly covering the other 4 in bud, sepals caducous, hypanthium persisting in fruit, forming a calyx ring; **petals** 5, free, imbricate, obovate to oblanceolate, 4 – 10 mm long. **Stamens** 10, free, filaments pubescent, particularly on the lower half. **Ovary** glabrous to pubescent. **Fruit** flattened, membranaceous to chartaceous, oblong to fusiform (occasionally falcate), apex rounded to obtuse, base acute, dehiscing along the middle of the valves, or near the margin of the fruit, but never on the margins. 10 – 50 x 4 – 15 mm, 1 – 3-seeded. **Seeds** oblong to reniform, flattened, 6 – 12 x 3.8 – 5 mm.

Geographical distribution: *Haematoxylum* comprises five species: two in Central America (Salvador to Costa Rica), Mexico, South America (Colombia and Venezuela) and the Caribbean (perhaps introduced), two endemic to Mexico and one in South Africa (Namibia).

Habitat: deserts, seasonally dry tropical semi-deciduous scrub and thorn scrub, sandy river beds and dry rocky hillsides. One species (*H. campechianum*) is known to grow in marshy areas, frequently inundated by rivers.

Etymology: From *haemato-* (Greek: bloody) and *xylon* (Greek: wood), alluding to the blood-red heartwood of *H. campechianum* L. which produces a brilliant red dye.

Notes: There is a key to species by Cruz Durán & Souza, in Novon 23(1): 31 – 36 (2014). While we are not changing the delimitation of this genus, we list here all the species and their types, as they have never before been presented in a single work.

Haematoxylum brasiletto H. Karst., in Fl. Columb. 2: 27 (1862). Type: Habitat regions calidas et aridas montanas ad pedes Andium Colubiae septentrionalis, ad incolis "Brasil" vel "Brasiletto" dicta.
Haematoxylum boreale S. Watson, in Proc. Amer. Acad. Arts & Sci. 21: 426 (1886). Type: Mexico, SW Chihuahua, Sierra Madre, Hacienda San Miguel, 1 mile from Batopilas, 1885, *E. Palmer* 247.

Haematoxylum calakmulense Cruz Durán & M. Sousa, in Novon 23(1): 32 – 35 f.1 (2014). Type: Mexico, Quintana Roo: Mpio. Othón P. Blanco, camino al poblado de Reforma, 17 March 2006 (fl., fr.), *J. Chavelas & M. Chavelas* 6276 (holotype, MEXU; isotypes FCME, MEXU, MO).

Haematoxylum campechianum L., in Sp. Pl. 1: 384 (1753). Type: Mexico, Habitat in Campeche Americes (Lectotype: LINN-538.1, designated by Howard & Staples, J. Arnold Arbor. 64: 529 (1983)).
Cymbosepalum baronii Baker, in Bull. Misc. Inform. Kew 1895: 103 (1895). Type: Madagascar, *Baron* 6422 (holotype K!).

Haematoxylum dinteri Harms, in Repert. Spec. Nov. Regni Veg. 12: 555 (1913). Type: SW Africa, "Gross-Namaland: Inachab-Berg", Nov. 1897. *Dinter* 1169 ("original!").

Haematoxylum africanum Stephens, in Transactions of the Royal Society of South Africa 3: 255. (1913). Type: SW Africa, Great Namaqualand, among rocks near Holoog, Feb. 1909, *Pearson* 4134.

Haematoxylum sousanum Cruz Durán & J. Jiménez Ram., in Novon 18(1): 26 (2008). Type: Mexico, Guerrero: Mpio. Atenango del Río, ca. 3.16 km al NO de Atenango del Río, 18°06′43.7″N, 99°07′14.2″W, 25 September 2003, *A. A. Rivas* 65 (holotype FCME, isotype MO).

References: Standley & Steyemark (1946); Ross (1977:122 – 114); Roux (2003); Curtis & Mannheimer (2005: 215); Durán & Ramírez (2008); Barreto Valdes (2013); Durán & Sousa (2014).

4. ***Paubrasilia*** E. Gagnon, H.C. Lima & G.P. Lewis, **gen. nov.**

Diagnosis: *Paubrasilia* is closely related to *Caesalpinia*, but differs in habit, as the new genus consists of medium-sized to large trees, 5 –15 m+ tall, armed with small to large upturned prickles, these usually arising from woody protuberances (vs. shrubs or small to medium sized trees, usually 1 – 6 m tall, unarmed or armed with curved deflexed prickles, these either occurring in pairs at the base of leaves, or scattered along the branches (or both), or on woody protuberances sometimes present at the base of trunks). *Paubrasilia* also differs from *Caesalpinia* by having pinnae with consistently alternate leaflets (vs. pinnae with opposite to alternate leaflets), yellow flowers (the median petal with a blood red central blotch) with a melittophilous pollination system (vs. flowers that are more variable in colour: yellow, white, red, orange or green) and with a wider range of pollination systems (including mellittophyly, ornitophily, psychophily and chirophily), and a spiny, woody, finely pubescent, sub-lunate, 1 – 2-seeded pod (vs. an unarmed, glabrous oblong-elliptic, generally 3 – 7-seeded pod, with a marcescent style forming an acute apex and).

Type species: *Paubrasilia echinata* (Lam.) E. Gagnon, H.C. Lima & G.P. Lewis

Description: **Medium sized to large trees**, 5 – 15m+ tall, armed with small to large upturned prickles, these usually arising from woody protuberances, 1 – 20 mm long (the prickles are often sparse or lacking on more mature specimens and larger, older branches). **Bark** chestnut brown to almost black with greyish pustular lenticels, flaking in large woody plates; heartwood red, with the trunk exuding a red sap when injured. **Stipules** lanceloate, acute to acuminate, caducous. **Leaves** pari-bipinnate; petiole and rachis finely tomentose; pinnae alternate, the terminal pair opposite to subopposite, with 1 – 20 pairs of pinnae per leaf. **Leaflets** alternate, with 2 – 19 leaflets per pinna (generally the number of leaflets is inversely proportional to their size), 0.9 – 5 x 0.5 – 3.6 cm (although some specimens have leaflets up to 12 cm long), leaflet blades coriaceous, broadly oblong to subrhombic, apex rounded, obtuse or emarginate, base asymmetric, eglandular, glabrous, midvein excentric, secondary veins brochidodromous. **Inflorescence** a terminal, or occasionally axillary, finely tomentose raceme or panicle, with c. 15 – 40 flowers; bracts broadly ovate-triangular, apex acute to acuminate, less than 1 mm long, pubescent, caducous. **Corolla** zygomorphic, bright yellow, the median petal with a blood-red blotch on the inner face,; **calyx** a tomentose hypanthium with 5 sepals, that are c. 5 – 9 mm long, the lowest sepal cucullate, covering the other 4 in bud, all sepals caducous but the hypanthium persisting as a free ring around the pedicel as the pod matures; **petals** 5, free, c. 11 – 15 x 4 – 10 mm, all petals eglandular, broadly-obovate to slightly spathulate, the petal claws pubescent. **Stamens** 10, free, 7 – 9 mm long, eglandular, densely pubescent on lower half. **Ovary** pubescent with small spines intermixed; stigma a subterminal fringed-chamber. **Fruit** a spiny, finely pubescent, sub-lunate, woody, 5.5 – 7.3 x 1.9 – 2.6 cm, elastically dehiscent pod with twisting valves, 1 – 2-seeded. **Seeds** laterally compressed, ovate-obovate.

Geographic distribution: A monospecific genus endemic to Eastern Brazil, in the states of Pernambuco, Bahia, Espirito Santo and Rio de Janeiro. Widely cultivated in Brazil as an ornamental street or park tree, and sometimes in plantations.

Habitat: dry coastal cactus scrub with rocky outgroups, inland in Mata Atlantica, and in tall restinga on well-drained sandy soil.

Etymology: “Pau Brasil” is the national tree of Brazil, and has long been associated with the history of the country. Its red sap was once used for dying cotton and cloth and its wood is much prized for the manufacture of high quality violin bows. Originally described as *Caesalpinia echinata* by Lamarck in 1785, it is appropriate that this phylogenetically isolated taxon should be placed in its own monospecific genus and a Latinization of the well-known and much used common name of the plant recognises the importance of the species to Brazil. For a detailed account of this iconic species refer to Pau Brasil by E. Bueno [et al.], São Paulo, Axis Mundi (2002).

Paubrasilia echinata (Lam.) E. Gagnon, H.C. Lima & G.P. Lewis, **comb. nov.**
Caesalpinia echinata Lam. Encycl. Meth. Bot. 1:461 (1785). Type: Brazil (holotype P, n.v.)
Guilandina echinata (Lam.) Spreng., Syst. 2: 327 (1825).
Caesalpinia vesicaria Vell., Fl. Flum.: 172 (1825), Ic. 4. Tab. 89 (1835). (“*vessicaria*”), non L. (1753).
Caesalpinia obliqua Vogel in Linnaea 11:407 (1837). Type: Brazil, *Sellow* s.n. (holotype ? B †)

References: Lewis (1998: 152-158); Bueno (2002); Cardoso & al. (2005).

5. ***Caesalpinia*** L. (sensu stricto), Sp. Pl. 1: 380 (1753), emend E. Gagnon & G.P. Lewis

Diagnosis: *Caesalpinia* is closely related to *Guilandina*, but differs in habit, as it consists of armed shrubs and small trees (vs. armed lianas and scrambling/trailing shrubs). It also differs in having inflorescences consisting of racemes of bisexual flowers (vs. inflorescences racemes of unisexual flowers), sepals that are imbricate in bud, with a pronounced lower cucullate sepal (vs. sepals valvate in bud), zygomorphic corollas that are variable in color (yellow, white, red, orange or green), with petals extending well beyond the sepals (vs. zygomorphic to sub-actinomorphic, yellow corollas, with petals barely extending beyond the sepals), coriaceous, oblong-elliptic to linear, laterally compressed, glabrous pods(vs. oblong-elliptic inflated pods, usually armed with 5 – 10 mm long spinescent bristles), and obovoid, laterally compressed seeds (vs. obovoid to globular seeds).

Type species: *Caesalpinia brasiliensis* L.

Poinciana L., in part (1753).
Brasilettia (DC.) Kuntze (1891), non sensu Britton & Rose (1930).

Description: Shrubs or small trees, usually 1 – 6 m tall, armed with curved deflexed prickles (*C. nipensis* is unarmed) these either occurring in pairs at the base of leaves, or scattered along the branches (or both), or on woody protuberances sometimes present at the base of trunks and stems; young branches terete, glabrous and eglandular. **Stipules** not seen**. Leaves** alternate, pari-bipinnate (without a single terminal pinna), c. 4 – 30 cm long, unarmed, or sometimes with a pair of prickles at the insertion of the pinnae on the leaf rachis, sometimes also at the insertions of the leaflets on the pinnae rachis; pinnae opposite, in (1–) 2 – 6 pairs per leaf. **Leaflets** alternate to opposite, in 3 – 13 pairs per pinna, short-petiolulate, blades suborbicular, obovate or elliptic, apex mucronate, rounded or emarginate, base cuneiform, rounded or oblique; main vein centric, secondary veins reticulate. **Inflorescence** a terminal or axillary raceme or panicle, c. 5 – 37 cm long, with pedicellate, bisexual flowers, unarmed; bracts lanceolate or ovate, apex acute to acuminate, caducous. **Corolla** zygomorphic, variable in colour (yellow, white, red, orange or green) and shape (related to different pollination systems: bees, butterflies, birds and bats), c. 13 – 25 mm long; **calyx** comprising a hypanthium with 5 sepals, that are each c. 7 – 17 mm long, glabrous to occasionally finely puberulous, always eglandular, the lower sepal strongly cucullate and covering the other 4 sepals in bud, all sepals caducous, but hypanthium persistent as a free ring around the pedicel as the fruit matures; **petals** 5, free. **Stamens** 10, free, c. 10 – 65 mm long, the filaments pubescent, eglandular. **Ovary** glabrous and eglandular. **Fruit** a wingless, unarmed, coriaceous, glabrous, eglandular, oblong-elliptic, or linear pod, with a marcescent style forming an acute apex, c. 34 – 120 x 7 – 26 mm, explosively dehiscent, with twisting valves, 3 – 7-seeded. **Seeds** laterally compressed, obovate, up to 10 mm in diameter.

Geographic distribution: *Caesalpinia* sensu stricto is here reduced to a genus of approximately nine species (a detailed revision and full synonymy of the genus remains to be done). One species (*C. cassioides*) occurs in the Northern Andes from Peru to Colombia, one (*C.pulcherrima*) in Central America (native in Mexico and Guatemala), two occur in the

Caribbean (one, *C. nipensis*, endemic to Cuba, the other widely distributed and possibly consisting of six species, all of which are listed below). *Caesalpinia pulcherrima* is a widely cultivated ornamental plant across the tropics. It includes red, orange and pure yellow flower forms and cultivated specimens are most often unarmed and lack bristles (unlike wild specimens which are armed and bristly).

Habitat: seasonally dry tropical woodland, coastal thicket, bushland and thorn scrub, dry plains and riparian woodland, on limestone or sandstone soils.

Etymology: Named for Andrea Cesalpino (1519–1603), Italian naturalist, botanical collector, systematist and philosopher, physician to Pope Clement VIII, professor of medicine and botany in Pisa and Rome.

Caesalpinia anacantha Urb., in Ark. Bot. 20A(5): 11 (1926). Type: Haiti, Montagnes du Trou d`Eau in Morne à Cabrits, *Ekman* H986 (holotype S, isotype NY!, US!)

Caesalpinia bahamensis Lam., in Encycl. Méth., Bot. 1(2): 461. 1785. Type: based on Catesby's plate, vol. 2, pl. 51.

Caesalpinia reticulata Britton, in Bull. New York Bot. Gard. 4(13): 118 (1906). Type: Inagua, *Nash & Taylor* 1012.

Caesalpinia rugeliana Urb., in Symb. Antill. 2(2): 278 (1900). Type: Cuba, Wright 2364 (syntype); prope Matanzas, ad Punta Brava, *Rugel* 621 (hb. Griseb., syntype).

Caesalpinia bahamensis subsp. *rugeliana* (Urb.) Borhidi, in Acta Botanica Academiae Scientiarum Hungaricae 22: 300 (1977).

Caesalpinia barahonensis Urb., in Symb. Antill. 7(4): 509 (1913). Type: Santo Domingo, prov. Barahina, prope Barahona, *Fuertes* 285.

Caesalpinia brasiliensis L., in Sp. Pl. 1:380 (1753). Type: "Habitat in Jamaicae, Carolinae collibus" RCN: 2996 (Lectotype chosen by Lewis & Reveal in Jarvis et al., Regnum Veg. 127:

28. 1993: [icon] “*Caesalpinia polyphylla, aculeis horrida*” in Plumier, Codex Boerhaavianus (University Library Groningen).

Caesalpinia cassioides Willd., in Enumeratio Plantarum Horti Botanici Berolinensis, 444 (1809). Type: “in America meridonali”,
Caesalpinia andreana Micheli, in J. Bot. (Morot) 6: 193. 1892. Type: “N. Gr. [Colombia] frequens ad flumen S. Jorge in valle Cauca”, Apr. 1876, *E. André* 2914.
Caesalpinia bicolor C.H. Wright, in Bull. Misc. Inf. Kew 1896: 22 – 23. 1896. Type: Peru, Chachapoyas, *Lobb* s.n.; Vitor, *Maclean* s.n.; Colombia, Patia valley and Magdalena valley, near Garzon, *R.B. White* 11 (syntypes).
Caesalpinia cassioides var. *pardoana* (Harms) J.F. Macbr., in Publ. Field Mus. Nat. Hist., Bot. Series 13(3/1): 191 (1943).
Caesalpinia insignis (Kunth) Spreng., in Syst. Veg., ed. 16, 2: 344 (1825).
Caesalpinia pardoana Harms, in Bot. Jahrb. 42(1): 92 – 94 (1908). Type: Peru, prope Caraz in Dep. Ancachs, June 1903, *Weberbauer* 3258.
Poinciana insignis Kunth, in Nov. Gen. et Sp. Pl. 6: 333 (1823[1824]). Type: “ad confluentem fluminis Amazonum et Chinchipes (Provincia Jaen de Bracamoros)”, plus ref. therein to *Poinciana insignis* in Pl. Legum.: 147, t. 44.

Caesalpinia monensis Britton, in N.L. Britton & P. Wilson, Sci. Surv. Porto Rico & Virgin Islands 5: 377 (1924). Type: Puerto Rico, Mona Island, on limestone plateau. No collector or number cited in the protologue.

Caesalpinia nipensis Urb., in Symbolae Antillanae seu Fundamenta Florae Indiae Occidentalis 9(4): 444–445 (1928). Type: Cuba, Prov. Oriente, Sierra de Nipe, at the so called Bio path. 27 April 1919, *Ekman* 9572. (holotype S, isotype NY).
Poincianella nipensis (Urb.) Britton & Rose, in N. Amer. Fl. 23(5): 335 (1930).

Caesalpinia pulcherrima (L.) Sw., in Observ. Bot. Pl. Ind. Occ.: 166 (1791).

Poinciana pulcherrima L., in Sp. Pl. 1: 380 (1753). Type:'Frutex pavonius, Crista pavonis' Breynius, Exot. Pl. Cent., 61, t. 22 (1678), fide Roti-Michelozzi in Webbia 13: 214 (1957). From India calidiore, *Linnaeus* 529/1 (LINN).

Poinciana bijuga Lour., in Flora Cochinchinensis 1: 260 (1790). Type: "agrestis in orâ Africae Orientali". *Crista pavonis*. Rumph. 1. 6. c. 24. tab. 20. Forsk. Arab. pag. 86. *Poinciana foliis duplicato-pnnatis, foliolis oppositis, oblongis, caule inermi.* Hort. Cliff. pag. 158.

Poinciana elata Lour., in Flora Cochinchinensis 1: 261 (1790). Type: "in Sylvis Cochinchinae".

Caesalpinia secundiflora Urb. , in Ark. Bot. 21A(5): 92 (1927). Type: Haiti, Ile de la Tortue, in coastal thickets at plage des Coquillages. 11 June 1927, *Ekman* H-4278. (holotype S, isotype NY!, US!)

References: Britton & Rose (1930); MacBride (1943: 191, 194 – 195); Ulibarri (1996); Barreto Valdes (2013).

6. *Denisophytum* R. Vig., in Notul. Syst. (Paris) 13(4): 349 (1948), emend E. Gagnon & G.P. Lewis

Diagnosis: *Denisophytum* is phylogenetically closely related to *Tara*, but differs in having flowers with a lower cucullate sepal with an entire margin (vs. a lower cucullate sepal with a pectinate margin), and in having dehiscent, coriaceous, laterally compressed (except for *D. madagascariense* which has inflated fruits*)* pods (vs. indehiscent, somewhat fleshy, coriaceous pods that are slightly turgid). Morphologically, species of *Denisophytum* are most likely to be confused with those of *Caesalpinia* s.s., but no reliable synapomorphy has been found to unambiguously differentiate these two genera. The corolla of *Denisophytum* species is consistently yellow and flowers are bee pollinated, whereas *Caesalpinia* s.s. species display a wide range of flower colour (yellow, orange, red, pink and white) and pollination syndromes (chirophily, ornitophily, psychophily and mellitophily).

Type species: *Denisophytum madagascariense* R. Vig.

Description: **Shrubs to small trees**, 0.5 – 2(–5) m tall, armed with straight or curved, deflexed prickles, these scattered along the branches and also found in pairs at the petiole base (*D. madagascariense* is unarmed); young twigs glabrous to pubescent, eglandular. **Stipules** either minute or foliaceous and conspicuous, caducous (persistent in *D. stuckertii*). **Leaves** alternate, pari-bipinnate (without a single terminal pinna); petiole and rachis glabrous and eglandular, with membranaceous or spinulose stipels at the insertions of pinnae on the leaf rachis, occasionally also at the insertion of the leaflets on the pinnae; pinnae opposite, in 1 – 6 pairs per leaf. **Leaflets** opposite, in 2 – 10 (–11) pairs per pinna, elliptic, obovate to orbicular, with a rounded, acuminate or emarginate apex, c. 2 – 25 x 3 – 12 mm, leaflet blades glabrous to pubescent, eglandular. **Inflorescence** a terminal or axillary raceme, with pedicellate, bisexual flowers; bracts caducous (acuminate and filiform in *D. stuckertii*). **Corolla** zygomorphic, yellow (the median petal sometimes with red markings on the inner face of the blade); **calyx** a short hypanthium with 5 sepals that are c. 4 – 10 mm long, eglandular, glabrous to finely pubescent, lower sepal cucullate and covering the other 4 sepals in bud, all sepals caducous, leaving a persistent free hypanthium ring on the pedicel as the fruit develops; **petals** 5, free, c. 5 – 10 mm long; obovate, petal claw almost absent (present in *D. madagascariense*). **Stamens** 10, free, filaments pubescent and eglandular (8 – 11 mm long in *D. madagascariense*), anthers dorsifixed, glabrous to pubescent. **Ovary** glabrous; **Fruits** coriaceous, oblong-elliptic, laterally compressed (but inflated in *D. madagascariense*), glabrous, eglandular pods with a tapering, sharp beak, 18 – 49 x 5 – 15 mm, elastically dehiscent, with twisting valves. **Seeds** ovoid, laterally compressed.

Geographical distribution: *Denisophytum* comprises nine taxa in eight species, found across North America, South America and in Africa. Three species are distributed in Mexico, Florida, and the Caribbean, one species is endemic to Paraguay and Argentina, one is endemic to northern Madagascar, and the other three occur in northern Kenya, in Somalia and Arabia. A revision and evaluation of species limits is needed in this group.

Habitat: low deciduous woodland or scrubland, also in open pineland or coastal plains and foothills. Species in Madagascar and Africa grow in limestone soils.

Etymology: There is no indication of the etymology of *Denisophytum* in the posthumous publication of the generic name. Nevertheless, it is quite likely that the author, René Viguier, had intended to honour his friend and collaborator, Marcel Denis, a botanist with expertise in the genus *Euphorbia* in Madagascar. Sadly, M. Denis passed away prematurely at the age of 33 in 1929 (Allorge & Allorge, 1930).

Notes: *Denisophytum bessac* is based on depauperate material and is of dubious status (Thulin, 2008, flora of Somalia).

Denisophytum bessac (Chiov.) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia bessac Chiov. in Flora Somala 1: 156 (1929). Type: Somalia, Uebi, Aug. 1891, *Robecchi-Bricchetti* 622 (FI).

Denisophytum buchii (Urb.) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia buchii Urb., in Symb. Antill. 7(4):510 (1913). Type: Haiti, "inter Gonaïves et Grosmorne ad Perou", *Buch* 322.

Denisophytum erianthera (Chiov.) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia erianthera Chiov., in Fl. Somala 1: 155 (1929).Types: Somalia, from Obbia to Wuarandi, Aug. 1891, *Robecchi-Bricchetti* 534 (syntype FI, fragments K!); and Boscaglia between Attod and Doldobscio, Apr. 1924, *Puccioni & Stefanini* 450 (syntype FI).

Denisophytum erianthera* var. *erianthera

Denisophytum erianthera* var. *pubescens (Brenan) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia erianthera var. *pubescens* Brenan, in Kew Bull. 17(2): 203 (1963). Type: Kenya, Northern Frontier Province, Banessa-Ramu, 23 May 1952, *Gillett* 13274 (holotype K!, isotype EA).

Denisophytum madagascariense R. Vig, in Notul. Syst. (Paris) 13(4): 349 (1949). Type: Madagascar, Loky R. basin, *Perrier de la Bâthie* 4147 (holotype P).

Caesalpinia madagascariensis (R. Vig.) Senesse, in Bull. Mus. Nat. Hist. Nat., B, Adansonia. 10(1): 79 (1988).

Caesalpinia antsiranensis Capuron, Adansonia, sér. 2, 7: 203 (1967). Type: Madagascar, NE of Diego Suarez [Antsiranana], Orangea, *Capuron* 22990-SF (holotype P).

Denisophytum pauciflora (Griseb.) E. Gagnon & G.P. Lewis, **comb. nov.**
Libidibia pauciflora Griseb., in Cat. Pl. Cub.: 78 (1866), (as "Lebidibia"). Type: Cuba or. et occ., *Wright* 2361.
Poinciana pauciflora (Griseb.) Small, in Fl. SE United States: 591(1903).
Caesalpinia pauciflora (Griseb.) C. Wright ex Sauvalle, in Anal. Acad. Cienc. Med. Habana 5: 404 (1868 [1869]).

Denisophytum rosei (Urb.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia rosei Urb., in Repert. Sp. Nov. Regni Veg. 15: 314 (1918). Type: Santo Domingo prope Azua, *Rose, Fitch & Russell* 3861.

Denisophytum sessilifolia (S. Watson) E. Gagnon & G.P. Lewis, **comb. nov.** *Caesalpinia sessilifolia* S. Watson, in Proc. Amer. Acad. Arts and Sci. 21: 450 (1886). Types: Mexico, Bolson de Mapimi, 10 May 1847, *Gregg* s.n. (syntype NY); Mexico, Coahuila, on hills and mesas about Jumulco, May 1885, *Pringle* 202 (syntypes BR, CAS, CORD!, E, F, GH, GOET, JE, K!, MO, PH, SI!, US).
Poinciana sessilifolia (S. Watson) Rose, in Contribs. U. S. Nat. Herb. 13(9): 303 (1911).

Denisophytum stuckertii (Hassl.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia stuckertii Hassl., in Repert. Sp. Nov. Reg. Veg. 12: 201 (1913). Type: Argentina, Prov. Tucuman, Dept. Bunyacu: prope Cañada Alegre, 5 January 1900, *Stuckert* 21276 (? holotype SI).
Caesalpinia herzogii Harms, in Meded. Rijks-Herb. 27: 38 (1915). Type: Gran Chaco: near Camoteras, Nov. 1910, *Herzog* 1077 (? holotype L).
Caesalpinia stuckertii var. *robusta* Hassl., in Repert. Sp. Nov. Reg. Veg.12: 202 (1913). Type: Argentina, Prov. Tucuman, Depto. Bunyacu: Cañada Alegre, 31 December 1908, *Stuckert* 19726 (? holotype SI).

References: Britton & Rose (1930); Burkart (1936: 84- – 86); Viguier (1948); Roti-Michelozzi, G. (1957); Brenan (1967); Capuron (1967); Thulin (1983: 16 –18; 1993: 344 – 347); Ulibarri (1996); Du Puy & Rabevohitra (2002); Barreto Valdes (2013).

7. *Tara* Molina, in Saggio Chili 283 (1789), emend E. Gagnon & G.P. Lewis

Diagnosis: *Tara* differs from closely related *Coulteria* in having inflorescences of racemes and panicles with bisexual flowers (vs. inflorescences of racemes with unisexual flowers), and in indehiscent, laterally compressed, oblong, straight, slightly turgid and somewhat fleshy, coriaceous, sessile pods (vs. membranaceous to papyraceous, laterally-compressed, oblong to elliptic (occasionally suborbicular) pods, with a stipe ca. 4 – 13 mm long), and ellipsoid seeds (vs. ovate-orbicular to sub-quadrate, compressed seeds).

Type species: *Tara tinctoria* Molina = *Tara spinosa* (Molina) Britton & Rose

Coulteria Kunth (1824), in large part (excluding *C. mollis* Kunth).
Nicarago Britton & Rose (1930).
Russellodendron Britton & Rose (1930).

Description: Shrubs or trees, 3 – 5 (– 8) m tall, armed with downward curved prickles along the branches; twigs glabrous to puberulent. **Stipules** not seen. **Leaves** alternate, pari-bipinnate, sometimes armed with prickles at the base of the pinnae and at the base of leaflets; pinnae in 2 – 5 opposite pairs. **Leaflets** opposite, in 1 – 8 pairs per pinna, obovate, broadly elliptic to oblong-elliptic, apex rounded, obtuse, to slightly emarginate, base equal or asymmetrical, rounded to cuneate, 10 – 46 x 7 – 35 mm, eglandular, glabrous or pubescent on lower surface; primary vein centric, secondary venation reticulate. **Inflorescences** in terminal or axillary racemes or panicles, flowers bisexual, rachis c. 5 – 30 cm long, glabrous or puberulous, eglandular, unarmed; bracts minute, usually under 3 mm long, with a long acuminate tip, caducous. **Corolla** zygomorphic, yellow, the median petal with red markings; **calyx** a hypanthium with five sepals that are 6 – 9 mm long, eglandular, glabrous to puberulous, lower sepal cucullate with a pectinate margin, covering the other 4 sepals in bud; sepals caducous, but the hypanthium persisting as a calyx ring around the pedicel as the pod matures; **petals** 5, free, c. 10 mm long. **Stamens** 10, free, the filaments pubescent, eglandular. **Fruit** an indehiscent, straight, oblong, laterally compressed, slightly turgid and somewhat fleshy, coriaceouspod, 4 – 15 x 1.2 – 4 cm, eglandular, often puberulent when young, glabrescent. **Seeds** ellipsoid, c. 8 – 10 mm diameter, brown, shiny.

Geographical distribution: A genus of three species, one in South America (*T. spinosa* is thought to be native to Peru and Ecuador), and two species in Mexico (one extending into the Caribbean). *Tara spinosa* is also widely cultivated across the tropics and subtropics as a source of tannins, and as an occasional ornamental (including in the Canary Islands).

Habitat: seasonally dry tropical forest to semi-arid thorn scrub.

Etymology: Derived from the vernacular name 'tara' in Peru, Bolivia and Chile.

Tara cacalaco (Humb. & Bonpl.) E. Gagnon & G.P. Lewis, **comb. nov.** *Caesalpinia cacalaco* Humb. & Bonpl., in Pl. Aequin. 2: 173, pl. 137 (1817). Type: Mexico, between Chilpantzingo and Zumpango "en allant d'Acalpulco à Mexico".

Coulteria mexicana DC., in Prodr. Syst. Nat. Reg. Veg. 2: 481 (1825). Type: "Novâ-Hispaniâ".

Poinciana horrida Sessé & Moc., in Naturaleza [Sociedad Méxicana de Historia Natural], ser. 2, 1, app. 66 (1888).

Russellodendron cacalaco (Humb. & Bonpl.) Britton & Rose, in N. Amer. Fl. 23(5): 320 (1930).

Tara spinosa (Molina) Britton & Rose, in N. Amer. Fl. 23(5): 320 (1930). Type: Peru, Lima, fide Britton & Rose.

Poinciana spinosa Molina, in Sag, Stor. Nat. Chili 158 (1782), nom. nud.. Type: not specified.

Caesalpinia pectinata Cav., in Descr. Pl. 467 (1802). Type: "Nueva España, flowered for the first time in the Real Jardin in July 1802"

Caesalpinia spinosa (Molina) Kuntze, in Rev. Gen. Pl. 3(3): 54 (1898).

Caesalpinia tara Ruiz & Pav., in Fl. Peru. et Chil. 4: pl. 374 (1802). Type: ? Plate 374 in Ruiz & Pavon, Flora Peru et Chile 4 (1802).

Caesalpinia tinctoria Dombey ex DC., in Prod. Syst. Nat. Reg. Veg. 2: 481 (1825). Type: no type material cited in the protologue.

Coulteria tinctoria Kunth, in Nov. Gen. et Sp. Pl. 6: 331, pl. 569 (1823[1824]). Type: “in Provincia Popayanensi prope Carthagineum”.

Coulteria horrida Kunth, in Nov. Gen. et Sp. Pl. 6: 330, pl. 568 (1823[1824]). Type: “crescit cum sequente”, i.e. in the same locality as *Coulteria tinctoria* Kunth.

Tara vesicaria (L.) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia vesicaria L., in Sp. Pl. 1: 381 (1753). Type: “in America calidiore”; Linnaeus cited “Sloan. jam. 149. hist. 2. p. 150. t. 181. f. 12. Raj. dendr. 111”.

Poinciana bijuga L., in Sp. Pl., ed.2: 544 (1762). Type: “in Indiis”.

Caesalpinia bijuga (L.) Sw., in Obs. Bot. 166 (1791).

Nicarago vesicaria (L.) Britton & Rose, in N. Amer. Fl. 23(5): 319 (1930).

Poinciana bijugata Jacq., in Enum. Syst. Pl. 20 (1760). Type: No type given.

Acacia bancroftiana Bertero, in Hort. Ripul. 1 (1824). Type: “Antillis”, “Hab. ad sepes locis sylvest. aridisque sems viam Spanish Town prope Ferry”.

References: Britton & Rose (1930); Sprague (1931); MacBride (1943); Ulibarri (1996); Barreto Valdes (2013).

8. *Coulteria* Kunth, Nov. Gen. Sp. 6 ed. fol. 258 (1824), 6 ed. qu. 328 (1824), (excluding t. 568 et 569 which = *Tara spinosa* (Molina) Britton & Rose); (1824); emend E. Gagnon, Sotuyo & G.P. Lewis.

Diagnosis: *Coulteria* differs from *Tara* by its racemose inflorescences of unisexual flowers (vs. inflorescences of racemes and panicles with bisexual flowers), by its membranaceous to papyraceous, laterally-compressed, oblong to elliptic (occasionally suborbicular) stipitate pods, the stipe ca. 4 – 13 mm long (vs. indehiscent, laterally compressed but slightly turgid and somewhat fleshy, coriaceous, straight, oblong, sessile pods), and compressed, ovate-orbicular to sub-quadrate, compressed seeds (vs. ellipsoid seeds).

Type species: No type designated in the original publication, or since. Type chosen here: *Coulteria mollis* Kunth.
Brasilettia sensu Britton & Rose (1930), non (DC.) Kuntze (1891).
Guaymasia Britton & Rose (1930).

Description: Trees or shrubs, 3 – 20 m tall, unarmed; young twigs with a dense velvety-bronze pubescence, glabrescent. **Stipules** not seen. **Leaves** alternate, pari-bipinnate, petiole and rachis glabrous or with a dense-velvety pubescence; pinnae in 2 – 4 pairs. **Leaflets** in (2 –)4 – 12(–14) pairs per pinna, 0.6 – 8 cm long, elliptic, oblong to ovate, apex obtuse to acute, base narrow, rounded or obtuse, eglandular, glabrous to velvety pubescent; main vein centric, secondary veins brochidrodomous. **Inflorescence** racemose, axillary or terminal, 5 – 16(– 25) cm long; flowers unisexual; bracts minute, with an acute tip, pubescent, caducous. **Corolla** zygomorphic, yellow; **calyx** comprising a hypanthium with 5 sepals that are 8 – 10 mm long and velvety-pubescent, lower sepal cucullate, glandular-pectinate, covering the other 4 sepals in bud; **petals** 5, free. **Stamens** 10, free, filaments pubescent, eglandular. **Fruit** membranaceous to papyraceous, laterally-compressed, oblong to elliptic (occasionally suborbicular), indehiscent (or sometimes opening along one suture), wingless, 3 – 15 x 2 – 4 cm, with a stipe 4 – 13 mm long, pendulous, often persisting on tree to next flowering season, eglandular, glabrous to densely velvety-pubescent, 1 – 6-seeded. **Seeds** ovate orbicular or sub-quadrate, compressed.

Geographic Distribution: A genus of seven species in Mexico and Central America, one species extending to Cuba, Jamaica and Curaçao, one to Venezuela (including Isla Margarita) and Colombia.

Habitat: seasonally dry tropical forest, deciduous woodland and dry thorn scrub, some species on limestone.

Etymology: Named for the Irish botanist Thomas Coulter (1793–1846) who collected in Central Mexico (1825–1834) and was curator of the herbarium at Trinity College, Dublin, Ireland.

Notes: The genus is currently being revised by S. Sotuyo, E. Gagnon and G.P. Lewis. A list of accepted species is given below, but excludes types and synonymy.

Coulteria glabra (Britton & Rose) Sotuyo & G.P. Lewis, ined.
Coulteria mollis Kunth
Coulteria linnaei (Benth.) Sotuyo & G.P. Lewis
Coulteria platyloba (S. Watson) N. Zamora
Coulteria pringlei (Britton & Rose) Sotuyo & G.P. Lewis, ined.
Coulteria pumila (Britton & Rose) Sotuyo & G.P. Lewis, ined.
Coulteria velutina (Britton & Rose) Sotuyo & G.P. Lewis, ined.

References: Kunth (1824); Britton & Rose (1930: 320 – 322); Zamora Villalobos (2010); Sotuyo, Gagnon & Lewis (in prep.)

9. ***Gelrebia*** E. Gagnon, G.P. Lewis & C.E. Hughes, **gen. nov.**

Diagnosis: *Gelrebia* is closely related to *Caesalpinia* sensu stricto. Nevertheless, species of *Gelrebia* differ somewhat in habit, as they are erect to scrambling shrubs (vs. erect shrubs or small trees), in having flowers varying in colour from a dark pinkish mauve to a light pinkish-white (vs. flowers that are variable in colour, from yellow, white, red and orange to green), and in having coriaceous, broadly oblong-ovoid to obliquely pyriform pods, with a large, oblique, rounded base (vs. coriaceous, oblong-elliptic to linear pods, with an oblique cuneate base).

Type species: *Gelrebia rubra* (Engl.) E. Gagnon, G.P. Lewis & C.E. Hughes
(*Hoffmanseggia rubra* Engl.).

Description: Erect to scambling **shrubs**, 0.3 – 5 m tall, armed with scattered, straight to curved, deflexed prickles (these 7 – 20 mm long); stems puberulous to pubescent when young, glabrescent. **Leaves** alternate, pari-bipinnate, pinnae opposite, in 1 – 17 pairs. **Leaflets** opposite (except in *G. glandulosopedicellata*), in 1 – 33 pairs per pinna, narrowly oblong or oblong-elliptic (3 – 11 x 2 – 5 mm), apex rounded to emarginate, sometimes mucronate, glabrous or with a sparse pubescence, lower surface of the blades with numerous subepidermal glands or translucent dots (best seen with a 10x hand lens or microscope). **Inflorescence** a terminal or axillary raceme, with pedicellate, bisexual flowers, c. (1–) 2 – 19 (–25) cm long, unarmed; bracts broadly ovate to suborbicular, apex aristate, 3 – 10 mm long, caducous. **Corolla** zygomorphic, varying in colour from a dark pinkish mauve to a light pinkish-white; **calyx** comprising a short hypanthium with 5 sepals that are c. 5 – 13 mm long, eglandular, glabrous to finely pubescent, lower sepal strongly cucullate (occasionally with a beaked apex), covering the other 4 sepals in bud before anthesis, all sepals caducous, but hypanthium persisting as a free ring around the pedicel as the pod matures; **petals** 5, free, c. 7 – 24 x 5 – 15 mm, eglandular. **Stamens** 10, free, filaments 8 – 20 mm long, pubescent and eglandular. **Ovary** glabrous. **Fruit** a coriaceous, broadly oblong-ovoid to obliquely pyriform pod, apex acute, with a large, oblique, rounded base, c. 15 – 40 x 12 – 23 mm, dehiscent along both margins, glabrous to minutely pubescent, eglandular. **Seeds** obovoid, laterally compressed.

Geographical distribution: A genus of nine taxa in eight species, restricted to Africa, occuring in Namibia, Botswana, South Africa, Northern Kenya, Ethiopia, and Somalia. One species also found in the Democratic Republic of the Congo (Zaire, Katanga).

Habitat: deciduous bushland, dry woodlands, on rocky ridges, often also found along dry river beds, or on sandy valley floors. One species also found in degraded savannahs, close to termite mounds.

Etymology: Gelreb or gelrib is a Somali name for *Gelrebia trothae* subsp. *erlangeri* and appears on the field labels of Dale K724 ("gelrib") and of Gillett 13223 ("gelreb"), both collections from Kenya deposited in the Herbarium at Kew. This translates as camel trap and must allude to the robust armature of the taxon that is assumed to prevent the passing of camels. Such armature is characteristic of most species in the genus.

Gelrebia bracteata (Germish.) E. Gagnon, G.P. Lewis & C.E. Hughes **comb. nov.**

Caesalpinia bracteata Germish., in Bothalia 21 (2): 153 (1991). Type: [South Africa, Cape Province]: 2819 (Ariamsvlei): Kenhardt District, on farm Skroef, near hot spring (Warmbad Noord) on Orange River (-DA), 29 September 1987, *Van Hoepen* 1941 (holotype PRE).

Gelrebia dauensis (Thulin) E. Gagnon, G.P. Lewis & C.E. Hughes **comb. nov.**
Caesalpinia dauensis Thulin, in Kew Bull. 34(4): 819(1980). Type: Kenya, 30 km on the Ramu-Malka road, c. 4º 04' N, 40º 59' E, 8 May 1978, *Gilbert & Thulin* 1583 (holotype UPS, isotypes BR, EA, K!).

Gelrebia glandulosopedicellata (R. Wilczek) E. Gagnon, G.P. Lewis & C.E. Hughes **comb. nov.**
Caesalpinia glandulosopedicellata R. Wilczek, in Bull. Jard. Bot. Brux. 21: 83 (1951). Type: "Congo Belge", district du Haut-Katanga: environs de Niemba, *Schmitz* 1595.

Gelrebia merxmuelleriana (A. Schreiber) E. Gagnon, G.P. Lewis & C.E. Hughes **comb. nov.**
Caesalpinia merxmuelleriana A. Schreiber, in Mitt. Bot. St. Munchen 16, Beih., Die Gattung *Caesalpinia* in Südwestafrica, 64 (1980). Type: Südwestafrica, Dist. Lüderitz-Süd, Farm Uitsig, *Wendt* in herb. *W. Giess* 14713 (holotype M; isotypes K!, PRE, WIND).

Gelrebia oligophylla (Harms) E. Gagnon, G.P. Lewis & C.E. Hughes **comb. nov.**
Caesalpinia oligophylla Harms, in Engl., Bot. Jahrb. Syst.33: 160 (1902). Type: Ethipoia, "Arussi Galla", Apr. 1901, *Ellenbeck* 2038 (holotype B †); Somalia, rive dello Scebelia Bulo Burti, 25 Feb. 1924, *Puccioni & Stefanini* 134 (neotype FI, selected by G. Roti-Michelozzi in Webbia 13: 207 (1957).

Gelrebia rostrata (N.E.Br.) E. Gagnon, G.P. Lewis & C.E. Hughes **comb. nov.**
Caesalpinia rostrata N.E.Br., in Hooker's Icon. Pl., 28: t. 2702 (1901). Type: from cultivation in Durban Botanic Garden (South Africa), raised from seed obtained from "Delagoa Bay", Maputo (Lourenço Marques), *Wood* 7943 (holotype K!, isotypes BOL, NH, PRE).

Gelrebia rubra (Engl.) E. Gagnon, G.P. Lewis & C.E. Hughes **comb. nov.**

Hoffmanseggia rubra Engl., in Engl., Bot. Jahrb. Syst. 10: 25 (1889). Type: Namibia, Karibib Dist., Usakos, *Marloth* 1432 (holotype B, isotypes BOL, PRE).
Caesalpinia rubra (Engl.) Brenan, in Kew Bull. 17(2): 202 (1963).

Gelrebia trothae (Harms) E. Gagnon, G.P. Lewis & C.E. Hughes **comb. nov.**
Caesalpinia trothae Harms, in Engl., Bot. Jahrb. Syst., 26: 277 (1899), as "trothaei".
Type: Tanzania, ?Dodoma District, Ugogo, Chumo Pass, Jan. 1897, *von Trotha* 186 (holotype B †).

Gelrebia trothae subsp. ***trothae***

Gelrebia trothae subsp. ***erlangeri*** (Harms) E. Gagnon, G.P. Lewis & C.E. Hughes **comb. nov.**
Caesalpinia erlangeri Harms, in Engl., Bot. Jahrb. Syst. 33: 160 (1902).Type: Ethiopia, Galla Sidama, Borana, Tarro Gumbi, *Ellenbeck* 2071 (holotype B †). Somalia, Dolo, sul Daua, 6 May 1893, *Riva* 1104 (neotype FI, selected by G. Roti-Michelozzi in Webbia 13: 209 (1957).
Caesalpinia trothae subsp. *erlangeri* (Harms) Brenan, in Kew Bull. 17(2): 201 (1963).

References: Wilczek (1951); Roti-Michelozzi (1957); Brenan (1963); Brenan (1967); Ross (1977: 122 – 130); Thulin (1980, 1983: 16 – 18; 1993: 344 – 347); Germishuizen (1991); Roux (2003); Curtis & Mannheimer (2005: 226 – 228); Brummitt & al. (2007).

10. ***Hultholia*** E. Gagnon & G.P. Lewis, **gen. nov.**

Diagnosis: *Hultholia* is closely related to *Guilandina*. While both genera are armed lianas, *Hultholia* differs in having stems with dome-shaped glands intermixed with the dense slender, patent, needle-like prickles (vs. stems eglandular and with prickles in *Guilandina*); both genera have sharp recurved prickles on the leaf and pinnae rachises. *Hultholia* has bisexual flowers in racemes (vs. dioecious flowers in separate female and male racemes), a zygomorphic corolla, with petals extending beyond the sepals, and the median (standard) petal smaller than the other four (vs. a sub-actinomorphic corolla, with petals barely extending beyond the sepals in *Guilandina*), unarmed, obovoid, falcate, pubescent, vesicular pods (vs. oblong-elliptic, coriaceous, eglandular, inflated pods, usually armed with 5 – 10 mm long, slender spinescent bristles), and sub-globose, oblong, grey, ca. 10 x 7 mm seeds (vs. obovoid to globular c. 20 mm in diameter, smooth, grey, pale to dark brown or orange seeds, with parallel fracture lines concentric with the small apical hilum).

Type species: *Hultholia mimosoides* (Lam.) E. Gagnon & G.P. Lewis (*Caesalpinia mimosoides* Lam.)

Description: Climbing woody shrub; branches densely armed with short, needle-like, robust trichomes. Young stems pubescent, with rust-coloured, hyaline hairs and dome shaped-glands, topped with a few hairs. **Stipules** awl-shaped, 7 – 15 mm long, pubescent, caducous. **Leaves** alternate, 22 – 40 cm long; pinnae opposite, in 10 – 30 pairs per leaf, about 3 – 5 cm long, pubescent, with a pair of spines at the insertion of the pinnae on the leaf rachis, and at the insertion of leaflets on the pinnae rachises. **Leaflets** opposite, in 7 – 20 pairs per pinna, oblong, asymmetric at base, c. 9 x 4 mm, glabrous, eglandular. **Inflorescences** terminal, lax racemes, with 50 or more bisexual flowers, 20 – 40 cm long; rachis and pedicels armed with needle-like, robust trichomes, pubescent and covered with domed, hair-tipped glands. **Corolla** zygomorphic, bright yellow; **calyx** comprising a hypanthium with 5 sepals that are c. 13 – 16 x 6 mm.; hypanthium and sepals pubescent and glandular, the sepal margins sometimes with small stipitate glands, less than 1 mm long; **petals** 5, free; dark glands present on the blade; median (standard) petal c. 8 mm wide and smaller than the other 4 lateral petals, that are c. 1.7 x 1.3 cm. **Stamens** 10, free, filaments 1.8 cm long, pubescent. **Ovary** densely pubescent, and with glandular dots (often obscured by the dense pubescence). **Fruit** an obovoid, falcate, vesicular, unarmed, dehiscent pod, sparsely pubescent, particularly along the margin, and covered in gland dots, c. 5 – 6 x 2.5 – 3 cm, 1 – 3-seeded. **Seeds** sub-globose, oblong, 10 x 7 mm, grey.

Geographical distribution: One species distributed across Asia, in China (Yunnan), Bangladesh, India, Laos, Myanmar, Thailand and Vietnam.

Habitat: near roads, in secondary thickets and clearings, up to 1500 m in altitude. More information on the habitat preferences of this genus is needed.

Etymology: The name *Hultholia* is in the honour of the botanist Dr. Sovanmoly Hul Thol (born 1946), whose doctoral thesis, “Contribution à la revision de quelques genres de Caesalpiniaceae, representés en Asie” (1976), is an important revision of the species and genera of the Caesalpinia Group present in Asia, particularly of *Pterolobium*. Dr. Hul Thol is today in charge of curation at the Museum National d’Histoire Naturelle in Paris, and a specialist of the flora of Cambodia and of South East Asia. Since 1995, she has been directing the publication of the multiple volumes of the Flora of Cambodia, Laos and Vietnam. She is also one of the co-founders of the National Herbarium of Cambodia at the Royal University of Phnom Penh, her country of origin.
Notes: While this species is not cultivated, the young, pungent, flowering twigs are sold as vegetables in the markets of Vientiane (Laos) (Vidal & Hul Thol 1976).

Hultholia mimosoides (Lam.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia mimosoides Lam., in Encycl. Méth., Bot. 1(2): 462 (1785). Type: Specimen originally from Malabar, communicated to Lamarck by Sonnerat (P: Herb. Lamarck, fide Vidal & Hul Thol 1976).
Biancaea mimosoides (Lam.) Tod., Hort. Bot. Panorm. 1(1): 3 (1875).

References: Vidal & Hul Thol (1976); Chen & al. (2010: 42 – 43).

11. *Guilandina* L., in Sp. Pl.: 381 (1753).

Type species: *Guilandina bonduc* L.

Bonduc Mill (1754)
Caesalpinia subgenus *Guilandina* (L.) Gillis & Proctor (1974).

Description: Lianas, woody climbers, scrambling or trailing shrubs, often forming dense tangled clumps, strongly armed with recurved prickles along the branches, as well as in pairs at leaf bases. (*Caesalpinia murifructa* and closely related species in in the West Indies are completely unarmed). **Stipules** foliaceous to subulate, sub-persistent to caducous. **Leaves** bipinnate, large, prickles present in pairs at the insertion of pinnae on the leaf rachis, scattered along the main rachis, and also at the insertion of leaflets on the pinnae rachises. **Leaflets** oblong, apex obtuse and mucronulate to acuminate, base rounded. **Inflorescences** supra-axillary or terminal racemes, 30 – 60 cm long; bracts narrow, lanceolate, aristulate, 1 mm long, to conspicuous and exceeding floral buds, caducous; flowers dioecious, in male and female racemes; female flowers are cryptically bisexual with 10 fully formed stamens, but these produce no pollen; male flowers have a highly reduced, non-functional pistil. **Corolla** zygomorphic to sub-actinomorphic, yellow; **calyx** with a hypanthium and 5 almost equal sepals, these valvate in bud, the lower sepal not cucullate, the hypanthium and sepals caducous, leaving no persistent calyx ring, eglandular, without spines (except the calyx armed with slender prickles in Madagascan *Caesalpinia. delphinensis*); **petals** 5, free, barely exceeding the sepals. **Stamens** 10, free, pubescent near the filament base. **Ovary usually** covered in bristly trichomes (with some exceptions, including *Caesalpinia solomonensis* and *Caesalpinia murifructa*). **Fruits** oblong-elliptic, inflated pods, usually armed with 5 – 10mm long spinescent bristles, apex terminating in a beak, base acute, 1 – 4-seeded. **Seeds** obovoid to globular, c. 2 cm in diameter, smooth, grey, pale to dark brown or orange, with parallel fracture lines concentric with the small apical hilum.

Geographic distribution: The genus needs to be revised across its total pantropical distribution. The exact number of "good" species is unknown, and total species number varies between seven to as high as 19. Species occur from as far north as Japan, south to South Africa, three occur in the Caribbean, one in China, India, Myanmar, Indo China, Hong Kong and Taiwan, one is endemic to Madagascar, one in Australia, and two species are widespread across the Old and New World tropics.

Habitat: coastal thickets on sand, in secondary forest, lowland rain forest, occasionally on limestone.

Etymology: Named for Melchior Wieland (1515–1589), Prussian naturalist, traveller and scholar from Königsberg, who settled in Italy and italianised his name to 'Guilandini' and latinised it as Guilandinus; he was sent to the Levant, Asia and Africa (1559–1560), was captured by pirates and finally ransomed by Gabriele Falloppio.

Notes: The list of 19 names provided below is a guide to potential species content in *Guilandina*, but we have included no synonymy and no information on types, neither have we proposed new combinations for the five species of *Caesalpinia* that belong here, but as yet have no published name in *Guilandina*.

Guilandina barkeriana (Urb. & Ekman) Britton
Guilandina bonduc L.
Guilandina caymanensis (Millsp.) Britton & Rose
Guilandina ciliata Bergius ex Wikstrom
Guilandina culebrae Britton & Wilson ex Britton & Rose
Caesalpinia delphinensis Du Puy & Rabev.
Guilandina glaucophylla (Urb.) Britton & Rose
Caesalpinia homblei R. Wilczek
Guilandina intermedia (Urb.) Britton & Rose
Guilandina major (DC.) Small
Caesalpinia minax Hance
Caesalpinia murifructa Gillis & Proctor
Guilandina portoricensis Britton & Wilson
Guilandina socorroensis Britton & Rose
Caesalpinia solomonensis Hattink
Guilandina sphaerosperma (Urb. & Ekman) Britton
Guilandina urophylla (Donn. Sm.) Britton & Rose
Caesalpinia volkensii Harms
Guilandina wrightiana (Urb.) Britton & Rose

References: Britton & Rose (1930: 336 – 341); Wilczek (1951); Brenan (1967); Gillis & Proctor (1974); Hattink (1974); Vidal & Hul Thol (1976); Heald (1994); Du Puy & Rabevohitra (2002: 46 – 48); Chen & al. (2010).

12. *Moullava* Adans., Fam. Pl. 2: 318 (1763), emend E. Gagnon & G.P. Lewis

Diagnosis: *Moullava* is related to *Mezoneuron*, but differs by its fleshy, oblong-elliptic, indehiscent, sub-torulose, wingless pods, with thickened sutures (vs. fruit a laterally compressed, chartaceous, coriaceous or ligneous, indehiscent pod, with a longitudinally wing along the upper suture), and by its subglobular seeds (vs. compressed seeds).

Type species: "H.M. 6 t. 6" (= Rheede`s Hortus Malabaricus 6, plate 6, 1686).

Wagatea Dalzell (1851).
Cinclidocarpus Zoll. & Moritzi (1846).
Caesalpinia sect. *Cinclidocarpus* (Zoll. & Moritzi) Benth. & Hook. (1865).

Description: Lianas and scrambling shrubs, armed with downwardly curved prickles along the branches. **Stipules** not seen. **Leaves** alternate, pari-bipinnate, 12 – 40 cm long, glabrous to pubescent-tomentose, with a pair of prickles at the insertion of each pinna; pinnae opposite, in 7 – 20 pairs. **Leaflets** in 5 – 40 opposite pairs per pinna, sessile, narrowly oblong to ovate-oblong, apex rounded to emarginate, sometimes mucronate, base asymmetrical to rounded, blades eglandular, glabrous to pubescent, 4 – 20 x 2 – 6 mm. **Inflorescence** an elongated terminal or axillary raceme, the bisexual flowers subsessile to pedicellate (pedicel, when present, 10 – 25 mm long), the racemes sometimes aggregated into panicles, 8 – 60 cm long, unarmed or with a few prickles at the base of the inflorescence. **Corolla** sub-actinormophic or zygomorphic, yellow, the median and lateral petals sometimes streaked with red,; **calyx** comprising a hypanthium with 5 sepals that are c. 6 – 12 x 2 – 4 mm, the lower sepal strongly cucullate, covering the other 4 sepals in bud, all sepals eglandular and glabrous; **petals** 5, free, eglandular. **Stamens** 10, free, barely exserted from the corolla, densely pubescent on lower half of filaments, c. 8 – 15 mm long. **Ovary** glabrous or pubescent. **Fruit** fleshy, oblong-elliptic, unarmed, indehiscent, sub-torulose, with thickened sutures, the apex apiculate, 35 – 50 (–80) x 15 – 30 mm, drying black (red-tomentose in immature fruit of *M. spicata*), exocarp and endocarp strongly adnate, glabrous, 1 – 4-seeded. **Seeds** sub-globular, about 12 – 20 mm in diameter, olive-brown to black.

Geographic distribution: A genus of four species, three distributed in Southern Asia, India, Nepal, Myanmar (Burma), Thailand, Laos, Cambodia, Sri Lanka, Southern China (Yunnan & Hainan), and the Malaysian peninsula and archipelago; one species in Africa (Cameroun, Gabon, the Democratic Republic of Congo, Angola, Zambia (Kabompo Dist.), Uganda and Tanzania (Kigoma Dist.).

Habitat: in Asia, species are found in seasonally dry tropical semi-evergreen forest margins, in secondary thickets, and also on mountain slopes, up to 1200 m in altitude. The African species is most often found occupying riverine habitats in lowland rainforests.

Etymology: Derived from the vernacular name of *Moullava spicata*, "mulu" (Malayalam: spiny), a spiny climber.

Moullava digyna (Rottl.) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia digyna Rottl., in Ges. Naturf. Freude Berlin Neue Schriften 4:198– 200, pl. 3 (1803). Type: [S. India] Marmelon (near Madras), 9 October 1799, *Rottler* s.n. (B: Herb. Willdenow, K!).

Caesalpinia gracilis Miq., in Fl. Ned. Ind. 1:110 (1855). Type: from India, *Roxburgh (n.v.)*.

Caesalpinia oleosperma Roxb., in Hort. Bengal. 32 (1814). Type: Java, *Horsfield* 138 (holotype K!, isotype BM).

Caesalpinia flavicans Grah., in Cat.: 5825 (1832), *nom. nud.*

Moullava spicata (Dalzell) Nicolson, in Bot. Hist. Hort. Malabaricus [K.S.Manilal]: 184 (1980).

Caesalpinia spicata Dalzell, in Hooker's J. Bot. Kew Gard. Misc. 3: 89 (1851). Type: Western India, Bombay Presidency.

Wagatea spicata Dalzell, in Hooker's J. Bot. Kew Gard. Misc. 3: 89 (1851). Type: Western India, Bombay presidency.

Caesalpinia digyna Graham, in Cat. 60 (1839), non Rottl. (1803), nom illeg.

Caesalpinia mimosoides Heyne & Wall, in Numer. List n. 5837 (1831), non Lam. (1785), nom illeg.

Caesalpinia ferox Hohen., Pl. Ind. Or. Exs. No. 414, non Hassk. Type: to be identified.

Moullava tortuosa (Roxb.) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia tortuosa Roxb., in Fl. Ind. (ed. 1832) 2: 365 (1832). Type: Specimen originating from Sumatra, cultivated in the Botanical Garden of Calcutta, “Hort. Calc. E. Sumatra”, *Roxburgh* s.n. (K!).

Caesalpinia acanthobotrya Miq., in Fl. Ned. Ind. 1(Suppl.): 108 (1860) & 293 (1861). Type: W. Sumatra, in prov. Priaman, 1855 – 60, *Diepenhorst* HB2240 (holotype U; isotype BO).

Caesalpinia microphylla Buch.-Ham ex Prain, in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 66: 471 (1897), non Mart. ex G. Don (1832). Type: Goyalpara, 6 August 1908, *Wallich* 5826 (K!).

Caesalpinia tortuosa var. *grandifolia* Craib, in Fedde Repert. Spec. Nov. Reg. Veg. 12: 392 (1913). Type: Myanmar [Burma], Kowpok, January 1912, *Meebold* 17208 (K!).

Caesalpinia cinclidocarpa Miq., in Fl. Ned. Ind 1: 110 (1855). Type: Java, as for *Cinclidocarpus nitidus*, non *Caesalpinia nitida* Hassk. (1844).

Cinclidocarpus nitidus Zoll. & Moritzi, in Naturr-Geneesk. Arch. Ned.-Indie 3: 82 (1846). Type: Java, *Zollinger* 3462 (holotype L, isotypes A, BM, P).

Caesalpinia tortuosa Wall., in Numer. List n. 5827 D (1831), nom. nud.

Moullava welwitschiana (Oliv.) E. Gagnon & G.P. Lewis, **comb. nov.**

Mezoneuron welwitschianum Oliv., in Fl. Trop. Afr. 2: 261 (1871). Type: Lower Guinea, Golungo Alto (flower) and Pungo Andongo (fruit), Angola, *Welwitsch* s.n.

Caesalpinia welwitschiana (Oliv.) Brenan, in Kew Bull. 17(2): 203 (1963).

References: Brenan (1963); Brenan (1967); Hattink (1974); Vidal & Hul Thol (1976); Nicolson (1980); Ansari (1990); Sanjappa (1992: 33); Brummitt et al. (2007, see both *Moullava* and *Mezoneuron welwitschianum*); Chen et al. (2010).

13. ***Biancaea*** Tod., Nuovi Gen. Sp. Orto Palermo (1860), emend E. Gagnon & G.P. Lewis

Diagnosis: *Biancaea* is closely related to *Mezoneuron,* but differs mostly in its fruit type, which is a coriaceous, laterally compressed, wingless, dehiscent pod (with the exception of *B. decapetala*, which is somewhat inflated and boat-shaped, and can occasionally have a narrow wing or ridge along the upper suture). In contrast, *Mezoneuron* has a chartaceous, coriaceous or ligneous pod, which is also laterally compressed, but is indehiscent, and has a wing along the upper suture. In addition, the ovary of *Biancaea* species always has a velvety indumentum (vs. a glabrous to pubescent ovary in *Mezoneuron*).

Type species: *Biancaea scandens* Tod. = *Biancaea decapetala* (Roth) Deg.

Campecia Adans. (1763); no type species designated, and no species names ever published in this genus. It is thus not possible to know how to apply the name which will need to be rejected against *Biancaea*.
Caesalpinia sect. *Sappania* DC. (1825).

Description:

Lianas or climbing or trailing shrubs (1 – 3 m), **or trees** (2.5 – 10 m), armed with short, slightly recurved prickles, scattered along the branches; young branches pubescent or glabrescent. **Stipules** lanceolate-oblong to broadly-ovate, sometimes with an amplexicaul base, from 3 – 4 mm up to 4.5 cm long, caducous or sub-persistent to persistent. **Leaves** alternate (except in *B. oppositifolia*), pari-bipinnate, rachis pubescent (glabrous in *B. oppositifolia*), armed with pairs of prickles inserted at the base of each pinna, sometimes also scattered along the rachis; pinnae in 4 – 19 opposite to alternate pairs. **Leaflets** in 5 – 18 opposite to alternate pairs per pinna, blade membranous, eglandular, glabrous to pubescent, 10 – 35 x 4 – 15 mm (4 – 10 x 1.5 – 4.5 cm in *B. oppositifolia*), oblong-elliptic, apex acute, obtuse, rounded to emarginate, base asymmetric. **Inflorescences** erect, showy, terminal or axillary racemes or panicles of bisexual flowers; rachis eglandular, pubescent, unarmed or with a few scattered prickles, mainly near the base; bracts ovate-lanceolate, acuminate, 2 – 8 mm long, caducous. **Corolla** zygomorphic, yellow to white; **calyx** with a short hypanthium and 5 sepals, the lower sepal cucullate and covering the other 4 in bud, sepals pubescent (except in *B. sappan*), caducous, but the hypanthium persists as a calyx ring around the pedicel as the fruit matures; **petals** 5, free, eglandular, with pubescent claws; the median petal smaller than the other 4, and inrolled towards the centre; lateral petals oblong, obovate to spathulate, 4 – 10 x 2 – 8mm. **Stamens** 10, with densely pubescent filaments, the indumentum most evident at the base, eglandular, c. 10 – 15 mm long. **Ovary** covered in a dense, velvety pubescence. **Fruit** a coriaceous, glabrous, eglandular, oblong-elliptic to obovate, dehiscent, wingless, laterally compressed (but can be somewhat inflated in *B. decaptala* which also frequently has a narrow wing along the upper suture), 4.5 – 10 x 2 – 4 cm pod, this usually much broader at the rounded to truncate apex, which terminates in a sharp beak, 2 – 8-seeded. **Seeds** flat, elliptic, ovoid to orbicular, c. 2 cm in diameter, black or brown.

Geographic distribution: This genus of six species is widespread across Southern Asia, from India, to Myanmar (Burma), Thailand, Cambodia, Vietnam, Southern China, Japan, the Philippines, and the Malaysian peninsula and Archipelago. One species is endemic to Northern Borneo (near Sandakan). *Biancaea decapetala*, while originally from Asia, has been introduced across the tropics as a hedge plant or ornamental. It is considered to be invasive in South Africa and Hawaii.

Habitat: primary forest and forest margins, grasslands, scrub vegetation, riverine habitats, secondary thickets and clearings. From the coast to mountain slopes.

Etymology: Unknown.

Biancaea decapetala (Roth) O. Deg., in Fl. Hawaiiensis K7 (1936).

Reichardia decapetala Roth, in Nov. Pl. Sp. 212 (1821). Type: India, (fl.), *Heyne* s.n. (isotype K!).

Caesalpinia decapetala (Roth) Alston, in Handb. Fl. Ceylon 6:89 (1931).

Caesalpinia decapetala (Roth) Alston var. *pubescens* P.C. Huang, in Sylva Sinica 2: 1187 (1985), nom. illeg., without Latin description or type.

Caesalpinia decapetala var. *pubescens* (T. Tang & F.T. Wang ex C.W. Chang) X.Y. Zhu, in Legumes of China: 5 (2007). Type: China.

Biancaea scandens Tod., in Nuov. Gen. Sp. Pl.: 22 (1860). Type: "Cortivasi da lungo tempo nel Real Orto Botanico [di Palermo] in piena terra, col nome di *Caesalpinia sepiaria*".

Caesalpinia benguetensis Elmer, in Leafl. Philipp. Bot. 1:226 (1907). Type: Philippines, Luzon, Benguet prov. Baguio, (fl. fr.), March 1907, *Elmer* 8720 (BO, K!, L, PHN).

Mezoneuron benguetense (Elmer) Elmer, in Leafl. Philipp Bot 1: 362 (1908).

Caesalpinia japonica Sieb. & Zucc., in Abh. Math.-Phys. Cl. Königl. Bayer Akad. Wiss. 4(2): 117 (1845). Type: Japan, *Siebold & Zuccanini.*

Caesalpinia sepiaria var. *japonica* (Siebold & Zucc.) Gagnep., in Fl. Indo-Chine 2:180 (1913).

Caesalpinia sepiaria var. *japonica* (Siebold & Zucc.) Makino, in Ill. Fl. Nippon: 431 (1940).

Caesalpinia decapetala var. *japonica* (Siebold & Zucc.) H. Ohashi, in Fl. E. Himalaya 3:58 (1975).

Caesalpinia decapetala var. *japonica* (Siebold & Zucc.) Isely, in Mem. New York Bot. Gard. 24(2): 193 (1975).

Caesalpinia ferox Hassk., in Ind. Sem. Hort. Amst. (1841). Type: probably a living plant in Hort. Bog., fide Hattink (1974).

Biancaea ferox (Hassk.) Tod., Hort. Bot. Panorm. 1(1): 3 (1875).

Caesalpinia sepiaria Roxb., in Fl. Ind. (ed. 1832) 2: 360 (1832). Type: India, *Roxburgh* without number (isotypes: BM, K!, in *Hb. Wallich* 5834A).

Biancaea sepiaria (Roxb.) Tod., in Hort. Bot. Panorm. 1(1): 3 (1875).

Caesalpinia sepiaria Roxb. var. *pubescens* T. Tang & F.T. Wang ex C.W. Chang, in Flora Tsinlingensis 1(3): 444 (1981). Type: the item "holotypus" was erroneously written as "lectotypus".

Caesalpinia sepiaria Roxb. var. *pubescens* T. Tang. & F.T. Wang, Illust. Treat. Prin. Pl. China (Leguminosae): 96 (1955), without Latin description.

Biancaea godefroyana (Kuntze) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia godefroyana Kuntze, in Rev. Gen. Pl. 1: 166 (1891). Type: Vietnam (South), Cap St-Jacques (Vung Tau), 18 March 1875, *Godefroy* s.n. (lectotype K!, selected by Vidal & Hul Thol, 1976).

Caesalpinia thorelii Gagnep., in Notul. Syst. (Paris). 2: 207 (1912). Type: Indo-China, "Cochinchine: Baria, no. 104 *Baudouin*], [*Talmy*]; Bien-hoa, no. 848 [*Thorel*], nov. 1866 et no. 130 [*Pierre*]; prè Saïgon, no. 145 [Lefèrre], [*Thorel*], [Godefroy]", syntypes.

Biancaea milletii (Hook. & Arn.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia milletii Hook. & Arn., in Bot Beechey Voy. 182 (1841[1833]). Type: China, *Millett* s.n. (K!).
Pterolobium subvestitum Hance, in J. Bot. 22(12): 365 (1884). Type: China, Kwangtung, Lo Fau Sahn, *Faber in herb. Hance* 22291 (BM).
Cantuffa subvestita (Hance) Kuntze, in Rev. Gen. Pl. 1: 168 (1891).

Biancaea oppositifolia (Hattink) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia oppositifolia Hattink, in Reinwardtia 9(1): 43 (1974). Type: Malesia, Sabah [North Borneo], Ranau Distr. Hot Spring track, 15 February 1961, *J. Singh* 24026 (holotype SAN, isotypes K!, L).

Biancaea parviflora (Prain ex King) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia parviflora Prain ex King, in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 66: 230 (1897). Type: Malaya, Perak, Relau Tugor, May 1888, *Wray* 1909 (lectotype CAL, chosen by Hattink 1974; isolectotypes K!, SING).
Caesalpinia parviflora var. *stipularis* Prain, in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 66: 230 (1897). Type: Malaya, Perak, Larut, *Wray* 3983, 3991, 4261 (syntypes).
Caesalpinia parviflora var. *typica* (Prain ex King) Prain, in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 60: 230 (1897), *nom. illeg.*
Caesalpinia borneensis Merr., in Univ. Calif. Publ. Bot. 15: 104 (1929). Type: Borneo, Tawao, Elphinstone Prov., October 1922 – March 1923, *Elmer* 21449 (holotype MO; isotypes A, BM, BO, K!, L, NY, P, U, UC, SING).
Caesalpinia macra Craib, in Bull. Misc. Inform. Kew 1927(2): 386 (1927). Type: Thailand, Saraburi, Muak Lek, 10 Nov. 1924, *Marcan* 1866 (syntype K), Pak Chwng, 30 Dec. 1923, *Marcan* 1532 (syntype K).

Caesalpinia minutiflora Elmer, in Leafl. Philipp. Bot. 5: 1803 (1913). Type: Philippines, Palawan, Puerto Princesa, Mt. Pulgar, April 1911, *Elmer* 12969 (BM, K!, L, P, PNH, U).
Caesalpinia stipularis Ridl., in Fl. Malay Penin. 1: 651 (1922), *nom. illeg.*, non *Caesalpinia stipularis* (Vogel) Benth. (1870) (= *Pomaria stipularis* (Vogel) B.B. Simpson & G.P. Lewis).

Biancaea sappan (L.) Tod., Hort. Bot. Panorm. 1(1): 3 (1875).
Caesalpinia sappan L., in Sp. Pl. 1: 381 (1753). Type: Ceylon, *Hb. Hermann*, vol. 4, fol. 31 (BM).
Caesalpinia angustifolia Salisb. in Prod.: 326 (1796), *nom. illeg.*

References: Hattink (1974); Vidal & Hul Thol (1976); Jansen (2005); Brummitt et al. (2007); Chen et al. (2010).

14. *Pterolobium* R. Br. ex Wight & Arn., Prodr. 283 (1834), (nom cons.)

Type species: *Pterolobium lacerans* R.Br. ex Wight & Arn., nom. illeg. (*Cantuffa exosa* J.F. Gmel. = *Pterolobium exosum* (J.F. Gmel.) E.G. Baker; this now considered a synonym of *Pterolobium stellatum* (Forsskal) Brenan).

Cantuffa J.F. Gmel. (1791).
Reichardia Roth (1821), nom. illeg., non Roth (1787), nec Roth (1800).

Description:
Lianas or climbing or trailing shrubs, armed with prickles along the branches, as well as in pairs at the base of leaves. **Stipules** small, inconspicuous, subulate or triangular-subulate, caducous. **Leaves** alternate, pari-bipinnate, 6 – 30 cm long, petiole and rachis pubescent to sparsely pubescent or glabrous; pinnae opposite, in 5 – 20 pairs. **Leaflets** opposite, in 6 – 25 pairs per pinna, linear-oblong to elliptic-oblong, apex rounded to emarginate, sometimes mucronate, eglandular or punctate-glandular, 6 – 15 x 1.5 – 10 mm. **Inflorescences** terminal or axillary racemes, these often aggregated into panicles, pubescent to glabrous, 4 – 25 cm long,

flowers pedicellate, bisexual; bracts small, caducous. **Corolla** sub-actinomorphic to zygormophic, yellow to white; **calyx** comprising a short hypanthium and 5 sepals, glabrous to pubescent, the lower sepal cucullate, covering the other 4 sepals in bud; **petals** 5, free, equal to slightly differentiated, their claws pubescent, the median petal sometimes inrolled. **Stamens** 10, free, with pubescent filaments (occasionally glabrous); anthers dorsifixed, dehiscing by longitudinal slits. **Ovary** pubescent, stigma chambered. **Fruit** a samara, red to brown, the basal seed-containing portion (12 – 20 x 8 – 15 mm, reticulate or smooth, glabrous to pubescent) has an upper suture that is much prolonged and broadly winged (the wing 20 – 45 mm long and usually becoming wider distally), 1 (–2)-seeded.

Geographic distribution: A genus of 11 species; one in southern tropical Africa, East Africa and Arabia, ten in SE Asia (one endemic to India, two in China, four in Indo-China [one endemic to Thailand, two extending to Malesia], three species restricted to the Malesian Peninsula and Archipelago [one endemic to the Philippines]).

Habitat: seasonally dry tropical upland evergreen forest, riverine and humid forest, woodland and wooded grassland.

Etymology: From *ptero-* (Greek: wing) and *lobion* (Greek: pod, fruit), in reference to the samaroid fruit.

Notes: Vidal & Hul Thol (1974) published a revision of *Pterolobium*, with a key to species. We provide below a list of species currently accepted in the genus, including *P. sinense* published in 1976.

Pterolobium borneense Merrill
Pterolobium densiflorum Prain
Pterolobium hexapetalum (Roth) Santapau & Wagh
Pterolobium integrum Craib.
Pterolobium macropterum Kurz
Pterolobium membranulaceum (Blanco) Merrill
Pterolobium micranthum Gagnep., emend. Craib

Pterolobium microphyllum Miq.
Pterolobium punctatum Hemsl.
Pterolobium sinense J.E. Vidal
Pterolobium stellatum (Forsskal) Brenan

References: Roti-Michelozzi (1957); Brenan (1967: 40 – 42); Vidal & Hul Thol (1974, 1976); Hul Thol & Hideux (1977); Hou (1996: 654 – 700); Chen et al. (2010).

15. *Mezoneuron* Desf., in Mém. Mus. Hist. Nat. 4: 245 (1818).

Type species: *Mezoneuron glabrum* Desf. = *Mezoneuron pubescens* Desf.

Mezonevron Desf. and *Mezoneurum* DC. (1825), (orth.vars.).
Caesalpinia subg. *Mezoneuron* (Desf.) Vidal ex Herend. & Zarucchi (1990).

Description: Scrambling shrubs or lianas, occasionally small trees, usually armed with recurved prickles on stem and leaves, rarely unarmed. **Stipules** very small, often caducous. **Leaves** alternate or occasionally opposite, pari-bipinnate; pinnae opposite to sub-opposite. **Leaflets** opposite to alternate. **Inflorescences** terminal or axillary racemes (often aggregated into panicles) of pedicellate bisexual flowers; bracteoles small. **Corolla** zygomorphic, usually yellow with red markings on the median petal, or occasionally red, pink or cream; **calyx** comprising a hypanthium and 5 imbricate sepals, the lower sepal cucullate, and overlapping the other 4 in bud; **petals** 5, free, the median petal somewhat modified (either with a fleshy ligule or a patch of hairs on the inner surface between the petal blade and its claw, or the petal bilobed). **Stamens** 10, free, filaments alternately longer and shorter, usually all 10 pubescent or villous on lower half, or one or all glabrous; anthers dorsifixed, dehiscing by longitudinal slits. **Ovary** glabrous to hairy, 1-many ovuled**,** stigma cupular, funnel-shaped, terminal or laterally placed, glabrous, or the rim fimbriate (with papillate hairs), not peltate. **Fruit** laterally compressed, indehiscent, chartaceous, coriaceous or ligneous, venose, longitudinally and often broadly winged along the upper suture (wing 1 –18 mm wide). **Seeds** 1 – 13 per pod, ± transversely arranged in seed chamber, compressed, without endosperm.

Geographic distribution: A genus of approximately 24 species, mainly in Asia, extending to Australia, Polynesia, Madagascar and Africa; two species in mainland Africa (one species widespread in West Africa, the others found occurring in both West, East and Southeast Africa); one species endemic in Madagascar; five endemic in New Caledonia; one endemic in Hawaii; one in Vietnam; four species endemic to Australia (Queensland and New South Wales); one endemic in the Philippines; one in Australia and Papua New Guinea; nine species more widespread throughout Asia.

Habitat: tropical and subtropical riverine forest, lowland rain forest, swamp forest, seasonally dry forest, thicket, vine forest and wooded grassland, especially along forest and river margins.

Etymology: From *meso-* (Greek: middle) or *meizon* (Greek: greater) and *neuron* (Greek: nerve), the upper suture of the fruit is bordered by a usually broad lengthwise wing so that the suture appears as a subcentral prominent nerve or vein.

Notes: The genus is currently under revision by Ruth Clark at Kew, who kindly provided data for the genus description and species list. A list of currently accepted species, including three unpublished combinations, is given below, but excludes types, basionyms and synonymy.

Mezoneuron andamanicum Prain
Mezoneuron angolense Welw. ex Oliv.
Mezoneuron baudouinii Guillaumin
Mezoneuron benthamianum Baill.
Mezoneuron brachycarpum Benth.
Mezoneuron cucullatum (Roxb.) Wight & Arn.
Mezoneuron enneaphyllum (Roxb.) Wight & Arn. ex Voigt
Mezoneuron erythrocarpum (Pedley) R. Clark & E. Gagnon **comb. nov.**, ined.
Mezoneuron furfuraceum Prain
Mezoneuron hildebrandtii Vatke
Mezoneuron hymenocarpum Wight & Arn. ex Prain

Mezoneuron kauaiense (H. Mann) Hillebr.
Mezoneuron latisiliquum (Cav.) Merr.
Mezoneuron mindorense Merr.
Mezoneuron montrouzieri Guillaumin
Mezoneuron nhatrangense Gagnep.
Mezoneuron nitens (F. Muell. ex Benth.) R. Clark & E. Gagnon **comb. nov.**, ined.
Mezoneuron ouenensis (Guillaumin) R. Clark
Mezoneuron pubescens Desf.
Mezoneuron rubiginosum (Guillaumin) R. Clark
Mezoneuron schlechteri (Harms) R. Clark
Mezoneuron scortechinii F. Muell.
Mezoneuron sumatranum (Roxb.) Wight & Arn.
Mezoneuron traceyi (Pedley) R. Clark & E. Gagnon **comb. nov.**, ined.

References: Brenan (1967: 38 – 40); Hattink (1974); Vidal & Hul Thol (1976); Verdcourt (1979: 18 – 20); Lock (1989: 25); Herendeen & Zarucchi (1990); Pedley (1997); George (1998a: 59 – 67); Wagner et al. (1999); Du Puy & Rabevohitra (2002: 48 – 49); Brummitt & al. (2007); Clark & Gagnon (2015).

16. *Cordeauxia* Hemsl., in Bull. Misc. Inform. Kew 1907: 361 (1907).

Type species: *Cordeauxia edulis* Hemsl.

Description: Evergreen shrubs, multi-stemmed, up to 4 m tall, unarmed, red gland dots on the stems. **Leaves** alternate, pinnate. **Leaflets** in (1–) 2 – 4 (– 6) pairs per leaf, ovate-oblong, coriaceous with conspicuous red glands on the lower surface, elliptic-oblong, up to 3 (– 5) x 1.5 (– 2.5) cm. **Inflorescence** a terminal, few-flowered raceme, flowers bisexual, sub-actinomorphic. **Sepals** c. 1cm long, with red gland dots. **Corolla** yellow. **Petals** 5, free, c. 1.5 cm long, clawed. **Stamens** 10, free, filaments pubescent. **Ovary** with red gland dots. **Fruit** a compressed-ovoid, ligneous, dehiscent pod, 4 – 6 x 2 cm, with very hard, thick valves, and a cornute beak, 1 – 4-seeded. **Seeds** ovoid, 20 – 45 mm long.

Geographic distribution: A monospecific genus from NE Africa (Somalia and Ethiopia). Introduced in Israel, Kenya, Sudan, Tanzania, and Yemen (Orwa et al. 2009).

Habitat: seasonally dry tropical (semi-desert) bushland and thicket on sand.

Etymology: Named for Captain H.E.S. Cordeaux (1870–1943), one time H.M. Commissioner in Somalia.

Cordeauxia edulis Hemsl., in Bull. Misc. Inform. Kew 1907: 361 (1907). Type: Africa, Somalia, "without exact locality", *Church & Dunstan* s.n. (syntype, seeds only); *Cordeaux* s.n. (syntype, entire plant, detached flowers and pods).

References: Helmsley (1907); Brenan (1967); Roti-Michelozzi (1957); Thulin (1983: 20 – 21; 1993: 348); Brink (2006).

17. *Stuhlmannia* Taub., in Engler, Pflanzenw. Ost.-Afr. C: 201 (1895).

Type species: *Stuhlmannia moavii* Taub.

Description: Unarmed trees, up to 25 m tall. **Bark** brown, fissured and fibrous. Young stems eglandular or with small red glands. **Stipules** not seen. **Leaves** alternate, pinnate or pari-bipinnate, (1.5–) 5 – 11 (–20 cm) long, pinnae in (1–) 2 – 8 (– 11) pairs per leaf, with reddish glands. **Leaflets** opposite to sub-opposite, elliptic, 7 – 75 (– 120) x 3 – 30 (– 60) mm, obtuse at the base and apex, glabrous, eglandular or with red glands on the lower surface. **Inflorescence** a 2 – 11 cm long, terminal or axillary raceme of bisexual flowers; pedicels 3 – 13 mm long. **Calyx** comprising a hypanthium and 5 sepals, these 5 – 6.5 mm long, valvate in bud, caducous. **Corolla** sub-actinomorphic, yellow, with median petal with red markings; **petals** 5, free, obovate, 9 – 12 x 3 – 6 mm, apex rounded; median petal slightly smaller than the others. **Stamens** 10, free, 5.5 – 8 mm long, filaments pubescent. **Ovary** stipitate, with red sessile glands, glabrous to pubescent. **Fruit** a flattened, oblong, woody, elliptic pod with an acuminate apex, 4.5 – 6 x 1.5 – 2 cm, dehiscing along both sutures, valves twisting, glabrous to thinly puberulous. **Seeds** flattened, sub-circular to ovate, c. 10 – 13 x 8 – 9 mm, brown.

Geographic distribution: A monospecific genus of E Africa (Kenya and Tanzania) and N Madagascar.

Habitat: seasonally dry tropical forest, woodland on limestone and in riverine forest.

Etymology: Named for the German naturalist Franz Ludwig Stuhlmann (1863–1928).

Stuhlmannia moavii Taub., in Engler, Pflanzenw. Ost.-Afr. C: 201 (1895). Types: Tanzania, Tanga District, Pangani, [date unknown], *Stuhlmann* 467 & 616 (B, syntype †, BM, drawing of 616!)

Hoffmannseggia insolita Harms, in Notizbl. Bot. Gart. Berlin-Dahlem 13: 416 (1936). Type: Tanzania, Lindi District, *Schleiben* 5682 (holotype B†, isotypes BM, BR, K!, LISC).

Caesalpinia insolita (Harms) Brenan & J.B. Gillett, in Kew Bull. 17(2): 200 (1963).

Caesalpinia dalei Brenan & J.B. Gillett, in Kew Bull. 17(2): 198 (1963). Type: Kenya, Kwale District, Sept. 1936 (fl.), *Dale* in *Forest Herbarium* 3572 (holotype: K!, isotypes BM!, EA, P).

References: Brenan (1967: 45 – 47); Capuron (1967, under *Caesalpinia insolita*); Lewis (1996); Du Puy & Rabevohitra (2002: 48, 50, under *Caesalpinia insolita*); Lemmens (2010).

18. *Cenostigma* Tul., in Ann. Sci. Nat., Bot., sér. 2. 20: 140 (1843), emend E. Gagnon & G.P. Lewis

Diagnosis: *Cenostigma* is phylogenetically closely related to the genus *Libidibia*, but is morphologically most similar to the genus *Erythrostemon.* It differs from the latter by its leaves with alternate to subopposite (occasionally opposite) pinnae and leaflets (vs. leaves consistently with opposite pinnae and opposite leaflets in *Erythrostemon*). A number of other characters can help to distinguish between the two genera, but these are found inconsistently across species of *Cenostigma*. For example, a stellate indumentum can be found on the leaflets, inflorescences, and/or sepals of a number of *Cenostigma* species*,* but it is always lacking in species of *Erythrostemon.* Black subepidermal glands (best seen with ax 20 lens) can be found scattered in the undersurface of leaflets and/or in sepals in *Cenostigma* (vs. these always lacking in *Erythrostemon). Cenostigma* pods are generally more woody and have thickened margins or also can have an adaxial, proximal woody ridge or crest (vs. the pods less robust and lacking any woody ridge or crest in *Erythrostemon*).

Type species: *Cenostigma macrophyllum* Tul.

Description: Unarmed multi-stemmed shrubs or small compact trees, (0.3 –) 0.5 – 6 m, or large trees up to 35 m tall (species that become large trees have fluted trunks at maturity: *C. pluviosa*, *C. eriostachys*, *C. tocantinum* and *C. macrophyllum*). **Bark** smooth, or occasionally rough and flaking (*C. pluviosa*), brown, grey, or mottled silver or grey. Young stems terete, glabrous to pubescent, glandular to eglandular. **Stipules** red, with ciliate margins, broadly ovate with a rounded apex, and caducous in *C. pyramidalis,* not observed in other species. **Leaves** alternate, pinnate or impari-bipinnate, glabrous to densely pubescent, sometimes including stellate hairs or various types of sessile or stalked glands; petioles (0.1 –) 0.6 – 4.8 (–6) cm, rachis 0.5 – 17 (– 26.5) cm. Pinnate leaves are either with three leaflets or 2 – 9 pairs of opposite leaflets, (found in *C. tocantinum, C. marginata, C. pinnata,* and *C. macrophyllum*). Species with impari-bipinnate leaves have 1 – 11 pairs of opposite to alternate pinnae, plus a terminal pinna; each pinna has c. 3 –29 alternate to subopposite (occasionally opposite) leaflets. **Leaflets** vary greatly in size, 0.5 – 15 x 0.1 – 7 cm, are glossy on the upper surface, usually more or less coriaceous (chartaceous in *C. tocantinum*), ovate-elliptic, obovate, oblong-elliptic or suborbicular, apex rounded or emarginate, mucronate, base cuneate, cordate or truncate, the blade often inequilateral at the leaflet base, blade eglandular, or with black subepidermal glands (best seen with a x 20 lens) scattered in the undersurface, and/or with conspicuous, sessile or punctate glands on the undersurface or along the leaflet margins, in addition to stipitate glands;

veins usually prominent, main vein often excentric, secondary venation brochidodromous. **Inflorescences** either axillary or terminal racemes, these sometimes pyramidal in shape, or sometimes organized in large showy panicles of aggregated racemes, inflorescence rachis and pedicels densely tomentose to glabrescent, sometimes covered in stellate hairs, these occasionally intermixed with stipitate glands; pedicels 5 – 22 mm long, articulated; bracts 2.5 – 6 mm long, caducous. **Corolla** zygomorphic, bright yellow; **calyx** a short hypanthium with 5 sepals, that are 4.5 – 9 (– 11) mm long, the lower cucullate sepal generally slightly longer than the other four, apices entire or with a fimbriate-glandular margin; sepals puberulous or tomentose, sometimes with a dense stellate indumentum (*C. eriostachys*, *C. tocantinum* and *C. macrophyllum*), the sepal blades eglandular or with scattered dark, subepidermal glands, caducous, although the hypanthium persisting as a calyx ring in fruit; all 5 **petals** free and clawed, the median petal (7.5–) 9 – 15 (–19) x 5 – 13 (–17) mm , with red or orange markings on the inner surface of the blade, suborbicular to elliptic or spathulate, with a thickened, pubescent claw, the outer surface of which has short-stalked glands, these sometimes also found on the dorsal surface of the blade, lateral petals 0.9 – 2.7 x 0.4 – 2 cm, broadly elliptic, sub-rectangular, obovate or suborbicular, petal claws pubescent and with stalked-glands, these sometimes present also on the dorsal surface of the blade. **Stamens** 10, free, filaments (7 –) 8 – 14 (–21) mm long, pubescent on lower ⅔ to ½, with short-stipitate glands along their entire length (except in *C. macrophyllum)*. **Ovary** pubescent with glands intermixed, these sometimes obscured by the indumentum); stigma a terminal fringed-chamber. **Fruits** laterally compressed, coriaceous to woody pods, (3.8 –) 5 – 14 (–16) x 1.2 – 3.3 (– 3.7) cm, with conspicuously thickened margins (an adaxial, proximal woody ridge or crest in *C. macrophyllum*), elastically dehiscent (sometimes tardily) with twisting valves, at maturity either glabrous or pubescent, smooth or prominently reticulately veined (on herbarium specimens), usually eglandular or with a few scattered stipitate or sessile glands (densely glandular in *C. microphylla*). **Seeds** 2 – 6 (– 8) per pod, ovate-elliptic to ovate-orbicular, 9 – 19 x (6 –) 8 – 12 x 1 – 3 mm, ochre, brown, or mottled, shiny.

Geographic distribution: We recognise a total 20 taxa in 14 species of *Cenostigma,* all found in the Neotropics; only two of these taxa do not require new names. The majority of these species are found in central and NE Brazil, including in parts of the Amazon. Two species extend into the Amazonian arc of dry forests, including in Paraguay, Argentina and Bolivia, and one species is also found in the seasonally dry inter-Andean valleys of Peru. They are also found across Central America, from Panama northwards and in Mexico, with endemics in Cuba and Hispaniola.

Habitat: seasonally dry tropical bushland and thicket (restinga, caatinga, semi-arid thorn scrub), wooded grassland (cerrado and cerradão) and terra firme forest.

Etymology: From *ceno-* (Greek: empty) and *stigma*, presumably alluding to the chambered stigma (a character of many species of the Caesalpinia Group, and not restricted to *Cenostigma*)

Cenostigma bracteosa (Tul.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia bracteosa Tul. in Arch. Mus. Hist. Nat., Paris 4: 141 (1844). Type; Brazil, Piauí, *Gardner* 2144 (holotype P!, isotypes BM!, K!).
Poincianella bracteosa (Tul.) L.P. Queiroz, in Leguminosas da Caatinga: 122 (2009).

Cenostigma eriostachys (Benth.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia eriostachys Benth., Bot.Voy. Sulphur: 88 (1844). Type: Costa Rica, Cocos Island, *Barclay* s.n. (lectotype K!, chosen by Lewis, 1998).
Poincianella eriostachys (Benth.) Britton & Rose, N. Amer. Fl. 23(5): 332 (1930).
Schizolobium covilleanum Pittier in Contr. U.S. Natl. Herb. 18:231 (1917), pro parte (flowering material only). Type: Panama: Prov. Coclé, between Aguadulce and Chico River, *Pittier* 5105.

Cenostigma gardneriana (Benth.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia gardneriana Benth. in Mart., Fl. Bras. 15 (2): 68 (1870). Type: Brazil, Piauí, between Praya Grande and Boa Esperança, Feb. 1839, *Gardner* 2148 (holotype K!, isotype BM!).
Poincianella gardneriana (Benth.) L.P. Queiroz, in Leguminosas da Caatinga: 123 (2009).

Cenostigma gaumeri (Greenman) E. Gagnon & G.P. Lewis, **comb. nov.** *Caesalpinia gaumeri* Greenman in Publ. Field Mus. Nat. Hist., Bot. Ser. 2: 330 (1912). Type: Mexico, Yucatan, Progresso, 5 March 1899, *Millspaugh* 1675 (holotype F, n.v.).

Poincianella gaumeri (Greenman) Britton & Rose in N. Amer. Fl. 23(5): 333 (1930).

Poincianella guanensis Britton in N. Amer. Fl. 23(5): 333 (1930). Type: Cuba, Remates de Guane, Pinar del Rio, April 1926, *Fors* 3965 (holotype NY!).

Caesalpinia guanensis (Britton) León in Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle" 9:12 (1950).

Cenostigma laxiflora (Tul.) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia laxiflora Tul. in Arch. Mus. Hist. Nat., Paris 4: 143 (1844). Type: Brazil, Bahia, near Villa da Barra, *Blanchet* 3146 (holotype P., n.v., isotypes BM!, BR!, F!, GH!, K!, MG!).

Caesalpinia laxiflora Tul. var. *pubescens* Benth. in Mart., Fl. Bras. 15(2): 70 (1870). Type: Brazil, Bahia, near Maracás, *Martius* s.n. (holotype M!, isotypes M!).

Poincianella laxiflora (Tul.) L.P. Queiroz, in Leguminosas da Caatinga: 123 (2009).

Cenostigma macrophyllum Tul., Ann. Sc. Nat. 2 Sér. 20: 141, pl. 3 (1843).

Type: Brazil, Mato Grosso, *Gaudichaud*, Herb. Imp. Bras. No. 213 (holotype presumed to be at P, n.v.).

Cenostigma gardnerianum Tul. (1843:141). Type: Brazil, Piauí, *Gardner* 2523 (isotype K!).

Cenostigma angustifolium Tul. (1843: 141). Type: Brazil, Bahia, Gentio do Ouro: Serra do Açuruá, *Blanchet* 2798, (syntype K!, MO!).

Cenostigma marginata E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia marginata Tul. in Arch. Mus. Hist. Nat., Paris 4: 147 (1844). Type: Bolivia, Chiquitos, near San-Juan (Bois de la Tapira), without date, *d'Orbingy* 831 (holotype P!). *Cenostigma sclerophyllum* Malme in Bih. Kongl. Svenska Vetensk.-Akad. Handl. 25 (11): 24 (1900). Type: Paraguay, Colonia Risso, near Rio Apa, 20 Oct. 1893, *Malme* 1084 (lectotype S!, chosen by Lewis, 1998, isolectotype S!).

Cenostigma microphylla (Mart. ex G.Don) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia microphylla Mart. ex G. Don, Gen. Syst. 2: 431 (1832). Type: Brazil, Bahia, in sylvis catingas, *Martius* Obsv. 2274 (lectotype M!, chosen by Lewis, 1998, isolectotypes K!, M!).

Poincianella microphylla (Mart. ex. G.Don) L.P. Queiroz, in Leguminosas da Caatinga: 124 (2009).

Cenostigma myabensis (Britton) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia myabensis Britton in Mem. Torrey Bot. Club 16: 66 (1920). Type: Cuba, Oriente, between Holguin and Myabe, April 1909, *Shafer* 1403 (holotype NY!, isotype A!).

Libidibia pauciflora Griseb. var.? *puberula* Griseb. Cat. Pl. Cub.: 79 (1866). Type: Cuba, *Wright* 2362 (incorrectly given as "1362").

Caesalpinia subglauca Britton in Mem. Torrey Bot. Club 16: 66 (1920). Type: Cuba, Oriente, near Santiago, *Britton et al.* 12596 (holotype NY!).

Caesalpinia hornei Britton, loc. cit.: 67 (1920). Type: Cuba, Ciego de Avila, Camaguey, 3 Sept. 1905, *Horne* 95 (holotype NY!).

Poincianella myabensis (Britton) Britton & Rose in N. Amer. Fl. 23(5): 334 (1930).

Poincianella subglauca (Britton) Britton & Rose, loc. cit.: 333 (1930).

Poincianella hornei (Britton) Britton & Rose, loc. cit.: 333 (1930).

Poincianella clementis Britton, loc. cit.: 333 (1930). Type: Cuba, Oriente, Renté, Santiago, July 1919, *Clement* 135 (holotype NY!, isotype HAC!).

Caesalpinia clementis (Britton) León in Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle" 9: 12 (1950).

Caesalpinia hermeliae León, loc. cit: 12 (1950). Type: Cuba, Oriente, SW of Holguin, orillas del monte de Caguairanal, 18 March 1932, *León & Garcia* 15501 (holotype LS (transferred to HAC)!, isotypes HAC!, NY!).

Caesalpinia myabensis var. *clementis* (Britton) Barreto, in Acta Bot. Cub. 89: 6 (1992).

Caesalpinia myabensis var. *hermeliae* (León) Barreto, loc. cit.: 5 (1992).

Caesalpinia myabensis var. *hornei* (Britton) Barreto, loc. cit.: 5 (1992).

Caesalpinia myabensis var. *subglauca* (Britton) Barreto, loc. cit.: 6 (1992).

Cenostigma pellucida (Vogel) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia pellucida Vogel. in Linnaea 10: 601 (1836). Type: Dominican Republic, *Ehrenberg* s.n. (isotype NY!).
Poincianella pellucida (Vogel) Britton & Rose in N. Amer. Flora 23(5): 334 (1930).

Cenostigma pinnata (Griseb.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia pinnata (Griseb.) C. Wright in Suav., Anales Acad. Ci. Med. Habana 5: 404 (1869).
Libidibia pinnata Griseb. Cat. Pl. Cub.: 79 (1866). (As "Lebidibia pinnata"). Type: Cuba, *Wright* 2360 (holotype GOET!, isotypes GH!, K!, NY!).
Caesalpinia oblongifolia Urban, Symb. Ant. 2: 281 (1900). Type as for *C. pinnata.*
Poincianella pinnata (Griseb.) Britton & Rose in N. Amer. Fl. 23(5): 335 (1930).
Poincianella oblongifolia (Urban) Britton & Rose, loc. cit. (1930).
Poincianella savannarum Britton & Wilson, loc. cit (1930). Type: Cuba, Sancti Spiritus, 20 July 1915, *León & Roca* 7835 (holotype NY!).
Caesalpinia savannarum (Britton & Wilson) León in Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle" 10 (Fl. Cub. 2): 283 (1951).
Caesalpinia oblongifolia var. *savannarum* (Britton & Wilson) A. Borhidi & O. Muniz in Bot. Közlem. 62 (1): 25 (1975).

Cenostigma pluviosa (DC.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia pluviosa DC., in Prodr. 2: 483 (1825). Type: Brazil, *Leandro di Sacramento?* 7819 (holotype P, n.v.).

Cenostigma pluviosa var. ***pluviosa***

Caesalpinia floribunda Tul. in Arch. Mus. Hist. Nat., Paris 4: 140 (1844). Type: Bolivia, Prov. de Chiquitos, camino de San Rafel a Santa Ana, without date, *Orbigny* 1039 (holotype P!, isotype G).
Caesalpinia taubertiana S. Moore in Trans. Linn. Soc. London, Bot. 4: 345 (1895). Type: Brazil, near Corumbá, Jan. 1891 – 1892, *Moore* 1037 (holotype BM!, isotype BM!).
Poincianella pluviosa (DC.) L.P. Queiroz, in Leguminosas da Caatinga: 126 (2009).

Cenostigma pluviosa var. ***intermedia*** (G.P. Lewis) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia pluviosa var. intermedia G.P. Lewis, Caesalpinia: Revis. Poincianella-Erythrostemon group: 141 (1998). Type: Brazil, Bahia, Abaíra, road to Jussiape, 15 Feb. 1987, *Harley et al.* 24326 (holotype SPF, isotype K!).

Poincianella pluviosa var. *intermedia* (G.P. Lewis) L.P. Queiroz, in Leguminosas da Caatinga: 127 (2009).

Cenostigma pluviosa var. ***peltophoroides*** (Benth.) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia peltophoroides Benth. in *Mart*., Fl. Bras. 15(2): 72 (1870). Syntypes: Brazil, Rio de Janeiro, *Glaziou* 1032 (BM!, BR!, F!); *Glaziou* 6 (BR!).

Caesalpinia pluviosa var. peltophoroides (Benth.) G.P. Lewis, in Caesalpinia: Revis. Poincianella-Erythrostemon group: 146 (1998).

Poincianella pluviosa var. *peltophoroides* (Benth.) L.P.Queiroz, in Neodiversity 5(1): 11 (2010).

Cenostigma pluviosa var. ***cabraliana*** (G.P. Lewis) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia pluviosa var. *cabraliana* G.P. Lewis, in Caesalpinia: Revis. Poincianella-Erythrostmeon group: 148 (1998). Type: Brazil, Bahia, Mun. Santa Cruz de Cabrália, c. 12 km NW of Porto Seguro, 27 Nov. 1979, *Mori et al.* 13029 (holotype CEPEC!, isotypes K!, NY).

Poincianella pluviosa var. *cabraliana* (G.P. Lewis) L.P. Queiroz, in Neodiversity 5(1): 11 (2010).

Cenostigma pluviosa var. ***maraniona*** (G.P. Lewis & C.E. Hughes) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia pluviosa var. *maraniona* G.P. Lewis & C.E. Hughes, in Kew Bull. 65(2): 213-217 (2010). Type: Peru, Cajamarca, Celendín, Marañón Valley, km 50 rd from Celendín to Leimebamba, 23 April 2002, fl. & fr., *Hughes*, *Daza & Forrest* 2215 (holotype FHO!, isotype K!, MOL!)

Cenostigma pluviosa var. ***paraensis*** (Ducke) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia pluviosa var. *paraensis* (Ducke) G.P. Lewis, in Caesalpinia: Revis. Poincianella-Erythrostemon group: 150 (1998). Type: Brazil, Pará, near Monte Alegre, *Ducke* s.n. (BM!, K!, MG, RB).

Caesalpinia paraensis Ducke in Archiv. Jard. Bot. Rio de Janeiro 4:59 (1925).

Poincianella pluviosa var. *paraensis* (Ducke) L.P.Queiroz, in Neodiversity 5(1): 11 (2010).

Cenostigma pluviosa var. ***sanfranciscana*** (G.P. Lewis) E. Gagnon, & G.P. Lewis **comb. nov.**

Caesalpinia pluviosa var. sanfranciscana G.P. Lewis, in Caesalpinia: Revis. Poincianella-Erythrostemon group: 151 (1998). Type: Brazil, Bahia, 35 km S of Livramento do Brumado, 1 April 1991, *Lewis & Andrade* 1932 (holotype CEPEC!, isotype K!).

Poincianella pluviosa var. sanfranciscana (G.P. Lewis) L.P.Queiroz, in Leguminosas da Caatinga: 127 (2009).

Cenostigma pyramidalis (Tul.) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia pyramidalis Tul. in Arch. Mus. Hist. Nat., Paris 4: 139 (1844). Type: Brazil, Jacobina, 1841, *Blanchet* 3425 (holotype P, n.v., isotypes BM!, BR!, F!, MG!).

Cenostigma pyramidalis var. ***pyramidalis***

Caesalpinia pyramidalis var. *alagoensis* Tul. in Arch. Mus. Hist. Nat., Paris 4: 140 (1844) Type: Brazil, Alagoas, banks of the Rio St. Francisco at Propiá, Feb. 1838, *Gardner* 1278 (holotpye BM!, isotypes F!, GH!, K!, US!.)

Poincianella pyramidalis (Tul.) L.P. Queiroz, in Leguminosas da Caatinga: 128 (2009).

Cenostigma pyramidalis var. ***diversifolia*** (Benth.) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia pyramidalis var. *diversifolia* Benth. in *Mart.*, Fl. Bras. 15(2): 69 (1870). Type: Brazil, Maranhão, June 1841, *Gardner* 6006 (lectotype K!, chosen by Lewis, 1998, isolectotype BM!).

Cenostigma tocantinum Ducke in Arch. Jard. Bot. Rio de Janeiro 29, pl. 10 (1915). Type: Brazil, Pará, Alcobaça, Rio Tocantins, *Ducke* s.n., H.A.M.P. no. 15643 (holotype MG, n.v.).

References: Lewis (1987: 34 – 35); Freire (1994); Ulibarri (1996); Lewis (1998); de Queiroz (2009: 129 – 130, see also as *Poincianella,* 121 – 128) Warwick & Lewis (2009); Lewis & al. (2010).

19. *Libidibia* (DC.) Schltdl., in Linnaea 5: 192 (1830), emend E. Gagnon & G.P. Lewis

Diagnosis: *Libidibia* is closely related to the genus *Cenostigma*, but differs by its indehiscent, oblong-elliptic to suborbicular pods, that are eglandular and glabrous (vs. oblong-elliptic pods, that are elastically dehiscent with twisting valves, and with conspicuously thickened margins or with an adaxial, proximal woody ridge or crest, that is either glabrous or pubescent, and eglandular or with stipitate to sessile glands), as well as by its leaflets which are always opposite (vs. leaflets alternate to subopposite, except in species with pinnate rather than bipinnate leaves). All but two species of *Libidibia* also have a distinctive smooth patchwork bark in shades of grey, white and pale green (vs. smooth, or less commonly rough, and flaking brown, grey or mottled silver bark in species of *Cenostigma*). *Libidibia* also lacks a number of characters that are diagnostic of many species of *Cenostigma,* but not found ubiquitously throughout the genus, such as the presence of a stellate indumentum on leaves and/or inflorescences, or black sub-epidermal glands scattered in the undersuface of leaflets and/or in sepals (these best seen with a x20 lens).

Type species: *Libidibia coriaria* (Jacq.) Schltdl. (*Poinciana coriaria* Jacq.)

Caesalpinia section *Libidibia* DC. (1825).
Stahlia Bello (1881), **synon. nov.**

Description:

Small to medium-sized or large unarmed trees, 6 – 20+ meters in height. **Bark** smooth, with a patchwork of various shades of grey, white and pale green (except in *L. coriaria* and *L. monosperma,* where it is rough and furrowed). **Stipules** not seen. **Leaves** alternate, imparibipinnate (pinnate in *L. monosperma*); pinnae (in bipinnate species) in 2 – 10 opposite pairs, plus a single terminal pinna. **Leaflets** opposite, in 3 – 31 pairs per pinna, ovate, elliptic to oblong, apex rounded, mucronate or acute, base often oblique, subcordate, rounded or obtuse, eglandular or with subsessile gland dots on the undersurface of the blades, on either side of the midvein, glabrous to occasionally puberulous; in bipinnate leaves leaflets vary from (3–) 4–31 x 2.5 – 14 mm; in pinnate leaves, leaflets are much larger, c. 40 – 90 x 15 – 35 mm. **Inflorescences** in terminal or axillary racemes or panicles, sometimes corymbose, with pedicellate, bisexual flowers. **Bracts** not seen. **Corolla** zygomorphic, yellow or white, the median petal sometime flecked or blotched with orange or red; **calyx** comprising a hypanthium and 5 sepals, the lower sepal slightly longer and cucullate in bud, caducous, but hypanthium persisting as a calyx ring around the pedicel as the pod matures; petals 5, free. **Stamens** 10, free, pubescent on the lower half of the filaments, eglandular (except for *L. ferrea*, which has stipitate glands). **Ovary** eglandular, glabrous or pubescent. **Fruit** a coriaceous to woody, oblong-elliptic to suborbicular, straight (contorted in *L. coriaria*), indehiscent, eglandular, glabrous, black pod (red and somewhat fleshy in *L. monosperma*), 15 – 80 x 10 – 30 mm. **Seeds** oblong to elliptic, somewhat laterally compressed, smooth.

Geographic distribution: A genus of ten taxa in seven species in the Neotropics. One species in Mexico, one widespread in Brazil, one in Colombia, Venezuela and the Antilles, one in Colombia, Ecuador and Peru, one in Paraguay, Bolivia, Argentina and SW Brazil, one endemic to Puerto Rico and the Dominican Republic, and *L. coriaria* widespread throughout Mexico, Central America, the Caribbean and NW South America. Other species perhaps waiting to be discovered and described, both in the field and in herbaria; the genus needs revising.

Habitat: seasonally dry tropical forest and scrub, in thorn forest (including Brazilian caatinga) and savanna woodland. *Libidibia monosperma* occurs along the margins of tropical mangrove swamps and in marshy deltas, in drier edaphic conditions.

Etymology: Derived from the vernacular name ‘libi-dibi’ or ‘divi-divi’ used for some species.

Libidibia coriaria (Jacq.) Schltdl., in Linnaea 5: 193 (1830).

Poinciana coriaria Jacq., in Select. Stirp. Amer. Hist. 123, pl. 175, f. 36 (flower, fruit and seed) (1763). Type: Curação, “Habitat in Curação & Carthagenae frequens; in limosis praesertim inudatisque maritimis; ad salinas”, [no date], *Jacquin* s.n. (holotype probably in W, photo. Field Museum 1794 of probable isotype “Hb. Willdenow” (fl.) B y micro. Reprod. of the same Hb. *Willdenow* 8023: SI).

Caesalpinia coriaria (Jacq.) Willd., in Sp. Pl. 2: 532 (1799).

Caesalpinia thomaea Spreng., in Syst. Veg. 2:343 (1825). Type: "Ins. S. Thomae, Bertero".

Libidibia ferrea (Mart. ex Tul.) L.P.Queiroz, in Leguminosas da Caatinga: 130 (2009).
Caesalpinia ferrea Mart. ex Tul., in Arch. Mus. Hist. Nat. Paris 4: 137 (1844). Type: "Province of Alagoas, Tropical Brazil, [no date], *Gardner* 1277 (holotype: P, n.v., isotypes BM!, K!).

Libidibia ferrea var. ***ferrea***
Caesalpinia ferrea var. *petiolulata* Tul., in Arch. Mus. Hist. Nat. Paris 4: 138 (1844). Type: Brazil: Piaui ("Piauhy"), 1839, *Gardner* 2147 (syntype K); Bahia, *Blanchet* 3264 (syntype).
Caesalpinia ferrea var. *megaphylla* Tul., in Arch. Mus. Hist. Nat. Paris 4: 139 (1844). Type: Brazil: Piaui ("Piauhy"), dry woods near Villa do Crato, Jan. 1839, *Gardner* 1934 (isotype K).

Libidibia ferrea var. ***glabrescens*** (Benth.) L.P.Queiroz, in Leguminosas da Caatinga: 131 (2009).
Caesalpinia ferrea var. *glabrescens* Benth., in Mart, Fl. Brasil 15(2): 70 (1870). Type: Brazil: Sergipe-Alagoas, "banks of the Rio St. Francisco", Feb. 1838, *Gardner* 1276 (holotype K).

Libidibia ferrea var. ***leiostachya*** (Benth.) L.P.Queiroz, in Neodiversity 5(1): 11 (2010).

Caesalpinia ferrea Mart. ex Tul. var. *leiostachya* Benth. in Mart. Fl. Bras. 15(2): 70 (1870). Type: Brazil, "prope Rio de Janeiro juxta viam ad Jacarépaguá ducentem", *Glaziou* 2555.
Caesalpinia leiostachya (Benth.) Ducke, Mem. Inst. Oswaldo Cruz 51: 458 (1953).

Libidibia ferrea var. ***parvifolia*** (Benth.) L.P.Queiroz, in Leguminosas da Caatinga: 133 (2009).
Caesalpinia ferrea var. *parvifolia* Benth., in Mart., Fl. Brasil 15(2): 70 (1870). Type: "in sylvis catingas de interioribus prov. Bahia", *Martius* s.n.

Libidibia glabrata (Kunth) C.Castellanos & G.P. Lewis, in Revista Acad. Colomb. Ci. Exact. 36(139): 183 (2012).

Caesalpinia glabrata Kunth, in Nov. Gen. Sp. 6: 326 (1823). Type: Peru, "Crescit inter urbem Caxamarcae et pagum Madgalenae, Peruvia", *M.A. Bonpland* 3712 (holotype P, n.v., photo K!, photo and fragment F 937253).

Libidibia corymbosa (Benth.) Britton & Killip, Ann. N. Y.Acad. Sci. 35(3): 189 (1936).

Caesalpinia corymbosa Benth., in Pl. Hartw.: 117 (1832). Type: Ecuador, Guayaquil, without date, *Hartweg* 651 (holotype K; isotypes: fragment F [No. 937045], K, P (two sheets: P02737048!, P02737051!), photo[no. 1774] of the isotype at F).

Caesalpinia paipai Ruíz & Pav., in Fl. Peruv. 4, Ic. 375 (1830). Type: Peru, "Limae & Chancay" (lectotype: based on Ic. 375, fragment of the material probably used for the illustration "Hb. Ruíz & Pavon, Peru, Chacau" MA: F 842538).

Caesalpinia paipai var. *pubens* J.F. Macbr., in Field Mus. Nat. Hist. Bot. Ser. (Fl. Peru) 13, 3, 1: 193 (1943). Type: Peru, Dpto. Piura: Salitral y Serrán, III-1912, *Weberbauer* 5994 (holotype: F).

Libidibia monosperma (Tul.) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia monosperma Tul., in Arch. Mus. Hist. Nat. Paris 4: 148. (1844). Type: Puerto Rico, without location or date, *A. Plée* 713 (P barcode P03090076) (lectotype selected by Santiago-Valentín, Sánchez-Pinto & Francisco- Ortega, 2015).

Stahlia monosperma (Tul.) Urb., in Symb. Antill. 2(2): 285 (1900).

Stahlia monosperma var. *domingensis* Standl, in Trop. Woods 40: 16 (1934). Type: Dominican Republic, delta of Soco River, *J.C. Scarff* ("type" Hb. Field Mus. No. 7147180; Yale No. 27244).

Stahlia maritima Bello, in Anales Soc. Esp. Hist. Nat. 10: 255 (1881). Type: Puerto Rico, Guánica, in sylvis inter Barina et la Boca, 2 March 1886, *P.E.E. Sintensis* 3876 (neotype NY, selected by Santiago-Valentín, Sánchez-Pinto & Francisco- Ortega, in press 2015, isoneotypes BM, G, GH, NY, P, W).

Libidibia paraguariensis (D. Parodi) G.P. Lewis, in Mabberley, Pl. Book (ed. 3): 1021 (2008).

Acacia paraguariensis D. Parodi, in Revista Farm. 3: 7 (1862). Type: Paraguay, "Arbor sylvestris in ripa fluminis Paraguay" (holotype: probably at BAF, not found).

Caesalpinia paraguariensis (D. Parodi) Burkart, in Darwiniana 10(1): 26 (1952).

Caesalpinia melanocarpa Griseb., in Abh. Königl. Ges. Wis. Göttingen (Pl. Lorentz) 19: 80 (1874). Type: Argentina, Tucumán, infrecuens in sylvis subtropicis et in campis, pr. La Cruz, 20 – 24 IV 1872, *Lorentz* 196. (holotype: GOET, n.v.; isotypes: CORD, SI).
Caesalpinia coriaria Micheli, in Mem. Soc. Phys. Genève 29(7): 42 (1883), non Willd. Type: Paraguay, Assomption in hortis culta, *Balansa* 1397 and 1397a (syntypes BAF, G, K).

Libidibia punctata (Willd.) Britton, in Sci. Surv. Porto Rico & Virgin Islands 5: 378 (1924).
Caesalpinia punctata Willd., in Enum. Pl. 455 (1809). Type: Herb. Willd. 822, plant cult. Source erroneously attributed to Brazil.
Caesalpinia granadillo Pittier, in Bol. Cien. Técn. Mus. Com. Venez. 1:56 (1926). Type: Venezuela, Zulia: selva montañosa de San Martím, Río Palmar, 15-X-1922, *Pittier* 10515 (syntype probably in US and VEN, n.v.); Miranda: Lomas del Jalillal, 7-III-1923, *Pittier* s.n. (syntypes probably in US and VEN, seen.v.).
Libidibia granadillo (Pittier) Pittier, in Man. Pl. Usual. Venez. (Suppl.): 37 (1939).
Libidibia ebano (H. Karst.) Britton & Killip, in Ann. New York Acad. Sci. 35(4): 189 (1936).
Caesalpinia ebano H. Karst., in Fl. Columb. 2: 57, pl. 129 (1862). Type: Colombia, "regiones septentrionales calidus, siccas".

Libidibia sclerocarpa (Standl.) Britton & Rose, in N. Amer. Fl. 23 (5): 319 (1930).
Caesalpinia sclerocarpa Standl., in Contrib. U. S. Nat. Herb. 20(6): 214 – 215 (1919). Type: Mexico, Oaxaca, between San Geronimo and La Venta, alt. 50 m, 13 July 1895, *E.W. Nelson* 2784 (holotype: US 229315, n.v.).

References: Britton (1927); Britton & Rose (1930: 221, 318 – 319); Burkart (1936, *Caesalpinia melanocarpa:* 78 – 82); Macbride (1943, *Caesalpinia paipai*: 193 – 194); Little & Wadsworth (1964); Ford (1995); U.S. Fish and Wildlife Service (1995); Ulibarri (1996); de Queiroz (2009: 130 – 133); Borges et al. (2012); Barreto Valdes (2013).

20. *Balsamocarpon* Clos, in Fl. Chile. 2(2): 226; Atlas Botanico t. 20 (1846).

Type species: *Balsamocarpon brevifolium* Clos

Description:

Shrub 1 – 2 m tall, with long terete branches, and with leaves in fascicles on short brachyblasts; thin, straight, spines present along the branches, 3 – 5 mm long, often caducous. **Stipules** deltoid, hairy, glandular. **Leaves** alternate, pinnate, 3 – 8 mm long. **Leaflets** in 3 – 4 pairs, elliptic-obovate to orbicular, 1.5 – 4.5 x 1 – 2 mm, glabrous, fleshy. **Inflorescences** short (c. 8 – 12 mm long) racemes of pedicellate, bisexual flowers; pedicels and rachis hairy and glandular; bracts deltoid, hairy and glandular. **Corolla** sub-zygomorphic, yellow; **calyx** comprising a hypanthium and 5 sepals, c. 5 – 6 x 4.2 mm, fimbriate, hairy and with glandular trichomes, sepals persistent in fruit; **petals** 5, free, obovate, subequal, short-clawed, 10 x 3 – 4.5 mm, with glandular trichomes on the dorsal surfaces. **Stamens** 10, free, filaments pubescent, eglandular. **Ovary** glandular, with a fine pubescence, stigma a fringed chamber. **Fruit** a thick, turgid, resinous, indehiscent pod, 2.5 – 4 x 1.5 cm, 3 – 4-seeded.

Geographic Distribution: Endemic to Northern Chile, from the Coquibo and La Serena valleys.

Habitat: desert scrub, rocky hillsides.

Balsamocarpon brevifolium Clos, in Fl. Chile. 2 (2): 228-229; Atlas Botanico t. 20 (1846). Type: Chile, “In collibus Copiapo et Coquimbo”, without date, *Gay* s.n. (holotype: P00724077!)
Caesalpinia brevifolia (Clos) Benth., in Gen. Pl. 1(2): 566 (1865).

References: Burkart (1940: 162); Ulibarri (1996); Ulibarri (2008); Nores et al. (2012).

21. ***Zuccagnia*** Cav., Icon. 5: 2 (1799) (nom. cons.).

Type species : *Zuccagnia punctata* Cav.

Decription: **Shrubs**, 1 – 5 m. **Leaves** alternate, pinnate, (2–) 3 – 5 (–6) cm long. **Stipules** caducous. **Leaflets** in 5 – 13 subopposite pairs, elliptic-linear, rarely obovate, 4 – 14 x 1 – 3 mm, with glandular dots on both surfaces of the leaflet blades. **Inflorescences** terminal, erect racemes; bracts deltoid, glabrous, glandular, caducous. **Corolla** zygomorphic, yellow; **calyx** comprising a hypanthium and 5 glabrous sepals, persistent after fruit develops, the lower sepal cucullate and covering the other four in bud; **petals** 5, free,obovate to broadly obovate , short-clawed, glandular trichomes on the dorsal surface of the petal blades. **Stamens** 10, free, pubescent; anthers dorsifixed. **Ovary** pilose. **Fruit** an ovoid-acute, oblique, laterally compressed, indehiscent (?) pod, with a short stipe and long reddish brown bristles, c. 1 x 0.6 cm, 1-seeded.

Geographic Distribution: One species occurring in north-western Argentina and western Chile.

Habitat: dry temperate upland and montane brushland, thicket and sandy plains.

Etymology: Named for the Italian physician, traveller and plant collector, Attilio Zuccagni (1754–1807).

Zuccagnia punctata Cav., Icon. 5: 2, t. 403 (1799). Type: Chile, “Chilensibus montibus, in tractu a Portillo usque ad scaturigines vulgo Manantiales”.

References: Burkart (1952: 184 – 185); Ulibarri (in Kiesling & al. 1994: 286), Ulibarri (2005); Ulibarri (2008); Nores et al. (2012).

22. *Stenodrepanum* Harms, in Notizbl. Bot. Gart. Berlin-Dahlem 7: 500 (1921).

Type species: *Stenodrepanum bergii* Harms.

Description: Suffrutescent shrub, (10) – 20 – 40 cm tall, with gemmiferous or tuber-like roots; glabrous, with globose sessile glands scattered along the branches. **Stipules** ovate, membranous, 2.5 – 4 x 2 – 2.5 mm. **Leaves** alternate, impari-bipinnate, 4 – 10 cm long; pinnae in 1 – 3 pairs, plus a terminal pinna. **Leaflets** in 5 – 9 pairs per pinna, obtuse, 5 – 12 x 2 – 5.5 mm, with a crenulate, glandular margin, and with some embedded glands on the lower surface. **Inflorescence** a lax, terminal raceme, 4 – 14 cm long, with pedicellate, bisexual flowers. **Corolla** zygomorphic, yellow, the median petal with red markings; **calyx** comprising a hypanthium and 5 sepals, glabrous, glandular, the lower cucullate sepal covering the other four in bud; **petals** 5, obovate, with stipitate glands on their dorsal surfaces. **Stamens** 10, filaments pubescent and glandular. **Ovary** glandular. **Fruit** a linear to slightly falcate, cylindrical, torulose pod, 30 – 60 x 2 – 2.5 mm, 1 – 5-seeded. **Seeds** ovoid.

Geographic Distribution: A monospecific genus endemic to Central and Western Argentina.

Habitat: subtropical wooded grassland and scrub, especially on salt pans.

Etymology: From *steno-* (Greek: narrow) and *drepano-* (Greek: sickle), in allusion to the narrow sickle-shaped fruit.

Stenodrepanum bergii Harms, in Notizbl. Bot. Gart. Berlin-Dahlem 7: 500 (1921). Type: Argentina, “Am Rande der Sahsteooe bei Totoralejos nur an einer Stelle”, *C. Berg* 201 (May 1875).

References: Ulibarri (1978;and in Kiesling et al., 1994: 285); Ulibarri (2008); Caponio et al. (2012); Nores et al. (2012).

23. *Hoffmannseggia* Cav., Icon. 4: 63 (1798).

Type species: *Hoffmannseggia falcaria* Cav.

Larrea Ortega (1797), nom. rejec. against *Larrea* Cav. (1800) in the Zygophyllaceae.
Moparia Britton & Rose (1930).

Description: Perennial herbs (usually with a basal rosette habit), **or subshrubs**, unarmed, often with gemmiferous or tuberous roots, pubescent and with gland-tipped trichomes. **Stipules** not seen. **Leaves** alternate, impari-bipinnate; pinnae opposite. **Leaflets** small and numerous, glabrous, pubescent and glandular. **Inflorescences** terminal or axillary racemes of pedicellate, bisexual flowers; bracts often caducous. **Corolla** zygomorphic, yellow to orange, the median petal often with red markings; **calyx** comprising a hypanthium and 5 sepals, these weakly imbricate, persistent following pod maturation (except in two species, *H. microphylla* and *H. peninsularis*, where they are not always persistent); **petals** 5, free, their claws coarsely grooved. **Stamens** 10, free, filaments pubescent. **Ovary** glabrous to pubescent, eglandular to glandular; stigma apical, concave. **Fruit** a laterally compressed, straight or falcate pod, with the sutures almost parallel, papery to leathery, glabrous to pubescent, eglandular or with glandular trichomes, indehiscent or dehiscent, with twisting valves. **Seeds** compressed, ovoid.

Geographic distribution: *Hoffmannseggia* comprises 25 taxa in 23 species: 10 restricted to North America (southern USA and Mexico), 12 restricted to South America (Peru, Bolivia to south-central Argentina and Chile, and mainly Andean), one species (*H. glauca* (Ortega) Eifert) occurs throughout the range of the genus.

Habitat: subtropical desert and semi-desert grassland, often in open areas and on disturbed sites, on sandy, rocky or calcareous soils.

Etymology: Named for the German botanist, entomologist and ornithologist, Johann Centurius Graf von Hoffmannsegg (1766–1849).

Notes: A complete synopsis and key to species (with the exception of *H. aphylla)* is available in Simpson & Ulibarri (2006). A list of accepted species is given below, but excludes types and synonymy.

Hoffmannseggia arequipensis Ulibarri
Hoffmannseggia doelli Phil.
    subsp. ***doellii***
    subsp. ***argentina*** Ulibarri
Hoffmannseggia drepanocarpa A. Gray
Hoffmannseggia drummondii Torr. & A. Gray
Hoffmannseggia erecta Phil.
Hoffmannseggia eremophila (Phil.) Burkart ex Ulibarri
Hoffmannseggia glauca (Ortega) Eifert
Hoffmannseggia humilis (Mart. & Galeotti) Hemsl.
Hoffmannseggia intricata Brandegee
Hoffmannseggia microphylla Torr.
Hoffmannseggia minor (Phil.) Ulibarri
Hoffmannseggia miranda Sandwith
Hoffmannseggia oxycarpa Benth.
    subsp. ***oxycarpa***
    subsp. ***arida*** (Rose) B.B. Simpson
Hoffmannseggia peninsularis (Britton) Wiggins
Hoffmannseggia prostrata Lag. ex DC.
Hoffmannseggia pumilio (Griseb.) B.B. Simpson
Hoffmannseggia repens (Eastw.) Cockerell
Hoffmannseggia tenella Tharp & L.P. Williams
Hoffmannseggia trifoliata Cav.
Hoffmannseggia viscosa (Ruiz & Pav.) Hook.
Hoffmannseggia watsonii (Fisher) Rose
Hoffmannseggia yaviensis Ulibarri

References: Britton & Rose (1930, under *Larrea* & *Moparia*); Burkart (1936); Macbride (1943); Ulibarri (1979, 1996); Simpson (1999); Simpson et al. (2004, 2005); Lewis (1998, see *Caesalpinia pumilio:* 171 – 173); Simpson & Ulibarri (2006); Lewis & Sotuyo (2010).

24. *Arquita* E. Gagnon, G.P. Lewis & C.E. Hughes, Taxon 64(3): 479 (2015).

Type species: *Arquita mimosifolia* (Griseb.) E. Gagnon, G.P. Lewis & C.E. Hughes

Description: Small to medium-sized, often decumbent **shrubs**, 0.3 –2.5 m in height, slender in stature, usually with glandular trichomes on various parts of the plant. Young stems and inflorescence rachises red-orange to maroon. **Stipules** ovate-obovate to deltoid, chartaceous, 2.5–5.5 mm long, usually with a fimbriate-glandular margin and short-stalked glands (except in some specimens of *A. ancashiana*), caducous. **Leaves** bipinnate, with 1 to 5 pairs of pinnae, usually plus a single terminal pinna; petiole (0.3 –) 0.5 – 6 cm long; rachis 0.5 – 6 cm long (but sometimes absent). **Leaflets** usually in 4 to 12 opposite pairs per pinna, oblong-obovate, 2.5 – 10 (– 14) × 1 – 3.5 (– 6) mm, often with maroon/black glands in the depressions of the crenulated leaflet margins, and sometimes with occasional sessile black glands on the undersurface of leaflet blades (in *Arquita ancashiana* the glands occur in a submarginal position on the lower half of the basal leaflets of the pinnae.) **Inflorescences** leaf-opposed, in determinate racemes (with only 1 to 2 flowers open at a given time), (5–) 7 – 21 (– 41.5) cm long; bracts lanceolate, acuminate, either eglandular or covered in gland-tipped trichomes, 2.75–7 mm long, caducous; **Corolla** zygomorphic, yellow to orange; **calyx** comprising a hypanthium, and 5 sepals, that are 6 – 11 mm long, and caducous; the lower sepal is cucullate, and sepals either have an entire or glandular-fimbriate margin; **petals** 5, median petal 6 – 17 × 4 – 12 mm, claw pubescent at the base, either flat or inrolled, sometimes with stipitate-glandular trichomes on the dorsal surface of the whole petal; upper and lower lateral petals 6 – 17 × 3 – 12 mm. **Stamens** 10, free, 5 – 13 mm long, anthers 0.75 – 2.3 mm long, the stamens deflexed and loosely grouped around the gynoecium. **Ovary** usually covered with gland-tipped trichomes. **Fruits** laterally compressed, lunate-falcate pods with a marcescent style, covered sparsely to densely with gland-tipped trichomes, these sometimes dendritic, 2 – 4.7 ×(0.7 –)0.9 – 1 cm. **Seeds** laterally compressed, ovate-orbicular, 4.5– 6 × 3.5 – 4.5 × 1 mm, the testa shiny olive-grey, sometimes mottled or streaked black.

Geographic distribution: The genus *Arquita* comprises six taxa in five species. They occur in disjunct inter-Andean valleys, in Ecuador, Peru, Bolivia and Argentina.

Habitat: seasonally dry, montane, rupestral habitats in inter-Andean valleys.

Etymology: The genus name *Arquita* is the vernacular name of *Caesalpinia trichocarpa* in Argentina (Ulibarri, 1996).

Notes: A revision with a complete key to species is available in Gagnon et al. (Taxon 64(3): 468 – 490, 2015).

Arquita ancashiana (Ulibarri) E. Gagnon, G.P. Lewis & C.E. Hughes
Arquita celendiniana (G.P. Lewis & C.E. Hughes) E. Gagnon, G.P. Lewis & C.E. Hughes
Arquita grandiflora E. Gagnon, C.E. Hughes & G.P. Lewis
Arquita mimosifolia (Griseb.) E. Gagnon, G.P. Lewis & C.E. Hughes
Arquita trichocarpa (Griseb.) E. Gagnon, G.P. Lewis & C.E. Hughes
    var. ***trichocarpa***
    var. ***boliviana*** E. Gagnon, C.E. Hughes & G.P. Lewis

References: Burkart (1936); Ulibarri (1996); Lewis (1998: 167-171, 174-179); Lewis et al. (2010); Gagnon & al. (2015: 468 – 490).

25. *Pomaria* Cav., Icon. 5: 1 (1799).

Type species: *Pomaria glandulosa* Cav.

Melanosticta DC. (1825).

Cladotrichium Vogel (1837).

Description:

Small shrubs, subshrubs or perennial herbs, with an a moderate to dense indumentum of simple curled hairs on the stems, with sessile, oblate glands (drying black) intermixed amongst the hairs , and sometimes also with scattered plumose trichomes . **Stipules** laciniate, pubescent, glandular, persistent. **Leaves** alternate, impari-bipinnate; pinnae in 1 – 7 pairs, plus a terminal pinna. **Leaflets** small, numerous, always with multiple sessile glands on their lower surface (these orange in the field, drying black). **Inflorescence** a terminal or axillary raceme of bisexual, pedicellate flowers; bracts caducous. **Corolla** zygomorphic, yellow, white, red or pink; **calyx** comprising a hypanthium and 5 lanceolate sepals, the lower sepal cucullate, covering the other 4 in bud, and closely embracing the androecium and gynoecium at anthesis; **petals** 5, free. **Stamens** 10, filaments pubescent. **Ovary** eglandular or with glandular hairs; stigma in a lateral position. **Fruit** a linear or sickle-shaped, laterally-compressed pod, apex acute, glabrous or with a moderate to dense covering of plumose or stellate trichomes intermixed with sessile oblate glands (drying black), elastically dehiscent, with twisting valves. **Seeds** laterally compressed.

Geographic distribution: A genus of 17 taxa in 16 species: nine in North America (south-eastern USA, central and northern Mexico), four in South America (south-eastern Brazil, Paraguay, and Argentina), three in southern Africa (Namibia, Botswana and South Africa).

Habitat: mainly in subtropical dry areas of grassland and in degraded sites, many on limestone.

Etymology: Named for Dominic Pomar, botanist from Valencia, and doctor to Philip III (1598–1621), King of Spain.

Notes: Revisions of the species of *Pomaria* are available for North America (Simpson, 1998), for South America and Africa (Simpson & Lewis, 2003), and for Southern Africa (under the name of *Hoffmanseggia,* Brummit & Ross, 1974). A list of accepted species is given below, but excludes types and synonymy.

Pomaria austrotexana B.B.Simpson
Pomaria brachycarpa (A.Gray) B.B.Simpson
Pomaria burchellii (DC.) B.B.Simpson & G.P. Lewis
Pomaria canescens (Fisher) B.B.Simpson
Pomaria fruticosa (S. Watson) B.B. Simpson
Pomaria glandulosa Cav.
Pomaria jamesii (Torr. & A. Gray) Walp.
Pomaria lactea (Schinz) B.B. Simpson & G.P. Lewis
Pomaria melanosticta S. Schauer
Pomaria multijuga (S. Watson) B.B. Simpson
Pomaria parviflora (Micheli) B.B. Simpson & G.P. Lewis
Pomaria pilosa (Vogel) B.B. Simpson & G.P. Lewis
Pomaria rubicunda (Vogel) B.B. Simpson & G.P. Lewis
    var. *rubicunda*
    var. *hauthalii* (Harms) B.B. Simpson & G.P. Lewis
Pomaria sandersonii (Harv.) B.B. Simpson & G.P. Lewis
Pomaria stipularis (Vogel) B.B. Simpson & G.P. Lewis
Pomaria wootonii (Britton) B.B. Simpson

References: Burkart (1936: 86 – 90); Brummitt & Ross (1974, as *Hoffmannseggia*); Ulibarri (1996); Simpson (1998); Simpson & Lewis (2003); Simpson et al. (2006); Ulibarri (2008).

26. *Erythrostemon* Klotzsch, in Link, Klotzsch & Otto, Icon. Pl. Rar. Horti. Berol. 2: 97, t. 39 (1844), emend E. Gagnon & G.P. Lewis

Diagnosis: *Erythrostemon* is closely related to *Pomaria*, but differs in habit, consisting of shrubs and small to medium sized trees, and on occasion woody-based perennial herbs (vs. shrubs, suffrutescent shrubs, or perennial herbs in *Pomaria*). It also differs by its predominantly caducous sepals (two species are exceptions), that are ovate-lanceolate to orbicular in shape (vs. persistent, linear, laciniate sepals in *Pomaria*), by its leaflets that are either eglandular or with conspicuous black sessile glands along the margin, these sometimes sunken in the sinuses of the crenulated margin (vs. leaflets with multiple glandular dots on the lower surfaces, that are orange in the field, drying black), the androecium and gynoecium free (vs. the androecium and gynoecium cupped in the lower cucullate sepal), flowers with deflexed petals (vs. flowers with the two lower petals forming a horizontal platform above the lower cucullate sepal), and oblong-elliptic pods that are chartaceous to slightly woody, glabrous to pubescent, eglandular or with stipitate glands (vs. linear to sickle-shaped pods, that are glabrous or with plumose trichomes and stipitate glands).

Type species: *Erythrostemon gilliesii* (Hook.) Klotzsch

Poincianella Britton & Rose (1930).
Schrammia Britton & Rose (1930).

Description: Shrubs or small or medium-sized trees varying from (0.5 –) 1 –12 (– 20) meters tall, occasionally **woody-based perennial herbs** (e.g., *E. nelsonii* and *E. caudata*); unarmed (with the exception of *E. glandulosa*). **Bark** variable, smooth or rough, sometimes exfoliating, grey, greyish white, pale brown or reddish brown, sometimes with white or black pustular lenticels; young stems terete (angular in *E. angulata*), glabrous to densely pubescent, eglandular to densely covered in stipitate-glands. **Stipules** ovate-lanceolate, ovate to orbicular, apex acute to acuminate, caducous (persistent in *E. argentina* and *E. caudata*). **Leaves** alternate, bipinnate; petioles (0.2 –) 0.5 – 8 (– 10) cm long; rachis (0.5 –) 1.2 – 14.5 (– 21.5) cm long, or lacking; petiole and rachis glabrous to densely pubescent, eglandular or covered in stipitate glands; pinnae in 1 – 6 (–15) pairs, plus a terminal pinna (this occasionally lacking). **Leaflets** in 2 – 13 (–20) opposite pairs per pinna, size varying from a few mm in length and width (e.g., 1.4 – 3 x 0.75 – 2 mm in *E. exilifolia*), up to about 5.3 x 2.5 cm, elliptic, oblong-elliptic, obovate, ovate or sub-orbicular, leaflet blades eglandular or with conspicuous black sessile glands along the margin, these sometimes sunken in the sinuses of the crenulated margin. **Inflorescence** an axillary or terminal raceme, with pedicellate, bisexual flowers. **Corolla** zygomorphic, diverse in form and colour, ranging from bright golden yellow, to creamish yellow, salmon pink or pink-scarlet, the median petal often with red-orange markings; **calyx** a short hypanthium with 5 sepals, that are c. 4.5 – 25 mm long, glabrous to pubescent, eglandular or with stipitate-glands; lower sepal cucullate in bud; all sepals caducous, the hypanthium persistent and abscising to form a free ring around the pedicel as the fruit matures; **petals** 5, free, imbricate, the median petal 6 – 32 x 3.2 – 20 mm, the lateral petals 6 – 32 x 3.5 – 18.5 mm; petal blades eglandular or the dorsal surface covered with stipitate glands, claw margins glabrous to pubescent, eglandular or with gland-tipped trichomes. **Stamens** 10, free, 0.6 – 3.5 cm long (up to 10 cm long in *E. gilliesii*), filaments pubescent, eglandular or with stipitate glands. **Ovary** pubescent, eglandular or with sessile or stipitate glands; stigma a terminal fringed chamber. **Fruit** a chartaceous to coriaceous or slightly woody, laterally compressed pod, with a marcescent style persisting as a small beak, elastically dehiscent with twisting valves, 2.4 – 12.5 x 1 – 2.8 cm, glabrous to pubescent, eglandular or with stipitate glands, (1–) 2 – 7 (–8)-seeded. **Seeds** yellow to ochre-brown, or mottled with grey and black**.**

Geographic distribution: The genus comprises 34 taxa in 31 species. Its circumscription is emended here to include many species previously placed in Central American and Mexican *Poincianella*. A total of 22 species are found across the Southern USA, Mexico and Central America. One species occurs in the Caribbean (Cuba and Hispaniola). A total of eight species are found in South America, with one endemic in the caatinga vegetation of Brazil, wheras the seven other species are native from Argentina, Bolivia, Chile, and Paraguay.

Habitat: low-elevation seasonally dry tropical forests across Mexico, Central America, the Caribbean and in the caatinga vegetation in Brazil; also in patches of dry forests, deserts, yungas-puna transition zones, and chaco-transition forests in Argentina, Bolivia, Chile and Paraguay.

Etymology: From *erythro-* (Greek: red) and *stemon* (Greek: stamen), the type species *E. gilliesii* (Wall. ex Hook.) Klotzsch has long red exserted stamens.

Notes: Species descriptions (under *Caesalpinia* binomials) are available in Lewis (1998). A key is also available in that revision, but it includes species now considered to belong in *Cenostigma*, *Arquita*, and *Hoffmannseggia*.

Erythrostemon acapulcensis (Standl.) E. Gagnon & G.P. Lewis, **comb. nov.** *Caesalpinia acapulcensis* Standl., in Contr. U.S. Natl. Herb. 20:213 (1919). Type: Mexico, Guerrero, vicinity of Acapulco, Oct. 1894 – March 1895, *Palmer* 505 (holotype US!, isotypes F!, GH!, K!, MEXU!, NY!).
Poincianella acapulcensis (Standl.) Britton & Rose in N. Amer. Fl. 23(5): 329 (1930).

Erythrostemon angulata (Hook. & Arn.) E. Gagnon & G.P. Lewis, **comb. nov.**
Zuccagnia? angulata Hook. & Arn., Bot. Beechy's Voyage: 22 (1830).Type: Chile, Coquimbo (holotype ?E, n.v.).
Caesalpinia angulata (Hook. & Arn.) Baill., in Adansonia 9: 227 (1870).
Caesalpinia angulicaulis Clos, Fl. Chile: 223 (1846). Type: Chile, Coquimbo, Andacollo, near the Rio Hurtado (holotype ?TL, n.v.).

Erythrostemon argentina (Burkart) E. Gagnon & G.P. Lewis, **comb. nov.** *Caesalpinia argentina* Burkart in Revista Argent. Agron. 3: 105 (1936). Type: Argentina, Jujuy, Santa Cornelia, Sierra de Santa Bárbara, Nov. 1911, *Spegazzini* 2159 (holotype? LPS, n.v.).
Caesalpinia coulterioides Griseb. in Symb. Fl. Argent.: 113 (1879), pro parte.

Erythrostemon caladenia (Standl.) E. Gagnon & G.P. Lewis, **comb. nov.** *Caesalpinia caladenia* Standl., in Contr. U.S. Natl. Herb. 20: 214 (1919). Type: Mexico, Sonora, c. 5 miles below Minas Nuevas, 12 March 1910, *Rose et al.* 12660 (holotype US!, isotype NY!).
Poincianella caladenia (Standl.) Britton & Rose in N. Amer. Fl. 23(5): 329 (1930).

Erythrostemon calycina (Benth.) L.P. Queiroz, in Leguminosas da Caatinga: 121 (2009).
Caesalpinia calycina Benth., in Mart., Fl. Brasil. 15(2): 71 (1870). Type: Brazil, Bahia, near Rio de Contas, March 1817. *Prinz zu Wied-Neuwied* (Princeps Maximilianus Neovidensis) s.n. (holotype BR!).

Erythrostemon caudata (A. Gray) E. Gagnon & G.P. Lewis, **comb. nov.**
Hoffmannseggia caudata A. Gray, in Boston J. Nat. Hist. 6: 179 (1850). Type: USA, Texas, between the Nueces and the Rio Grande, *Wright* 146 (holotype GH, n.v. isotype K!).

Caesalpinia caudata (A. Gray) E.M. Fisher, in Bot. Gaz. 18: 123 (1893).
Schrammia caudata (A. Gray) Britton & Rose, in N. Amer. Flora 23(5): 317 (1930).

Erythrostemon coccinea (G.P. Lewis & J.L. Contr.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia coccinea G.P. Lewis & J.L. Contr., in Kew Bull. 49: 103 (1994). Type: Mexico, Oaxaca State, 27 March 1989, *Lewis et al.* 1802 (holotype MEXU!, isotypes FCME!, FHO!, K!, M!, NY!, SI!).

Erythrostemon coluteifolia (Griseb.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia coluteifolia Griseb., Symb. Fl. Argent.: 111 (1879). Type: Argentina, Tucumán, near El Alduralde on the route to Salta, Feb. 1873, *Lorentz & Hieronymus* 1004 (holotype GOET!, isotype CORD, n.v.)

Erythrostemon coulterioides (Griseb. emend Burkart) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia coulterioides Griseb., *emend.* Burkart, in Revista Argent. Agron. 3: 97 (1936). Type: Argentina, Jujuy, Depto. Tumbaya, El Volcán, 12 – 13 May 1873, *Lorentz & Hieronymus* 760 (holotype GOET, n.v., isotype CORD, n.v.)
Caesalpinia coulterioides Griseb., Symb. Fl. Argent: 113 (1879), (as "*coulteriodes*"), pro parte quoad material from El Volcán.

Erythrostemon epifanioi (J.L. Contr.) E. Gagnon & G.P. Lewis, **comb. nov.** *Caesalpinia epifanioi* J.L. Contr., in Anales Inst. Biol. Univ. Nac. Auton. Mexico, Bot. 58: 55 (1989). Type: Mexico: Guerrero, Mpio. of Mártires de Cuéllar, 18 Feb. 1986, *Contreras* 1825 (holotype FCME, n.v., isotype MEXU, n.v.).

Erythrostemon exilifolia (Griseb.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia exilifolia Griseb., Plant. Lorentz: 80 (1874). Type: Argentina, Catamarca, near San José, 4 Jan. 1872, *Lorentz* 352 (holotype GOET!).

Erythrostemon exostemma (DC.) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia exostemma DC., Prodr. 2: 483 (1825). Type: Mexico, a painting, one of the copies of Ic. Fl. Mex. 80, represented at G-DC by de Candolle plate 218.

Erythrostemon exostemma subsp. ***exostemma***

? Poinciana compressa Sessé & Mociño ex. G. Don, Gen. Hist. 2: 433 (1832). Type: Mexico, *Sessé & Mociño,* formerly in herb. Lambert – not located in recent times, but a specimen in the Sessé & Mociño herbarium (MA), no. 1097, labelled *Poinciana compressa,* represents *C. exostemma* according to P. Standley (fide McVaugh, 1987).

? Caesalpinia compressa (G. Don) D. Dietr. Syn. Pl. 2:1494 (1840).

Caesalpinia affinis Hemsl., Diag. Pl. Nov. Mexic. 8 (1878). Type: Guatemala, *Skinner* s.n. (holotype K!, isotype K!).

Poinciana conzattii Rose in Contr. U.S. Natl. Herb. 13:303 (1911). Type: Mexico, Tehuantepec, 1909, *Hugo & Conzatti* 2444 (holotype US!, national herbarium number 841055).

Poincianella exostemma (DC.) Britton & Rose in N. Amer. Fl. 23(5): 328 (1930).

Poincianella affinis (Hemsl.) Britton & Rose, loc. cit.: 328 (1930).

Poincianella conzattii (Rose) Britton & Rose, loc. cit.: 328 (1930).

Caesalpinia conzattii (Rose) Standl., in Trop. Woods 37: 34 (1934).

Erythrostemon exostemma subsp. ***tampicoana*** (Britton & Rose) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia exostemma subsp. *tampicoana* (Britton & Rose) G.P. Lewis, in Caesalpinia: Revis. Poincianella-Erythrostemon group: 72 (1998).

Poincianella tampicoana Britton & Rose in N. Amer. Fl. 23(5): 330 (1930). Type: Mexico, Vera Cruz, vicinity of Pueblo Viejo, 2 km S of Tampico, 1 and 2 June 1910, *Palmer* 556 (holotype US!).

Caesalpinia tampicoana (Britton & Rose) Standl., in Publ. Field Mus. Nat. Hist., Bot. Ser. 11(5): 159 (1936).

Erythrostemon fimbriata (Tul.) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia fimbriata Tul., in Arch. Mus. Hist. Nat. Paris 4: 145 (1844). Type: Bolivia: “Chivesivi, Vallé S de La Paz, alt. 8500 – 12000 ped. angl.”, *Pentland* 39 (holotype P!, isotype F!)

Caesalpinia bangii Rusby, in Mem. Torrey Bot. Club 3(3): 22 (1893). Type: Bolivia, 1891, *Bang* 757 (holotype NY!, isotypes E!, F!, GH!, K!).
Caesalpinia cromantha Burkart, in Revista Argent. Agron. 3(2): 100 (1936). Type: Argentina, Prov. Salta, Depto. Guachipas, Pampa Grande, Jan. 1897, *Spegazzini* 2198 (holotype SI!, isotype LP, n.v.).

Erythrostemon glandulosa (Bertero ex DC.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia glandulosa Bertero ex DC., Prodr. 2: 482 (1825). Type: Hispaniola, *Bertero* 84 (holotype G-DC, n.v.).
Poincianella glandulosa (Bertero ex DC.) Britton & Rose in N. Amer. Fl. 23(5): 336 (1930).

***Erythrostemon gilliesii* (**Hook.) Klotzsch, in Link, Klotsch & Otto, Ic. Pl. Rar. Horti. Berol. 2 (3): 97, t. 39 (1844).
Poinciana gilliesii Wall. ex Hook., Bot. Misc. 1: 129 (1829 [1830]). Type: Argentina, near Rio Quatro and Rio Quinto, and in La Punta de San Luis, *Gillies* s.n. (holotype K!).
Caesalpinia gilliesii (Hook.) D. Dietr., Synop. Pl. 2: 1495 (1840).

Erythrostemon hintonii (Sandwith) E. Gagnon & G.P. Lewis **comb. nov.**
Caesalpinia hintonii Sandwith in Kew Bull. 1937: 303 (1937). Type: Mexico, Guerrero, District of Coyuca, Cuajilote, 9 May 1935, *Hinton* 7746 (holotype K!, isotype A!, F!, GH!, MEXU).

Erythrostemon hughesii (G.P. Lewis) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia hughesii G.P. Lewis, in Caesalpinia: Revis. Poincianella-Erythrostemon group: 73 (1998). Type: Mexico, Oaxaca, 5 km W of Rio Grande, 25 March 1989, *Lewis et al.* 1795 (holotype K!, isotypes FCME!, FHO!, K!, MEXU!).

Erythrostemon laxa (Benth.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia laxa Benth., Pl. Hartw.: 60 (1840). Type: Mexico, Oaxaca, Teojomulco, *Hartweg* 455 (holotype BM!, isotypes E!, K!, photos F!, MEXU!).
Poincianella laxa (Benth.) Britton & Rose in N. Amer. Flora 23(5): 329 (1930).

Erythrostemon macvaughii (J.L. Contr. & G.P. Lewis) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia macvaughii J.L. Contr. & G.P. Lewis in Kew Bull. 47: 309 (1992). Type: Mexico, Guerrero, Mpio. Zirándaro de Chávez, 8 March 1988, *Contreras* 2343 (holotype FCME, isotypes K!, MEXU).
Caesalpinia laxa sensu McVaugh, pro parte quoad *McVaugh* 22517, non Benth.

Erythrostemon melanadenia (Rose) E. Gagnon & G.P. Lewis, **comb. nov.**
Poinciana melanadenia Rose in Contr. U.S. Natl. Herb. 13: 303 (1911). Type: Mexico, Puebla, near Tehuacán, 1 Sept. 1906, *Rose & Rose* 11249 (holotype US!).
Caesalpinia melanadenia (Rose) Standl., in Contr. U.S. Natl. Herb. 23: 425 (1922).
Poincianella melanadenia (Rose) Britton & Rose in N. Amer. Flora 23(5): 334 (1930).

Erythrostemon mexicana (A. Gray) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia mexicana A. Gray in Proc. Amer. Acad. Arts 5: 157 (1861). Type: Mexico, Nuevo Leon, near Monterrey, 11 Feb. 1847, *Gregg* s.n. (lectotype GH!, *fide* McVaugh, 1987).
Poinciana mexicana (A. Gray) Rose in Contr. U.S. Natl. Herb. 13: 303 (1911).
Poincianella mexicana (A. Gray) Britton & Rose in N. Amer. Fl. 23(5): 330 (1930).

Erythrostemon nelsonii (Britton & Rose) E. Gagnon & G.P. Lewis, **comb. nov.**
Poincianella nelsonii Britton & Rose in N. Amer. Fl. 23(5): 331 (1930).Type: Mexico, Guerrero, between Copala and Juchitango [Juchitan], 9 Feb. 1895, *Nelson* 2303 (holotype US!, isotypes GH!, NY!, photo MEXU).
Caesalpinia nelsonii (Britton & Rose) J.L. Contr., in Thesis, UNAM, Mexico D.F.: 91 (1991).

Erythrostemon nicaraguensis (G.P. Lewis) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia nicaraguensis G.P. Lewis, in Caesalpinia: Revis. Poincianella-Erythrostemon group: 86 (1998). Type: Nicaragua, Department of Esteli, *Hughes* 1406 (holotype MEXU!; isotypes EAP, FHO, K!, NY!).

Erythrostemon oyamae (Sotuyo & G.P. Lewis) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia oyamae Sotuyo & G.P. Lewis, in Brittonia 59: 34 (2007). Type: Mexico, Puebla, Mpio. Acatlan de Osorio, 20 km to the W of Acatlan on the road from Oaxaca City to Izucar de Matamoris (Hwy. 190), 18°17′N, 98°5′W, 19 February 1993, *J.A. Hawkins & C.E. Hughes* 23 (holotype MEXU, isotypes FHO!, K!, MEXU).

Erythrostemon palmeri (S. Wats.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia palmeri S. Wats., in Proc. Am. Acad. Arts 24: 47 (1889). Type: Mexico, Sonora, Guaymas, June 1887, *Palmer* 70 (holotype US!, isotypes GH!, K!, NY!).
Poinciana palmeri (S. Wats.) Rose in Contr. U.S. Natl. Herb. 13: 303 (1911).
Poincianella palmeri (S. Wats.) Britton & Rose in N. Amer. Flora 23(5): 332 (1930).
Poincianella arida Britton & Rose in N. Amer. Flora 23 (5): 332 (1930). Type: Mexico, Sonora, near Hermosillo, 7 March 1910, *Rose et al.* 12508 (holotype NY!).
Caesalpinia arida (Britton & Rose) Wiggins in Contr. Dudley Herb. 3(3): 69 (1940).

Erythrostemon pannosa (Brandegee) E. Gagnon & G.P. Lewis, **comb. nov.** *Caesalpinia pannosa* Brandegee, in Proc. Calif. Acad. Sci., Ser. 2: 150 (1889) and 3: 130 (1891). Type: Baja California, San Gregoria, 1 Feb. 1889, *Brandegee* s.n. (lectotype UC!, chosen by Lewis 1998).
Poinciana pannosa (Brandegee) Rose, in Contr. U.S. Natl. Herb. 13: 303 (1911).
Poincianella pannosa (Brandegee) Britton & Rose, in N. Amer. Flora 23(5): 331 (1930).
Caesalpinia mexicana A. Gray var. *californica* A. Gray, in Proc. Amer. Acad. Arts 5: 157 (1861). Type: Baja California, Cape St. Lucas, Aug. 1859 – Jan. 1860, *Xantus* 29 (lectotype GH!, chosen by Lewis 1998, isolectotype NY!).
Poinciana californica (A. Gray) Rose, in Contr. U.S. Natl. Herb. 13: 303 (1911).
Caesalpinia californica (A. Gray) Standl., in Contr. U.S. Natl. Herb. 23: 426 (1922).
Poincianella californica (A. Gray) Britton & Rose, in N. Amer. Flora 23(5): 331 (1930).
Caesalpinia arenosa Wiggins, in Contr. Dudley Herb. 3(3): 68 (1940). Type: Baja California, 4 miles S of Guadalupe, 21 March 1935, *Whitehead* 839 (holotype DS).

Erythrostemon phyllanthoides (Standl.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia phyllanthoides Standl., in Contr. U.S. Natl. Herb. 23: 425 (1922). Type: Mexico, Tamaulipas, Hacienda Buena Vista, 18 June 1919, *Wooton* s.n. (holotype US!, isotype NY!).

Poincianella phyllanthoides (Standl.) Britton & Rose in N. Amer. Fl. 23(5): 332 (1930).

Erythrostemon placida (Brandegee) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia placida Brandegee in Proc. Calif. Acad. Sci., Ser. 2, 3: 131 (1891). Type: Mexico, Baja California, La Paz, 4 Feb. 1890, *Brandegee* s.n. (lectotype UC!, chosen by Lewis 1998, isolectotype GH!).
Poinciana placida (Brandegee) Rose in Contr. U.S. Natl. Herb. 13: 303 (1911).
Poincianella placida (Brandegee) Britton & Rose in N. Amer. Fl. 23(5): 331 (1930).

Erythrostemon standleyi (Britton & Rose) E. Gagnon & G.P. Lewis, **comb. nov.**
Poincianella standleyi Britton & Rose, in N. Amer. Fl. 23(5): 330 (1930).Type: Mexico, Nayarit, Acaponeta, 9 April 1910, *Rose et al.* 14190 (holotype NY!).
Caesalpinia standleyi (Britton & Rose) Standl., in Publ. Field Mus. Nat. Hist., Bot. Ser. 11(5): 159 (1936).

Erythrostemon robinsoniana (Britton & Rose) E. Gagnon & G.P. Lewis, **comb. nov.**
Poincianella robinsoniana Britton & Rose, in N. Amer. Fl. 23(5): 330 (1930). Type: Mexico, Jalisco, Zapotlán, 25 May 1893, *Pringle* 5467 (holotype GH!, isotype MEXU!).
Caesalpinia robinsoniana (Britton & Rose) G.P. Lewis, in Caesalpinia: Revis. Poincianella-Erythrostemon group: 42 (1998).
Caesalpinia mexicana A. Gray var. *pubescens* B.L. Rob. & Greenm., in Proc. Amer. Acad. Arts 29: 386 (1894). Type as above.

Erythrostemon yucatanensis (Greenm.) E. Gagnon & G.P. Lewis, **comb. nov.**
Caesalpinia yucatanensis Greenman in Publ. Field Mus. Nat. Hist., Bot. Ser. 2: 252 (1907). Type: Mexico, Yucatan, near Izamal, 1895, *Gaumer* 371 (holotype F!, isotypes F!, K!, NY!).

Erythrostemon yucatanensis subsp. ***yucatanensis***

Caesalpinia recordii Britton & Rose, in Trop. Woods 7: 6 (1926). Type: Belize, Feb. 1926, *Record* s.n. (holotype US, isotypes F!, GH!, NY!).
Poincianella yucatanensis (Greenm.) Britton &Rose, in N. Amer. Fl. 23(5): 330 (1930).
Poincianella recordii (Britton & Rose) Britton & Rose in N. Amer. Fl. 23(5): 329 (1930).

Erythrostemon yucatanensis subsp. ***chiapensis*** (G.P. Lewis) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia yucatanensis subsp. *chiapensis* G.P. Lewis, in Caesalpinia: Revis. Poincianella-Erythrostemon group: 85 (1998). Type: Mexico, Chiapas, c. 4 km from Comalapa on road to La Trinitaria, 27 Feb. 1992, *Hughes et al.* 1684 (holotype K (sheet 2)!, isotypes E!, FHO!, K!, MEXU!, MO!, NY!).

Erythrostemon yucatanensis subsp. ***hondurensis*** (G.P. Lewis) E. Gagnon & G.P. Lewis, **comb. nov.**

Caesalpinia yucatanensis subsp. *hondurensis* G.P. Lewis, in Caesalpinia: Revis. Poincianella-Erythrostemon group: 86 (1998). Type: Honduras, Dept. Yoro, lower Aguan Valley, c. 31 km W of Olanchito, 25 March 1991, *Hughes* 1448 (holotype K!, isotype FHO!).

References: Britton & Rose (1930); Burkart (1936: 82 – 84, 97 – 108); Ulibarri (1996); Lewis (1998); de Queiroz (2009: 120 – 121).

?27. *Ticanto* Adans., Fam. Pl. 2: 319 (1763).

Type species: "H.M. 6: t. 19" (= Rheede`s Hortus Malabaricus 6, plate 19, 1686).

Caesalpinia sect. *Nugaria* DC. (1825).

Notes: More work is needed on this group of species to determine whether the clade in which they nest should be reinstated as a distinct genus or if the genus name *Ticanto* should be synonymised under another genus in the Caesalpinia Group. The list of species presented below includes those names that most probably belong in *Ticanto*, and includes their types and synonyms.

Caesalpinia caesia Handel-Mazzetti, in Öst. Bot. Z. 85:215 (1936). Type: China, Kwangsi, (fr.), *Fenzel* 3 (W).

Caesalpinia hypoglauca Chun & How, in Acta Phytotax. Sin. 7: 20, pl. 6 (1958). Type: China, Kwangtung, *H.Y. Liang* 69864 (GH).

Caesalpinia crista L. emend Dandy & Exell, in J. Bot. 76: 179 (1938). Type: no type cited in Dandy & Exell, Sri lanka (Ceylan), *Herb. Hermann,* vol. 1, fol. 68 (lectotype: BM).

Guilandina nuga L.., in Sp. Pl., ed. 2, 1: 546 (1762). Type: *Nugae silvarum* Rumph. Herb. Amboin. 5: 94, t. 50, 1747. Type: Ambon.

Caesalpinia nuga (L.) Ait. f., in Ait. Hort. Kew, ed. 2, 3: 32(1811).

Guilandina paniculata Lam., in Encycl. Meth., 1: 432 (1785). Type: India, Malabar, *Káku Múllú* Reede, Hort. Malabaricus 6: t. 19 (1686).

Caesalpinia paniculata (Lam.) Roxb., in Hort. Beng.: 32 (1814).

Genista scandens Lour., in Fl. Cochinch.: 428 (1790). Type: Cochinchina (n.v.)

Caesalpinia scandens Heyne ex Roth, in Nov. Pl. Sp.: 209 (1821). Type: Ind. Or., *Heyne* s.n. (BM, K!).

Caesalpinia chinensis Roxb., in Fl. Ind. 2: 361 (1832). Type: cultivated in the Botanic Garden at Calcutta, introduced from China.

Caesalpinia laevigata Perr., in Mém. Soc. Linn. Paris 3: 104 (1824). Type: Philippines, *Perrottet* (n.v.)

Caesalpinia elliptifolia S.J. Li, Z.Y. Chen & D.X. Zhang, in Nordic J. Bot. 22(3): 349 (2002). Type: China, Guangdong, Fengkai, Qizing, 20 July 2000, *Shi-Jin Li* 026 (holotpye IBSC).

Caesalpinia magnifoliolata Metcalf, in Lingan Sci. J. 19: 553 (1940). Type: China, Kwangsi, *Steward & Cheo* 583 (GH).

Caesalpinia rhombifolia J.E. Vidal, in Adansonia, sér.2, 15 (3): 394 (1975). Type: Vietnam (North), Quang Ninh, Dam Ha, *W.T. Tsang* 29830 (holotype P, isotypes C, E, G, K!, L, SING).

Caesalpinia sinensis (Hemsley) J.E. Vidal, in Bull. Mus. Natl. Hist. Nat., sér. 3, Bot. 27: 90 (1976). Type: China, Hupeh, Ichang, *Henry* 3113 (lectotype K!, chosen by Vidal & Hul Thol, 1976).

Mezoneuron sinense Hemsl., in J. Linn. Soc., 23: 204 (1887) (incl. var. *parvifolium* Hemsl.) Type: *Henry* 2238.

Caesalpinia tsongii Merr., in Philipp. J. Sci., 27: 162 (1925). Type: China, Szechuan, *Tsoong* 4190 (holotype: UC, isotype: GC).
Caesalpinia stenoptera Merr., in J. Arnold Arbor., 19: 35, fig. 1 (1938). Type: Vietnam, Cao Bang, Ban Gioc, *Pételot* 4757 (isotype: P!)

Caesalpinia szechuanensis Craib, Pl. Wilson., 2: 92 (1914). Type: China, Szechuan, *Wilson* 3255 (BM, E, GH, K!, US).
Caesalpinia kwangtungensis Merr., in J. Arnold Arbor. 8: 7 (1927). Type: Kwantung, *Wilson, in Canton Christ. Coll.* 12838 (LU, US, P, GH, BM).

Caesalpinia vernalis Champion, in Hook., J. Bot. & Kew Bull., Misc., 4: 77 (1852). Type: Hong Kong, “on the banks of a stream running towards little Hong-Kong”, *Champion* s.n. (? 502) in Herb. Bentham (K).

Caesalpinia yunnanensis S.J. Li, D.X. Zhang & Z.Y. Chen, in Novon 16: 78, pl. 1 & 2 (2006). Type: China, Yunnan, Xishuangbanna, *T.P. Zhu* 139 (holotype: KUN; isotype: IBSC).

References: Hattink (1974); Vidal & Hul Thol (1976); Chen et al. (2010).

2.7 Acknowledgements

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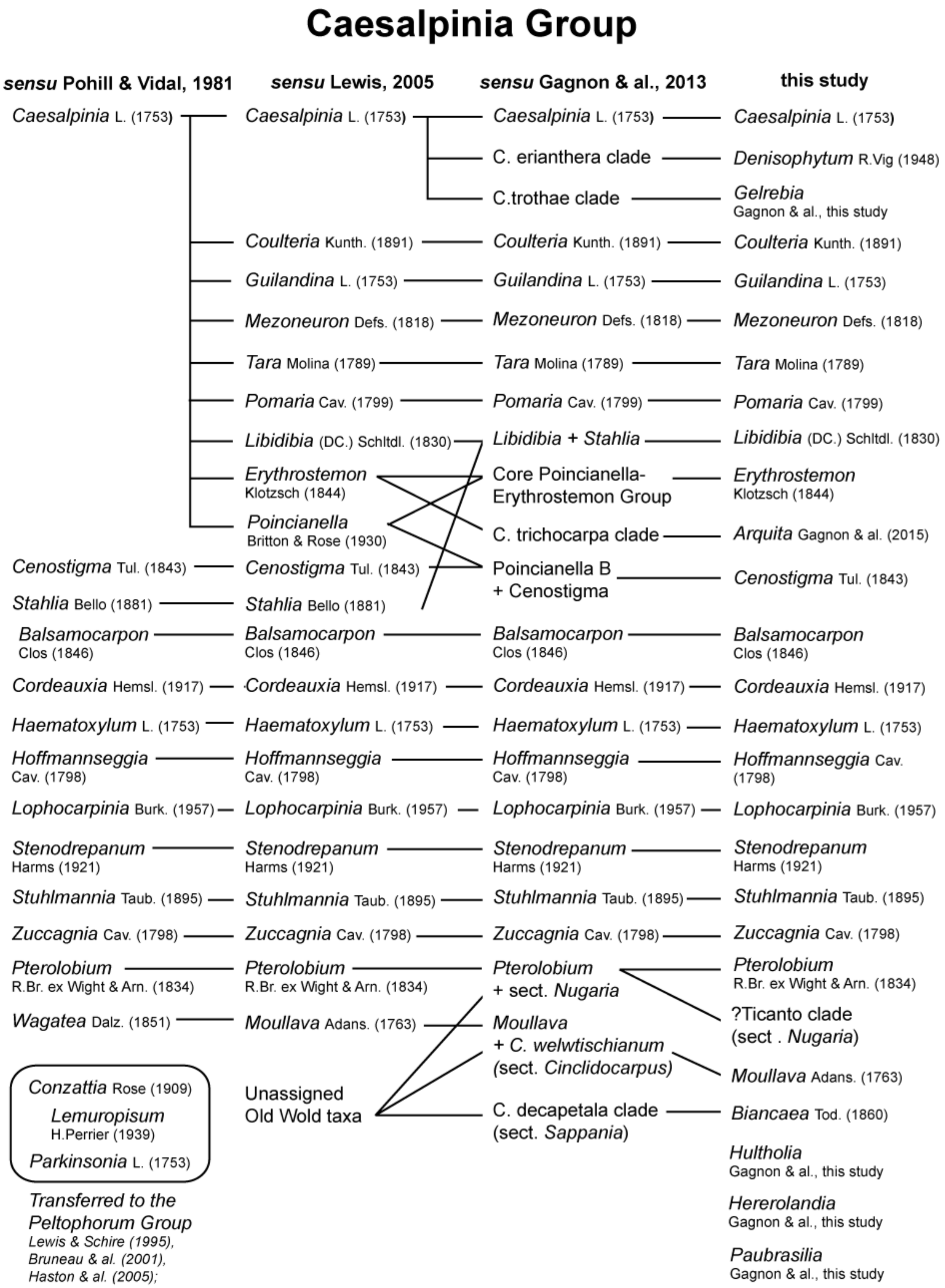
2.8 Authors contribution

EG, AB, CEH and GPL were involved in study conception and design; EG, AB, CEH, GPL, LPdQ, HCdeLima collected and provided herbarium and field samples for analysis; EG generated and assembled all the data, which she was also responsible for analysing and interpreting; EG drafted the manuscript, and critical revisions were provided by AB, CEH and GPL; EG also wrote the key, generic descriptions and provided the list of species belonging to each genus. These were all critically revised by GPL, who completed this work by verifying the nomenclature and identifying nomentaclural types for all species names and synonyms. GPL was also the main instigator behind the new generic names (*Paubrasilia*, *Hultholia*, *Hererolandia* and *Gelrebia*); Ruth Clark from Kew provided the description for *Mezoneuron* and helped revise the key when it came to the distinction between *Mezoneuron* and members of the putative genus *Ticanto.*

Figure 2.1 Comparison of generic classifications for the Caesalpinia Group proposed by Polhill & Vidal (1981), Lewis (2005), Gagnon & al., (2013, chapter 1).



Caesalpinia Group

Figure 2.2 Bayesian phylogram of the Caesalpinia Group based on 39 accessions, minimizing missing data while maximizing the taxonomic representation of each of the 27 putative genera within *Caesalpinia* s.l. Branch support values are indicated as follows: branches in bold indicate that maximum support has been attained in the parsimony, Maximum Likelihood and Bayesian analyses; otherwise, posterior probabilities are indicated above in bold, with bootstrap support from ML analyses (italicized) and parsimony analyses separated by a slash below the branches. The number of genes sampled for each taxa is indicated in parenthesis. The double asterix (**) indicates species for which genes were combined from multiple specimens.

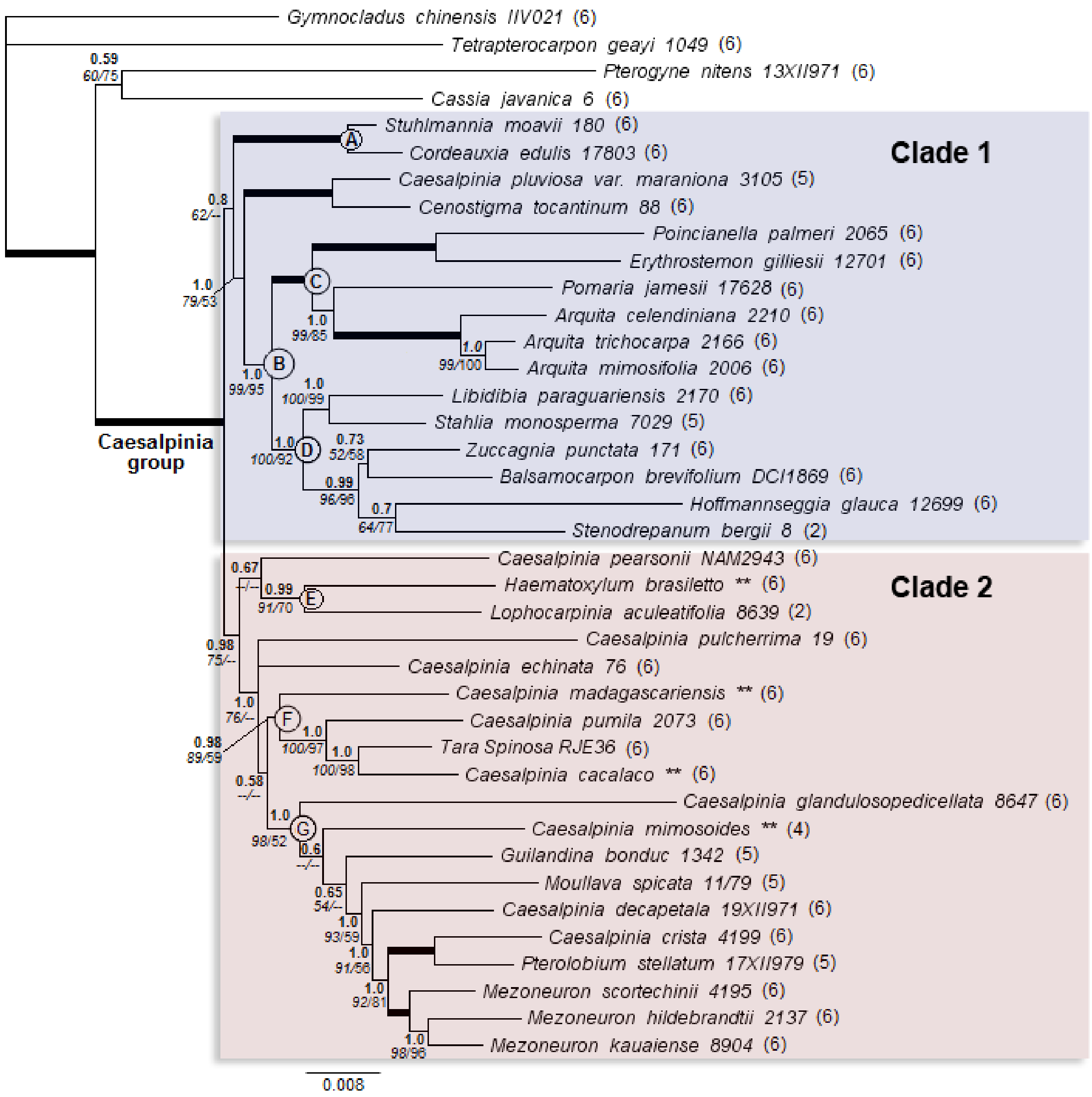
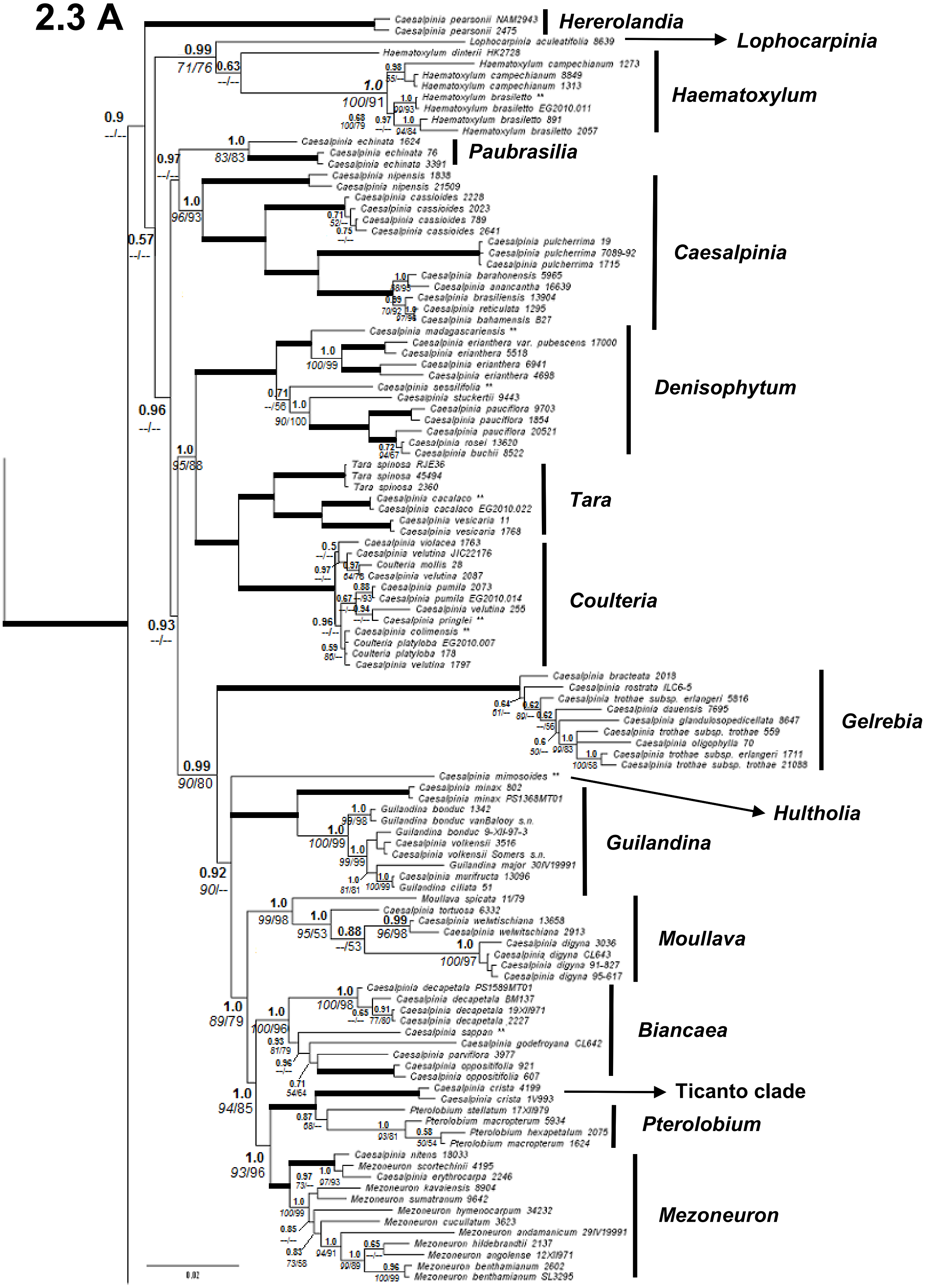


Figure 2.3 A-B-C. Bayesian phylogram of the Caesalpinia Group based on 312 accessions, including only accessions with two or more loci. Branch support values are indicated as follows: branches in bold indicate that maximum support has been attained in the parsimony, Maximum Likelihood and Bayesian phylogenetic analyses; otherwise, posterior probabilities are indicated above in bold, with bootstrap support from ML analyses (italicized) and parsimony analyses separated by a slash below the branches. The 26 genera accepted in the classification presented in this study are indicated in bold, as well as the Ticanto clade.

2.3 A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Lophocarpinia
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Haematoxylum campechianum 1273
Haematoxylum campechianum 8849
Haematoxylum campechianum 1313
Haematoxylum brasiletto **
Haematoxylum brasiletto EG2010.011
Haematoxylum brasiletto 891
Haematoxylum brasiletto 2057
Haematoxylum
Caesalpinia echinata 1624
Caesalpinia echinata 76
Caesalpinia echinata 3391
Paubrasilia
Caesalpinia nipensis 1838
Caesalpinia nipensis 21509
Caesalpinia cassioides 2228
Caesalpinia cassioides 2023
Caesalpinia cassioides 789
Caesalpinia cassioides 2641
Caesalpinia pulcherrima 19
Caesalpinia pulcherrima 7089-92
Caesalpinia pulcherrima 1715
Caesalpinia barahonensis 5965
Caesalpinia anancantha 16639
Caesalpinia brasiliensis 13904
Caesalpinia reticulata 1295
Caesalpinia bahamensis B27
Caesalpinia
Caesalpinia madagascariensis **
Caesalpinia erianthera var. pubescens 17000
Caesalpinia erianthera 5518
Caesalpinia erianthera 6941
Caesalpinia erianthera 4698
Caesalpinia sessilifolia **
Caesalpinia stuckertii 9443
Caesalpinia pauciflora 9703
Caesalpinia pauciflora 1854
Caesalpinia pauciflora 20521
Caesalpinia rosei 13620
Caesalpinia buchii 8522
Denisophytum
Tara spinosa RJE36
Tara spinosa 45494
Tara spinosa 2360
Caesalpinia cacalaco **
Caesalpinia cacalaco EG2010.022
Caesalpinia vesicaria 11
Caesalpinia vesicaria 1768
Tara
Caesalpinia violacea 1763
Caesalpinia velutina JIC22176
Coulteria mollis 28
Caesalpinia velutina 2087
Caesalpinia pumila 2073
Caesalpinia pumila EG2010.014
Caesalpinia velutina 255
Caesalpinia pringlei **
Caesalpinia colimensis **
Coulteria platyloba EG2010.007
Coulteria platyloba 178
Caesalpinia velutina 1797
Coulteria
Caesalpinia bracteata 2018
Caesalpinia rostrata ILC6-5
Caesalpinia trothae subsp. erlangeri 5816
Caesalpinia dauensis 7695
Caesalpinia glandulosopedicellata 8647
Caesalpinia trothae subsp. trothae 559
Caesalpinia oligophylla 70
Caesalpinia trothae subsp. erlangeri 1711
Caesalpinia trothae subsp. trothae 21088
Gelrebia
Caesalpinia mimosoides **
Hultholia
Caesalpinia minax 802
Caesalpinia minax PS1368MT01
Guilandina bonduc 1342
Guilandina bonduc vanBalooy s.n.
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Caesalpinia volkensii 3516
Caesalpinia volkensii Somers s.n.
Guilandina major 30IV19991
Caesalpinia murifructa 13096
Guilandina ciliata 51
Guilandina
Moullava spicata 11/79
Caesalpinia tortuosa 6332
Caesalpinia welwitschiana 13658
Caesalpinia welwitschiana 2913
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Caesalpinia digyna CL643
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Caesalpinia digyna 95-617
Moullava
Caesalpinia decapetala PS1589MT01
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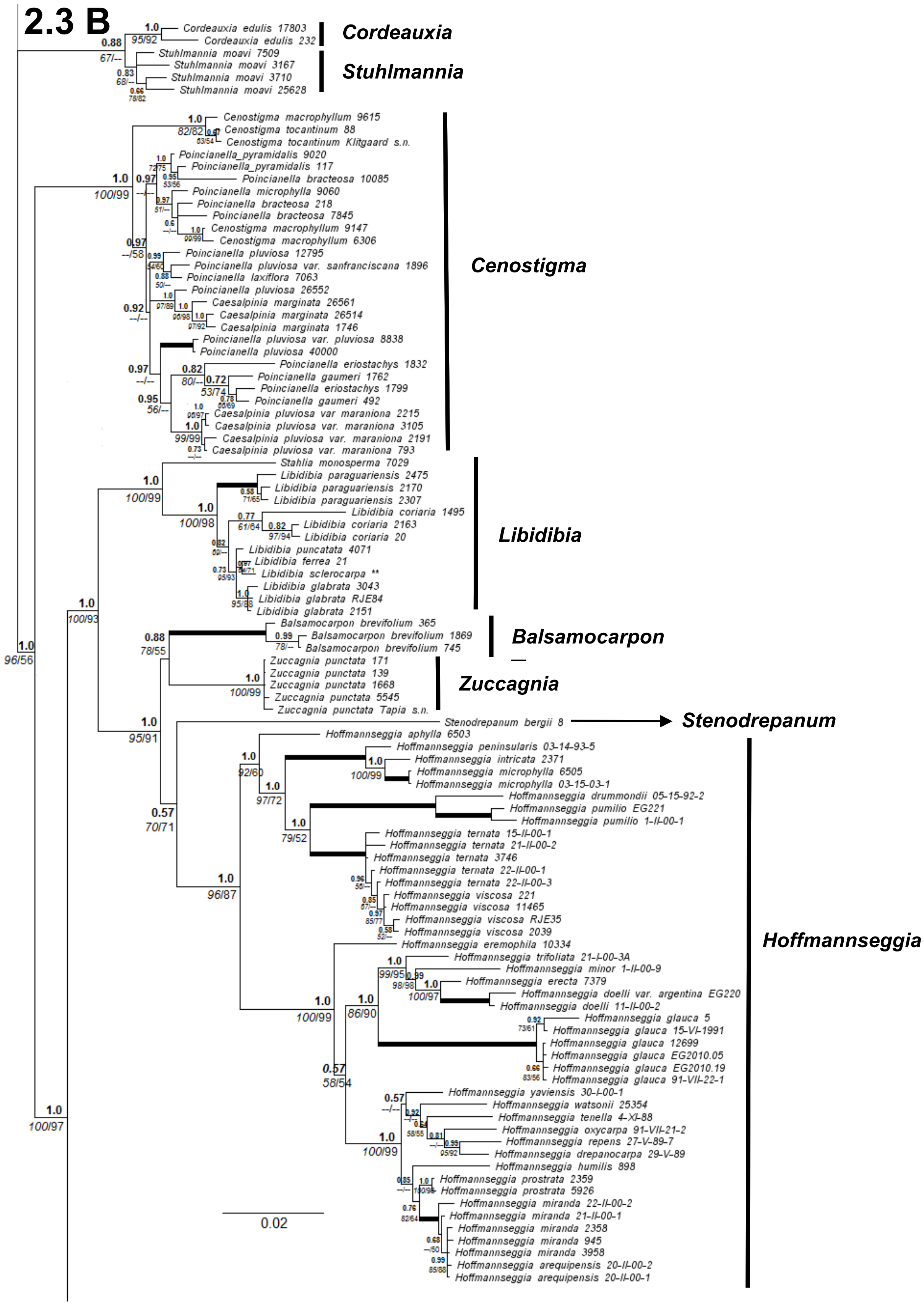
Caesalpinia decapetala 19XII971
Caesalpinia decapetala 2227
Caesalpinia sappan **
Caesalpinia godefroyana CL642
Caesalpinia parviflora 3977
Caesalpinia oppositifolia 921
Caesalpinia oppositifolia 607
Biancaea
Caesalpinia crista 4199
Caesalpinia crista 1V993
Ticanto clade
Pterolobium stellatum 17XII979
Pterolobium macropterum 5934
Pterolobium hexapetalum 2075
Pterolobium macropterum 1624
Pterolobium
Caesalpinia nitens 18033
Mezoneuron scortechinii 4195
Caesalpinia erythrocarpa 2246
Mezoneuron kavaiensis 8904
Mezoneuron sumatranum 9642
Mezoneuron hymenocarpum 34232
Mezoneuron cucullatum 3623
Mezoneuron andamanicum 29IV19991
Mezoneuron hildebrandtii 2137
Mezoneuron angolense 12XII971
Mezoneuron benthamianum 2602
Mezoneuron benthamianum SL3295
Mezoneuron
0.9 --/--
0.99 71/76
0.63 --/--
1.0 100/91
0.97 --/--
1.0 83/83
1.0 96/93
0.57 --/--
0.96 --/--
1.0 95/88
1.0 100/99
0.71 --/56
1.0 90/100
0.93 --/--
0.99 90/80
0.92 90/--
1.0 100/99
1.0 99/98
0.99 96/98
0.88 --/53
1.0 95/53
1.0 100/97
1.0 89/79
1.0 100/96
1.0 100/98
1.0 94/85
1.0 93/96
0.02

2.3 B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Stuhlmannia
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Caesalpinia marginata 26561
Caesalpinia marginata 26514
Caesalpinia marginata 1746
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Poincianella eriostachys 1832
Poincianella gaumeri 1762
Poincianella eriostachys 1799
Poincianella gaumeri 492
Caesalpinia pluviosa var maraniona 2215
Caesalpinia pluviosa var. maraniona 3105
Caesalpinia pluviosa var. maraniona 2191
Caesalpinia pluviosa var. maraniona 793
Cenostigma
Stahlia monosperma 7029
Libidibia paraguariensis 2475
Libidibia paraguariensis 2170
Libidibia paraguariensis 2307
Libidibia coriaria 1495
Libidibia coriaria 2163
Libidibia coriaria 20
Libidibia puncatata 4071
Libidibia ferrea 21
Libidibia sclerocarpa **
Libidibia glabrata 3043
Libidibia glabrata RJE84
Libidibia glabrata 2151
Libidibia
Balsamocarpon brevifolium 365
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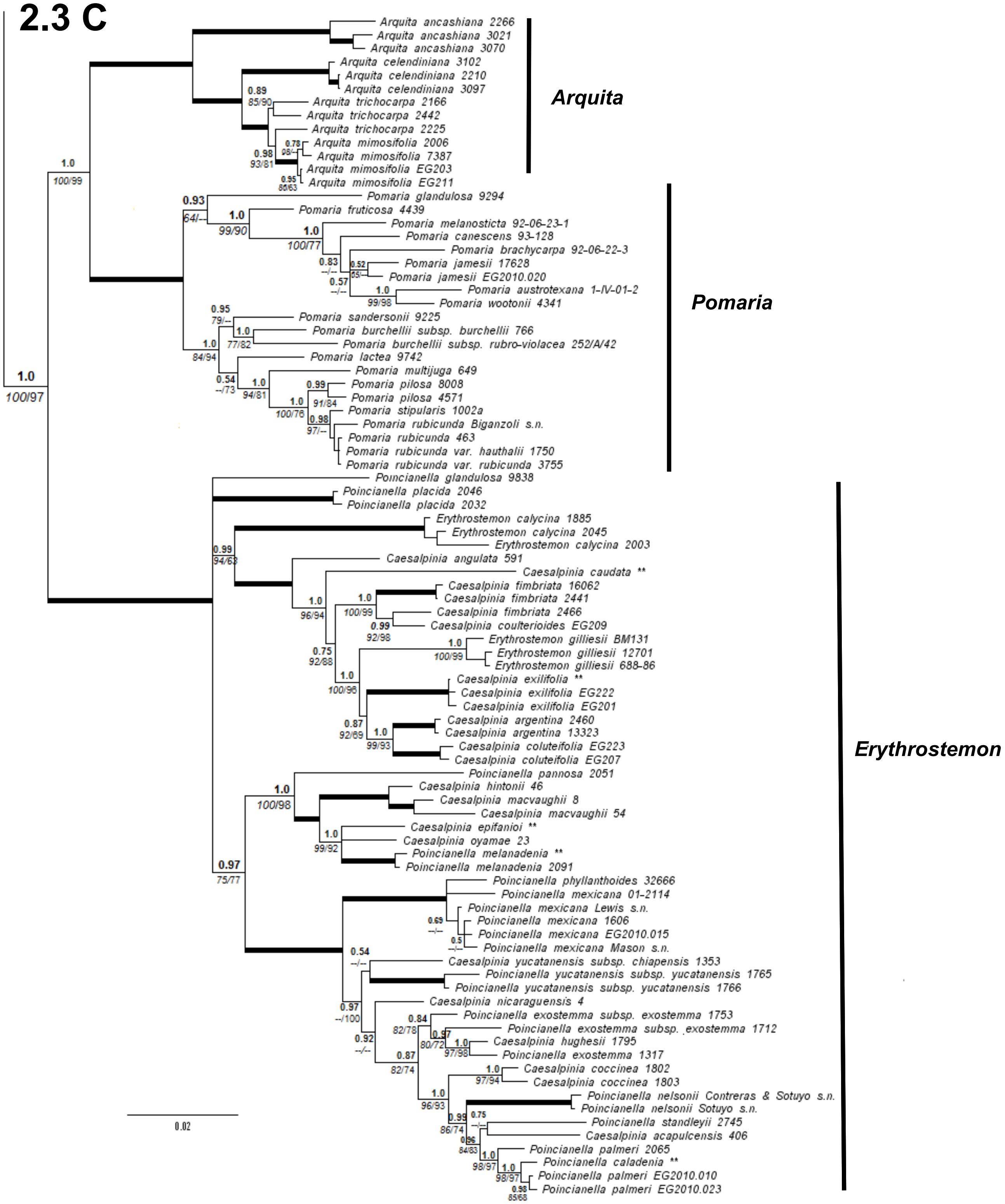
2.3 C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Arquita trichocarpa 2225
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85/90
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98/--
0.98
93/81
0.95
86/63
1.0
100/99
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Pomaria canescens 93-128
Pomaria brachycarpa 92-06-22-3
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Pomaria jamesii EG2010.020
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Pomaria wootonii 4341
Pomaria sandersonii 9225
Pomaria burchellii subsp. burchellii 766
Pomaria burchellii subsp. rubro-violacea 252/A/42
Pomaria lactea 9742
Pomaria multijuga 649
Pomaria pilosa 8008
Pomaria pilosa 4571
Pomaria stipularis 1002a
Pomaria rubicunda Biganzoli s.n.
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Pomaria rubicunda var. rubicunda 3755
Pomaria
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64/--
1.0
99/90
1.0
100/77
0.83
--/--
0.52
65/--
0.57
--/--
1.0
99/98
0.95
79/--
1.0
77/82
1.0
84/94
0.54
--/73
1.0
94/81
0.99
91/84
1.0
100/76
0.98
97/--
1.0
100/97
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Poincianella placida 2046
Poincianella placida 2032
Erythrostemon calycina 1885
Erythrostemon calycina 2045
Erythrostemon calycina 2003
Caesalpinia angulata 591
Caesalpinia caudata **
Caesalpinia fimbriata 16062
Caesalpinia fimbriata 2441
Caesalpinia fimbriata 2466
Caesalpinia coulterioides EG209
Erythrostemon gilliesii BM131
Erythrostemon gilliesii 12701
Erythrostemon gilliesii 688-86
Caesalpinia exilifolia **
Caesalpinia exilifolia EG222
Caesalpinia exilifolia EG201
Caesalpinia argentina 2460
Caesalpinia argentina 13323
Caesalpinia coluteifolia EG223
Caesalpinia coluteifolia EG207
Poincianella pannosa 2051
Caesalpinia hintonii 46
Caesalpinia macvaughii 8
Caesalpinia macvaughii 54
Caesalpinia epifanioi **
Caesalpinia oyamae 23
Poincianella melanadenia **
Poincianella melanadenia 2091
Poincianella phyllanthoides 32666
Poincianella mexicana 01-2114
Poincianella mexicana Lewis s.n.
Poincianella mexicana 1606
Poincianella mexicana EG2010.015
Poincianella mexicana Mason s.n.
Caesalpinia yucatanensis subsp. chiapensis 1353
Poincianella yucatanensis subsp. yucatanensis 1765
Poincianella yucatanensis subsp. yucatanensis 1766
Caesalpinia nicaraguensis 4
Poincianella exostemma subsp. exostemma 1753
Poincianella exostemma subsp. exostemma 1712
Caesalpinia hughesii 1795
Poincianella exostemma 1317
Caesalpinia coccinea 1802
Caesalpinia coccinea 1803
Poincianella nelsonii Contreras & Sotuyo s.n.
Poincianella nelsonii Sotuyo s.n.
Poincianella standleyii 2745
Caesalpinia acapulcensis 406
Poincianella palmeri 2065
Poincianella caladenia **
Poincianella palmeri EG2010.010
Poincianella palmeri EG2010.023
Erythrostemon
0.99
94/63
1.0
96/94
1.0
100/99
0.99
92/98
0.75
92/88
1.0
100/99
1.0
100/96
0.87
92/69
1.0
99/93
1.0
100/98
1.0
99/92
0.97
75/77
0.69
--/--
0.5
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0.54
--/--
0.97
--/100
0.84
82/78
0.97
80/72
1.0
97/98
0.92
--/--
0.87
82/74
1.0
97/94
1.0
96/93
0.99
86/74
0.75
--/--
0.96
84/83
1.0
98/97
1.0
98/97
0.98
85/68
0.02

Chapitre 3: Global phylogenetic biome conservatism and constant rates of diversification across the pantropical Caesalpinia Group (Leguminosae)

Edeline Gagnon[1], Colin E. Hughes[2], Gwilym P. Lewis[3] and Anne Bruneau[1]

1. Institut de recherche en biologie végétale and Département de sciences biologiques, Université de Montréal, H1X 2B2, Montréal, Canada;
2. Institute of Systematic Botany, University of Zürich, 8008, Zürich, Switzerland;
3. Comparative Plant and Fungal Biology Department, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, United Kingdom;

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3.1 Résumé/Abstract

Résumé

Objectifs : Mieux comprendre les origines et des patrons de diversification globaux des milieux arides à travers des études biogéographiques du groupe Caesalpinia (Leguminosae). Ce clade, incluant près de 205 espèces, se compose d'arbustes, d'arbres, de lianes et d'herbacées. Il se retrouve principalement dans le biome succulent, mais aussi dans le biome des savannes et le biome tempéré (déserts et prairies). La reconstruction de l'histoire biogéographique de ce clade permet de déterminer s'il existe des changements significatifs dans les taux de diversification au sein de celui-ci, et si ces derniers sont liés à l'histoire biogéographique du groupe, aux changements de biomes ou aux ports de plantes.

Localisation: Pantropical

Méthodes: Des analyses de datation phylogénétiques, incluant deux calibrations fossiles, ont été effectuées sur une matrice moléculaire contenant les 27 genres et 84% des espèces du groupe. Les aires ancestrales du clade ont été estimées, ainsi que les états ancestraux pour les biomes et ports de plantes. Les taux de diversifications ont été estimés et testés en utilisant la méthode bayésienne BAMM.

Résultats: L'origine du groupe Caesalpinia est retracée à la période Paléocène. L'ancêtre du clade, quant à lui, était probablement un arbre ou un arbuste du biome succulent, provenant de l'Amérique du Sud ou de l'Afrique. De plus, les dispersions intercontinentales ayant eu lieu au cours de son histoire ont été observé le plus fréquemment dans le biome succulent. Par ailleurs, aucun changement significatif de taux de diversification n'est détecté, et le taux de de spéciation montre une légère décélération à travers le temps.

Conclusions: L'âge et la persistance du groupe Caesalpinia, combiné avec l'absence de changement du taux de diversification, suggère que la stabilité et la résilience écologique sont caractéristiques du biome succulent. Les dispersions intercontinentales fréquentes au sein de ce biome suggèrent également un rôle important de la conservation des niches sur les dynamiques de diversification au sein de ce groupe.

Mots-clés: groupe Caesalpinia, clade Mimosoideae-Caesalpinieae-Cassieae, Leguminosae, biome succulent, forêts saisonnières tropicales sèches, biogéographie historique, taux de diversification, conservation de niche.

Abstract

Aim: To investigate the origins and global diversification patterns in arid habitats, using the Caesalpinia Group (Leguminosae) as a case study. This group of c. 205 species principally occurs in the Succulent Biome, but a subset also occur in the Savannah Biome, as well as in warm Temperate areas (deserts and prairies), and are found as shrubs, trees, lianas or herbaceous plants. In addition to reconstructing the biogeographic history of this group, we investigate whether diversification rates vary as a function of long-distance dispersal, evolution towards new biomes or changes in plant habits.

Location: Pantropical.

Methods: A molecular dataset with all 27 genera and 84% of species of the group was used to reconstruct a time-calibrated phylogeny, using two fossil calibrations. Ancestral areas occupied by this group were reconstructed, as well as the ancestral states for plant habit and biomes. Diversification rates were estimated and tested for shifts in macro-evolutionary processes using the Bayesian method BAMM.

Results: The Caesalpinia Group most likely appeared in the Paleocene period, and was most likely a tree/shrub species in the Succulent Biome, either from South America or Africa. Subsequent intercontinental dispersals events were estimated to occur most frequently in the Succulent Biome. Diversification analyses demonstrated a lack of any significant rate shifts, with speciation rates slightly decelerating through time.

Main conclusions: The age and the persistence of the Caesalpinia Group, in combination with the single evolutionary rates regime, suggests long-term stability and ecological resilience of the Succulent Biome. The frequent intercontinental dispersals within this biome points to niche conservatism acting to shape diversification of this clade on a global scale.

Keywords: Caesalpinia Group, Mimosoideae-Caesalpinieae-Cassieae clade, Leguminosae, Succulent Biome, Thicket Biome, seasonally dry tropical forests, historical biogeography, diversification rates, niche conservatism.

3.2 Introduction

Explanations for large-scale patterns of plant biodiversity have changed dramatically in the past decade with the introduction of the idea that, in addition to geo-historical vicariance events, ecology and metacommunity processes have played an important role in shaping and explaining the distribution of species and geographic structure of plant phylogenies (Lavin & al., 2004; Wiens & Donoghue, 2004; Donoghue, 2008). This paradigm shift has occurred as a result of an increasing number of phylogenetic trees that are incongruent with classical hypotheses of vicariance events linked to geological history. For example, cladistic area vicariance analyses have repeatedly failed to produce consistent patterns of area relationships in legume phylogenies (Beyra-Matos & Lavin, 1999; Lavin & al., 2000, 2001, 2004; Pennington & al. 2004; Thulin & al., 2004; Schrire & al. 2005; Lavin and Beyra-Matos, 2008). Instead, what has emerged as a better predictor of phylogenetic structure than geography is ecology, as revealed by patterns of taxon-biome relationships (Schrire & al., 2005)**.** A second line of evidence comes from time-calibrated phylogenies which have shown divergence time estimates for trans-continental crown nodes that are consistently, and often significantly, too young or too old to fit with established hypotheses of vicariance and continental history (Lavin & al., 2004; Pennington & al., 2004; Cody & al. 2010; Pennington & al., 2010; Särkinen & al., 2012). An important corollary of these repeated patterns is the idea that phylogenetic biome or niche conservatism, i.e. “the retention of niche-related ecological traits over time” (Wiens et al., 2010; Donoghue & Edwards, 2014), has been an important process that has shaped the distribution of species richness on a global scale for the Legumes, as well as in other plant families (Crisp & al., 2009). Questions remain though about what factors promote biome shifts. Are these related to biome sizes, spatial adjacency, ages and connections throught time, or do they depend more heavily on the development of particular traits (Donoghue & Edwards, 2014)?

At the moment, significant progress can be made from targeting case studies of particular clades that closely assess relevant abiotic and biotic factors to both examine biome shifts, and synthethize the general patterns of processes operating within individual biomes (Hughes & al., 2013; Donoghue & Edwards, 2014). For example, the comparative studies Crisp & al. (2009) revealed contrasting patterns of geographical, ecological and community structures in diverse ecological and geographical settings, including dry tropical/temperate, southern hemisphere and seasonally dry tropical forests (SDTF). One of the most intriguing examples of this type of biogeographical pattern, and one of the most striking examples of putative global biome conservatism to emerge from recent studies of legume phylogenies, is the observation of multiple examples of sister clades growing in the Succulent Biome spanning large geographic disjunctions, between the Horn of Africa and Namibia, the Caribbean, Central America, South America, and Madagascar (Lavin & al., 2004; Thiv & al., 2011). This Succulent Biome sensu Schrire & al. (2005) encompasses a range of seasonally dry tropical forests, from tall canopy deciduous forests to low thorn scrub and cactus scrub, which are strongly seasonal with a dry season of five to six months, and a flora that is sensitive to fire and frost. Despite this apparently repeated pattern of trans-continental disjunctions of taxa spanning the Succulent Biome documented in the pioneering study of Lavin & al. (2004) and subsequently amplified by Pennington & al. (2006; 2009), there are still only a handful of time-calibrated phylogenies that have analysed global biogeographic patterns of lineages from the Succulent Biome (e.g. the combined *Leucaena* and *Dichrostachys* clade of mimosoid legumes, the *Chapmannia* clade of dalbergioid legumes and the *Ormocarpum* clade of dalbergioid legumes, Lavin & al., 2004; *Parkinsonia,* Hawkins & al., 2007; Indigoferae*,* Schrire & al., 2009). Hence, whether this is really a general pattern specific to the Succulent Biome, repeated across many plant lineages, remains unclear.

The Succulent Biome is of particular importance in the Leguminosae where broad family-wide vicariance analyses using biomes instead of geographic areas have revealed that lineages from the Succulent Biome are older, often occuring as sister to Rainforest, Grassland and Temperate Biome lineages (Schrire & al., 2005). Based on these results and observations of the fossil record, Schrire & al. (2005) proposed a new biogeographic hypothesis, dubbed the "Tethys Seaway hypothesis", which suggested that Legumes originated in an arid belt surrounding the Tethys Seaway, a large body of water that crossed the Equator during the Eocene (56-43 Ma). Thus, the current distribution of the taxa from the Succulent Biome across the tropics would be linked to this original disitribution around this arid equatorial belt, which would have subsequently been fragmented by geological and climatic changes across the Tertiary. While this is a compelling hypothesis, it has yet to be tested extensively. With the exception of the biogeographic study of the Indigofereae clade (Schrire & al., 2009), few other studies have focused on taxa with global, pantropical distributions in the Succulent Biome, necessary to evaluate the importance of this biome in the evolution of the ecologically important plant family Leguminosae.

Biome shifts in plant evolution are of particular interest because they often are accompagnied by heterogeneous diversification rates and switches in plant habits and growth forms, ultimately leading to an increase in morphological and species diversity. For example, preliminary investigations into family-wide diversification patterns in the Leguminosae by Koenen & al. (2013) led to the important observation of a decrease in diversification rates in the Robineae tribe, a group of legumes with strong affinity to the Succulent Biome, which contrasted sharply with other lineages occurring in other type of biomes. Koenen & al. (2013) speculate that this deceleration may be related to the emerging view that the Succulent Biome is relatively stable and ecologicall resilient, with small clades of endemic species that are dispersal-limited and restricted to the geographically isolated disjunct patches of Succulent Biome habitats throughout the world. To what extent decreasing diversification rate is common for Succulent Biome lineages within legumes and other plant taxa remains to be tested. As for plant habits and growth, there are examples that show that switches in plant habit can accompany biome switches, and can thus have a role to play in in increasing or decreasing diversification rates. For example, herbaceous plants have also been linked to broader niches compared to woody plant taxa in several lineages of plants (Smith & Beaulien, 2009). Furthermore, there are also several examples of repeated evolution perennial, ligneous plant taxa in montane and alpine habitats, which have as sister lineages low-land, annual, herbaceous plant taxa (see Hughes & Atchison, 2015, and references cited therein; examples include New World *Lupinus, Androsace,* North American *Castilleja,* etc.). Another example is the evolution of the liana habit, which is possibly linked with adaptations to different environmental requirements in particular habitats. Examples include Calamoid palms in Asia, which evolved a number of key morphological characters that led to a liana habit and increases in diversification rates (Couvreur & al., (2015). In legumes from Brazil, lianas from the former subfamily Caesalpinioideae are six times more species-rich in the Amazon forest than in Cerrado habitats, with nearly four times more endemic species than the Cerrado and almost 10 times more than the Caatinga, typical of the Succulent

Biome (Souza-Neto & al., 2015). However, we know of no studies which have investigated in legumes whether the development of the liana habit are linked to biome switches.

The pantropical Caesalpinia Group, from the Mimosoideae-Caesalpinieae-Cassieae clade in the Leguminosae (Doyle, 2012; LPWG, 2013), is a clade of about 205 species of shrubs, trees, lianas and herbaceous plants, now classified in 26 genera (Gagnon & al., in prep., chapter 2). The genus *Caesalpinia* s.s., as previously defined by Lewis (2005) with ca. 25 species, was originally cited as one of the rare groups with a distribution of species that nearly perfectly matches the Succulent Biome across the globe (Schrire & al., 2005), and many other genera in the Caesalpinia Group also have strong affinities to this biome. Here we use the Caesalpinia Group as a case study to better understand global patterns of species diversification associated with Succulent Biome lineages. In addition to having strong affinities to the Succulent Biome, many of the related genera in the broader Caesalpinia Group also are associated with the Grassland Biome (sensu Schrire & al. 2005, i.e. a tropical savanna biome that includes the South American *Cerrado* and *Campos Rupestres*) and the Rainforest Biome. A few species also occur in mangroves or coastal beach habitats, and species in the genera of *Hoffmannseggia* (Simpson & al., 2005) and *Pomaria* (Simpson & al., 2006) also occur in the warm Temperate Biome, which include arid deserts and temperate grasslands. The historical biogeography and patterns of distribution of this large pantropical clade have remained poorly understood because until recently, a clear and comprehensive taxonomy and a well-resolved phylogeny have been unavailable.

Recent studies by Gagnon & al. (2013, chapter 1; see also Gagnon & al., in prep., chapter 2) have resulted in a new classification of this group into 26 genera, and provided a densely sampled well-resolved phylogeny for the clade. These new data provide the opportunity to examine geo-temporal patterns of diversification across the Succulent Biome on a global scale, and to evaluate the extent to which niches are conserved across and between continents. With the availability of this densely sampled species-level phylogeny for the Caesalpinia Group, insights can also be gained into the evolutionary dynamics of biome shifts into the Grassland, Rainforest, Warm Temperate, and Coastal Biomes. Here we use a highly resolved, time-calibrated phylogeny with all 26 genera and near-complete species sampling (around 84%) to reconstruct the biogeographic history of this clade in relation to the ecology and life history strategies of species. More specifically, we are interested in the following questions: What is the age and origin of the Caesalpinia Group, and when did the major lineages within this clade arise? Is it consistent with the Tethys seaway hypothesis? Is there directional bias among biome shifts? Do trans-continental disjunctions occur more frequently within certain biomes, or are they instead associated with biome shifts? Do switches in biomes, plant habit or intercontinental-dispersal have an effect on the diversification rates amongst lineages within the Caesalpinia Group? We hypothesize that clades in the Succulent and Temperate Biomes, which are composed of trees, shrubs, suffrutescent shrubs and herbaceous plants, will show constant species diversification rates, whereas clades with species in the Grassland and the Rainforest Biomes, which often have a liana habit, will have higher rates of diversification.

3.3 Material and Methods

3.3.1 Taxon sampling

To conduct our biogeographic analyses, we used the concatenated matrix of Gagnon & al. (in prep., chapter 2), which included five plastid markers (*rps16,* the *trnD-trnT* intergenic spacer, *ycf6-psbM,* the *matK* gene and *3'-trnK* intron, and the *trnL-trnF* intron-spacer region) and a nuclear ribosomal locus, the 5.8S subunit and flanking internal transcribed spacers ITS1 and ITS2. The matrix from Gagnon & al. (in prep, chapter 2) had a very large number of samples (408), which made several analyses lengthy and complex. This matrix was pruned down to 294 samples to make the analyses more feasible. Selection of taxa was based on preserving the maximum geographic and taxonomic representation within each group, and retaining a smaller set of multiple accessions of species (see Annex 2). For example, we conserved samples of species growing in different, disjunct geographical areas, because dating the divergence of these different geographic populations are of interest to us, and gives additional insight into how metacommunity processes might be acting on diversification within species (e.g. Pennington & al. 2010). Furthermore, we retained more than one accession of a species if we had indication that they were not forming monophyletic clades, which could either be attributed to insufficient phylogenetic signal, or possible undetected species diversity. In total the 294-terminal matrix included 169 species of the Caesalpinia Group (including 10 subspecies and varieties), representing all 26 genera and the as yet unresolved Ticanto clade (Gagnon & al., in prep., chapter 2). The outgroup consisted of nine species representing the Mimosoideae-Caesalpinieae-Cassieae (MCC) clade, including *Arcoa gonavensis*, *Gymnocarpus chinensis,* and *Tetrapterocarpon geayii* of the Umtiza grade, *Cassia javanica* and three *Senna* species from the Cassieae tribe, and *Conzattia multiflora* and *Colvillea racemosa* from the Peltophorum Group. In this matrix all samples have sequences of at least two loci, except for seven taxa (*Biancaea milletii, Caesalpinia vernalis, Cenostigma pellucida, Cenostigma pluviosa* var. *peltophorum, Erythrostemon laxa, Gelrebia rubra,* and *Pterolobium integrum)*, which were nonetheless included to maximise taxonomic and geographic representation of taxa, and because there was sufficient phylogenetic signal for these taxa to ascertain their phylogenetic positions (Gagnon & al., in prep., chapter 2). Ambiguous sequence regions were removed from the matrix prior to the analyses (see Gagnon & al., in prep., chapter 2), and we did not code indels in subsequent analyses.

3.3.2 Bayesian divergence-time estimates

Time-calibrated phylogenies were constructed using Beast v.1.8.0 (Drummond & al., 2012). The dataset was analysed using two partitions, the first consisting of the five plastid markers and the second consisting of ITS. We used the Aikake Criterion in Jmodeltest2 (Darriba & al., 2012) to select the best evolutionary model, which identified the GTR+I+G model for both partitions. Analyses were run using an uncorrelated log normal relaxed clock and a birth-death speciation model. A diffuse prior was used to estimate the UCLD.mean (Exponential prior distribution, mean 10, initial value 1.0).

The phylogeny was calibrated using a total of four calibration priors: two fossils previously used in time-calibrated phylogenetic analyses of the Leguminosae, one secondary calibration derived from previous phylogenetic analyses, and one geological constraint. The first fossil calibration was based on fruits attributed to the genus *Senna*, found in the South East U.S.A. and Mexico, estimated at 45 Ma (Herendeen 1992; Calvillo-Canadell & Cevallos-Ferriz, 2005). The second fossil calibration was based on winged fruits, attributed to the genus *Mezoneuron,* found in several sites across the South East and Western United States (the Middle Eocene Claiborne Formations in western Tennessee, the Eocene Green River Formation in Idaho, and the Miocene Clarkia, Whitebird, and Oviatt Creek sediments in Idaho), with the oldest of these fossils estimated to be 45 Ma (Herendeen & Dilcher, 1991). These membranous, indehiscent fossil pods are unequivocally assigned to the Mezoneuron clade, notably because of the apomorphy consisting of a broad placental wing with looping to longitudinal venation.

It is important to note that we discarded a fossil calibration point that was used by Bruneau & al. (2008) in their divergence time analyses of Caesalpinioideae. This calibration was based on fossils consisting of fruits with twisting valves and prominent seed chambers that were attributed to *Caesalpinia* s.s. These fossils also were found in the Claiborne Formation and dated to the Eocene, at ca. 45 Ma (Herendeen, 1992). However, the new phylogenetic analyses by Gagnon & al. (2013, chapter 1; in prep., chapter 2), which resolve multiple distinct clades for *Caesalpinia* s.s. as previously circumscribed, mean that these fossils could be assigned to a number of genera within the Caesalpinia Group, including *Cenostigma*, *Tara, Stuhlmannia*, *Erythrostemon*, *Caesalpinia* s.s., *Biancaea* and *Denisophytum*, and we thus dismissed these fossils to calibrate our phylogenies.

The two retained fossil calibrations were placed on the stem node of their respective genera as a minimum age of diversification. For both fossils, we specified a uniform prior, with a minimum age corresponding to the age of the fossil and a maximum age corresponding to the root height of the tree (see further below, in next paragraph). Careful selection of priors for calibrating time-divergence analyses in phylogenies is important, as the selected parameters have an enormous influence on the resulting age estimates (Ho & Philipps, 2009; Inoue & al., 2010; Warnock & al. 2012; 2015). It has been advocated that the most crucial step of selection of priors should be informed on paleobiological evidence (e.g. Nowak & al. 2013), and non-uniform priors have been advocated by authors (Yang & Rannala, 2006; Ho & Philipps, 2009). However, this is not always possible in the majority of studies, which leads to a subjective choice of priors (Warnock & al., 2012; Hispley & Müller, 2014); this is unfortunate, but there has yet been a study published with guidelines as to which type of prior is ideal in the absence of data. While the hard bound uniform priors are improper priors in Bayesian statistics, though they do not necessarily lead to improper posterior probability distributions (Huelsenbeck & al., 2002). More importantly, when several calibration points are used, it is important to check the shape of the effective prior distribution: often the priors specified by the users are not the resulting joint effective priors generated by Beast. For example, Koenen & al. (2015) found that the effective priors in his study in diversification time in Meliaceae were not uniform, as original specified, due to interactions with the root height prior, and he investigated the effect of different maximum age priors on the dates estimated in his phylogenies. These are issues that we plan on taking in consideration in future time-calibrated phylogenies of the Caesalpinia Group.

In addition to the two fossil calibrations, we also constrained the root height of the tree, corresponding to the crown node of the MCC clade. This was crucial as preliminary analyses leaving the root unconstrained resulted in significantly older ages for this clade, roughly around the middle of the Cretaceous (90 Ma), when in fact most studies based on fossil evidence agree to say that there is the lack of any definitive legume fossil before 58 Ma (Herendeen, 1992; Wing & al., 2009), and time-calibrated phylogenies in Legumes have estimated a crown age of 60-70 Ma for the family, based on time-calibrated phylogeniy based on 12 to 23 fossil calibrations, and dated with different methods (Beast: Simon & al., 2009; penalized likelihood: Lavin & al. 2005; Bruneau & al., 2008).). Nonetheless, Crown node ages for the Legume family and major tribes have remained uncertain as legumes diversified extremely rapidly, with almost of all of the major lineages appearing in the fossil record by 50 Ma (Herendeen, 1992). To increase the precision of these dating analyses it has been suggested that a larger analysis encompassing the entire Fabales and Rosids would be more appropriate in pinpointing the exact age of the major lineages of the Legume family (Koenen & al., 2013). Thus, for the moment a “de novo” dating analysis would thus appear to be simply repeating past analyses, and using a secondary calibration point seems appropriate to calibrate the root of our tree, which corresponds to the crown age of the MCC clade. Despite the uncertainty surrounding the age estimates of the MCC node, all previous time-calibrated phylogenies of the Leguminosae have estimated this node to be only slightly younger than the age of the family itself. For example, based on a *matK* phylogeny of the legume family, Simon et al. (2009) estimated the age of the MCC clade to be 60.8 Ma, (height range: 66.4-56.5, Beast analysis), whereas Bruneau et al. (2008) estimated the age to be 58.6 Ma (58.8-58.5, 95% confidence interval of penalised likelihood analysis repeated on 100 trees from the posterior distribution of a Bayesian analysis). Based on this evidence, we specified for the root height a uniform prior, with min age corresponding to the lowest value of the height range of Simon et al. (2009) and max age corresponding to the age of the MCC clade estimated by Simon et al. (2009).

Finally, because our phylogeny included *Mezoneuron kauaiense,* a species endemic to the dry/mesic forests of the islands of Kauai, Hawaii, Oahu and Maui, we placed a fourth calibration point based on the age of the Hawaiian archipelago. Because *M. kauaiense* was historically present on the oldest island of the archipelago (Kauai (Wagner & al., 1999)), we constrained the node of the minimum age of the most recent common ancestor (MRCA) of this species at 4.7 Ma, the estimated age of emergence of Kauai. However, it is entirely possible that *M. kauaiense* originated before the emergence of Kauai, dispersing from volcanic island to volcanic island. Models for the evolution of the chain of islands of the Hawaiian archipelago indicate that there could have been islands with peaks above 1000 m in elevation as old as 32 Ma (Price & Clague, 2002). To reflect this possibility, while biasing for the youngest age possible, we used an exponential prior with offset = 4.7 and mean = 7, with a maximum age cut-off of 32 Ma.

Several analyses were run to check the effect of these calibrations: 1) including only the root calibration; 2) including the root and two fossil calibrations; 3) including all four calibrations. For each analysis, an initial tree was specified, whose age calibrations were specified in order to avoid problems with low likelihood at the start of the analysis. The initial topology of these trees was generated using an exploratory run with Beast without any fossil constraints, with the default model for nucleotide evolution (JC) specified for each partition.The Maximum clade credibility (Mccr) tree obtained in this way was subsequently calibrated in R, using the function chronopl from the package “ape” (Paradis & al., 2004), in order to achieve node heights that were compatible with the constraints imposed by the fossil calibration.

For each of the three analyses with different fossil calibrations, we ran three chains for 20,000,000 generations, sampling trees at every 1000 generations. Initial analyses led us to find a highly unusually relationship for the genus *Lophocarpinia,* which was found nesting within *Paubrasilia echinata.* The position of this genus contradicts results from previous phylogenetic studies that analysed the same loci (Nores & al. 2012; Gagnon & al., in prep., chapter 2), and is highly unlikely based on the highly similar vegetative morphology of *Lophocarpinia* and *Haematoxylum* (Burkart, 1957; Nores & al., 2012), whereas there is no morphological evidence suggestion that *Lophocarpinia* and *Paubrasilia* are related. It is highly likely that the result we found is due to lack of information, given that only the two least informative loci (*matK*-3*'trnk* and *trnL-trnF*) are available for *Lophocarpinia.* Furthermore, we also found an unusual topology in which the clade containing the three *Mezoneuron* species *M. nitens*, *M. scortechinii* and *M. erythrocarpa* was sister to the rest of *Pterolobium* + *Ticanto* clade, rather than being sister to the remaining *Mezoneuron* species, an unexpected result that also contradicts previous phylogenetic analyses (Gagnon & al., in prep., chapter 2), but that is nonetheless plausible in that the small clade of three species have fruit that are similar but can be distinguished from the main clade containing the majority of *Mezoneuron* species. In order to have a tree that was consistent with previous results and the morphological similarities between genera, two topological constraints were imposed in the analyses, the first being the monophyly of the *Lophocarpinia* plus *Haematoxylum* clade, the second being the monophyly of the genus *Mezoneuron* as found by Gagnon & al. 2015. In retrospect, it would have been preferable to exclude this second topological constraint, but it is unlikely to seriously affect the overall results and conclusions of this present study.

Results of these analyses were examined in Tracer v.1.6 (Rambaut & al., 2014), to verify that chains had stabilized and converged to similar values and had reached appropriate estimated sampling size values. Burn-in values were estimated to be about 25%, and the three chains were combined using LogCombiner. The Mccr tree was generated in Treeannotator. Node heights were determined using the common Ancestor heights option, as there were conflicts in tree topologies leading to the annotation of negative branch lengths, which would have hindered subsequent analyses. These negative branch lengths were likely the result of problems of convergence in the analyses. While the phylogeny of the Caesalpinia Group always recovers the same generic clades, relationships amongst these clades or within clades are not always consistently resolved. Another option, which I intend to explore in future analyses, is to use the summary_tree utility from biopy (Heled, 2013), which uses an alternative way of creating a summary tree from the posterior trees found in Beast, by looking for a tree which minimizes the overall distances to the whole set of posterior trees.

3.3.3 Ancestral state reconstruction of characters and geographical areas

3.3.3.1 Coding of biomes and habit

We defined two multistate characters representing biomes and plant habit, which were coded for all the ingroup taxa. For habit, we defined three character states: (0) small to medium-sized shrubs and trees, (1) lianas and/or scrambling shrubs, (2) suffrutescent shrubs or perennial herbs. We also assigned each terminal to one or more of the four broad global biomes delineated by Schrire & al. (2005) in their cladistic vicariance analysis of legumes (Succulent, Temperate, Grassland and Rainforest (mapped on Fig. 3.1)), plus a fifth biome that we add here, a Coastal Biome to accommodate a few species which are confined to mangroves and other coastal vegetation. These five biomes are defined as follows:

The Succulent Biome (S) comprises a collection of semi-arid habitats, consisting predominantly of seasonally dry tropical forest, thicket and bushland biomes, with a fragmented distribution across the Neotropics, Africa and Madagascar. In the Neotropics, the Succulent Biome occurs in Mexico, Central America, the Caribbean, the Piedmont area of north-western Argentina and central Bolivia, the Misiones region of north-eastern Argentina and Paraguay, the inter-Andean dry valleys of Peru and Ecuador, northern South America in Colombia and Venezuela and the Caatinga of eastern Brazil (Pennington & al., 2000; Schrire & al., 2005; Pennington & al. 2009; Särkinen & al., 2011a). In the Old World, the Succulent Biome is present in Namibia, in southern and south-western Africa in the Succulent Karoo and Nama Karoo, which extends across to the horn of Africa and the Somalia-Masai regional centre of endemism, as highly fragmented, small pockets of thicket and dry forest ‘arid’. This biome also occurs in western and northern Madagascar, and extends to Arabia and north-western India (Schrire &

al., 2005; Cowling & al., 2005). All these regions are characterized by non-adaptation to fire, by a rich soil, and by seasonal rainfall (e.g. SDTF in the Neotropics receive less than 1800 mm yr−1, with a period of 5 to 6 months receiving less than 100 mm yr−1 (Pennington & al., 2009); in the Thicket Biome in Africa, between 200 to 1050 mm yr-1(Vlok & al., 2003) of rain occurs, of which 20% falls in winter (May-September months)). The Succulent Biome is also generally poor in grass taxa, but has a strong succulent component, such as Cactaceae in the Neotropics (Pennington & al., 2009), or succulent members Aizoaceae, Asphodelaceae, Euphorbiaceae, Apocynaceae and Crassulaceae in Africa (Cowling & al., 2005; Vlok & al., 2003). Although it has been argued that the South American Pacific coastal Lomas desert formations constitute a unique biota in their own right (Guerrero & al., 2013), they are here included in the Succulent Biome, due to the presence of succulent plants including Cactaceae and also because the climate there is considerably more homogeneous and milder than in the adjacent high altitude Andean desertic areas assigned to the Temperate Biome, due to the influence of the coast, with cool, sea-surface temperatures maintaining an uniform climate throughout the year, and causing the seasonal appearance of fog during winter months (Dillon & Rundel, 1990; Rundel & al., 1991).

In contrast, the Grassland Biome (G) consists of habitats that are fire-adapted, succulent-poor and grass-rich and includes the major tropical savannas including variably open woodlands (e.g. Miombo in Africa, Cerrado and Campos Rupestres in South America). The Grassland Biome comprises the Sudanian and Zambezian regional centres of endemism in Africa, to the monsoon forest and more open vegetation types in tropical Madagascar, tropical Asia and Northern Australia, plus the Cerrado, Campos Rupestres and Llanos of South America; these areas are much less fragmented than the Succulent Biome across the tropics (Schrire & al., 2005).

The Temperate (T) Biome of Schrire et al (2005), in the case of the Caesalpinia Group, corresponds to Warm Temperate semi-arid thickets, scrublands and deserts (often at higher altitudes), plus grasslands and Mediterranean-type habitats that can tolerate light frosts, without having a full winter season. Schrire & al. (2005) described this Warm Temperate Biome as also present in Eastern Asia, South America, South Africa and Australia. More specifically, we considered that desertic, high altitude areas in the Andes were part of this biome, as they experience considerable cold temperature fluctuations.

The Rainforest Biome (R), consisting of wet forests, is the least fragmented of the four biomes described by Schrire & al. (2005), and is essentially confined to the equatorial tropics. The main areas of rainforests are located from Amazonia to the Atlantic forests of Eastern Brazil in South America, and include the Guinea-Congolian and Swahelian wet forest regions of Africa, and the tropical forests of Indo-China and North-eastern India. They are also present in Madagascar, Central America, and the North Eastern coast of Australia. The fifth Coastal Biome (C) was added to accommodate the handful of species that grow in mangroves and coastal areas with salty to brackish water, in habitats that do not correspond to any of the four biomes described by Schrire & al. (2005).

It is important to note that the biome definitions used here are broad ones, compared to the perhaps more familiar categories (e.g. WWF Ecoregions; Olson & al., 2001; Donoghue & Edwards, 2014), especially with respect to the Succulent Biome here taken to span seasonally dry forests, xeric shrublands and deserts. In general, there is a striking lack of consistency and precision in how biomes are defined and mapped (Särkinen & al., 2011a; Hughes & al., 2013)

Plant habit and biome (Table 3.1) were scored based on an extensive review of the literature of *Caesalpinia* species, and on habitat information derived from herbarium specimen labels in numerous herbaria and in GBIF (for references, see Annex 3). When species appeared to be growing in two biomes or in transitions zones, they were coded as occupying several biomes. If information was insufficient to attribute a biome to a species, we coded the information as missing (indicated by "?"). We had most difficulty identifying the biomes of species occurring in Asia (see results and discussion below). The biome and habit characters were optimised on the phylogeny using the parsimony ancestral state reconstruction method in Mesquite (Maddison & Maddison, 2011).

Ideally, we would also have taken to reconstruct the biome and habit characters using maximum likelihood methods. These have the advantage of incorporating branch length information into the analyses, and provide estimates of variance and error in the reconstruction of the evolution of traits across a phylogeny (Huelsenbeck al., 2000). This could have been carried out in Mesquite, using a MK1 model of evolution, which assumes equal rate of transitions amongst taxa (Maddison & Maddison, 2011). Mesquite also allows to incorporate phylogenetic uncertainty with the option “trace over trees”, which would allow us to run the ML ancestrate state estimation over a subset of trees from the posterior probability. The only disadvantage is that our data would require to be recoded, as polymorphic states are not allowed in ML ancestral state estimates in Mesquite. Another option that would be interesting to explore would be the method of Stochastic character mapping (Huelsenbeck & al., 2003), that is available through the software SIMMAP (Bollback, 2006), as well as through the R package “phytools” (Revell, 2012).

3.3.3.2 Ancestral area reconstruction

To locate and estimate the number and timing of trans-continental disjunctions, we reconstructed ancestral areas on our phylogeny using the package BioGeoBEARS (Matzke, 2012). Six geographic areas were defined, corresponding to North America (Na), South America (Sa), the Caribbean (Car), Africa (Af) (including Madagascar and the Arabian Peninsula), Asia (As), and the Australian-Pacific (PA) region (based on Wallace’s line) (Fig. 3.2). We coded the presence of species in these areas based on different sources from the litterature, including floras, synopses, and taxonomic treatments of various groups (Table 3.1, see Annexe 3 for references).

The R package BioGeoBEARS was used to run a dispersal-extinction-cladogenesis (DEC) analysis, which uses an approach that calculates the relative likelihood of each possible ancestral range at each node of a tree, given a particular probability of dispersal and extinction amongst different areas (Ree & al., 2005). Running this analysis in BioGeoBEARS has several advantages, including the possibility of running the DEC model with an additional parameter consisting of a founder event leading to cladogenesis (J) and testing whether the addition of this parameter leads to a better likelihood of the DEC model, by calculating a likelihood ratio or using the Aikaike information criterion.

In the DEC model, it is all possible to test whether different probabilities of dispersal between geographic areas have an impact on the ancestral area reconstruction for each node by specifying a dispersal matrix in Lagrange that affects the Q matrix implemented in the DEC model. Several dispersal matrices can also be specified to reflect the changing connections between different geographic areas, such as the closing of the Isthmus of Panama and the closure of the Tethys seaway. Preliminary analyses, which will need to be refined, showed however that it had a relatively minimal impact on ancestral area estimates, but we hope to refine these analyses for the final publication of this chapter. Other plans for the final publication of the

Table 3.1 Geographic areas, biomes and habit of species included in the time-calibrated phylogeny of the Caesalpinia Group. Geographic areas: Na: North America; Sa: South America; Af: Africa; As: Asia; PA: Australia/Pacific region. Biomes: S: Succulent; G: Grassland; R: Rainforest; T: Temperate; C: Coastal. Habit: 0: Trees and shrubs; 1 lianas and scrambling shrubs; 2: suffrutescent shrubs and herbaceous perennials.

Species	**Geographic Areas**	**Biome**	**Habit**
Arquita ancashiana	Sa	S	0
Arquita celendiniana	Sa	S	0
Arquita grandiflora	Sa	S	0
Arquita mimosifolia	Sa	S	0
Arquita trichocarpa var. trichocarpa	Sa	S	0
Arquita trichocarpa var. boliviana	Sa	S	0
Balsamocarpon brevifolium	Sa	S	0
Biancaea decapetala	As+PA	G	1
Biancaea godefroyana	As	G	1
Biancaea milettii	As	R	0/1
Biancaea oppositifolia	As	?	1
Biancaea parviflora	As	R	1
Biancaea sappan	As	G/R	0
Caesalpinia anancantha	Car	S	0
Caesalpinia barahonensis	Car	S	0
Caesalpinia bahamensis	Car	S	0

Caesalpinia brasiliensis	Car	S	0
Caesalpinia cassioides	Sa	S	0
Caesalpinia nipensis	Car	S	0
Caesalpinia pulcherrima	Na	S	0
Caesalpinia reticulata	Car	S	0
Cenostigma bracteosa	Sa	S/G	0
Cenostigma eriostachys	Na	S	0
Cenostigma gaumeri	Na	S	0
Cenostigma laxiflora	Sa	S	0
Cenostigma macrophyllum	Sa	S/G	0
Cenostigma marginata	SA	G	0
Cenostigma microphylla	Sa	S	0
Cenostigma pellucida	Car	S	0
Cenostigma pluviosa var. pluviosa	Sa	S/G	0
Cenostigma pluviosa var. maraniona	Sa	S	0
Cenostigma pluviosa var. sanfranciscana	Sa	S	0
Cenostigma pluviosa var. peltophorum	Sa	?	0
Cenostigma pyramidalis	Sa	S	0
Cenostigma tocantinum	Sa	R	0
Cordeauxia edulis	Af	S	0
Coulteria pumila	Na	S	0
Coulteria velutina	Na	S	0
Coulteria pringlei	Na	S	0
Coulteria colimensis	Na	S	0
Coulteria platyloba	Na	S	0
Coulteria mollis	Sa	S	0
Coulteria violacea	Na	S	0
Erythrostemon acapulcensis	Na	S	0
Erythrostemon angulata	Sa	S	0
Erythrostemon argentina	Sa	S	0
Erythrostemon caladenia	Na	S	0
Erythrostemon calycina	Sa	S	0
Erythrostemon caudata	Na	T	2
Erythrostmeon coccinea	Na	S	0
Erythrostemon coluteifolia	Sa	S	0
Erythrostemon coulterioides	Sa	S	0

Erythrostemon epifanioi	Na	S	0
Erythrostemon exilifolia	Sa	T	0
Erythrostemon exostemma	Na	S	0
Erythrostemon fimbriata	Sa	S	0
Erythrostemon gilliesii	Sa	S	0
Erythrostemon glandulosa	Car	S	0
Erythrostemon hintonii	Na	S	0
Erythrostemon hughesii	Na	S	0
Erythrostemon laxa	Na	S	0
Erythrostemon macvaughii	Na	S	0
Erythrostemon melanadenia	Na	S	0
Erythrostemon mexicana	Na	S	0
Erythrostemon nelsonii	Na	S	0/2
Erythrostemon nicaraguariensis	Na	S	0
Erythrostemon oyamae	Na	S	0
Erythrostemon palmeri	Na	S	0
Erythrostemon pannosa	Na	S	0
Erythrostemon phyllanthoides	Na	S	0
Erythrostemon placida	Na	S	0
Erythrostemon standleyii	Na	S	0
Erythrostemon yucatanensis subsp. yucatanensis	Na	S	0
Erythrostemon yucatanensis subsp. chiapensis	Na	S	0
Hoffmannseggia aphylla	Sa	S	0
Hoffmannseggia arequipensis	Sa	S	0/2
Hoffmannseggia doelli var. doellii	Sa	T	2
Hoffmannseggia doelli var. argentina	Sa	T	2
Hoffmannseggia drepanocarpa	Na	T	2
Hoffmannseggia drummondii	Na	T	0
Hoffmannseggia erecta	Sa	T	2
Hoffmannseggia eremophila	Sa	T	2
Hoffmannseggia glauca	Na+Sa	T	2
Hoffmannseggia humilis	Na	S	2
Hoffmannseggia intricata	Na	S	0
Hoffmannseggia microphylla	Na	S	0
Hoffmannseggia minor	Sa	T	2
Hoffmannseggia miranda	Sa	S	0/2

Hoffmannseggia oxycarpa	Na	T	2
Hoffmannseggia peninsularis	Na	S	2
Hoffmannseggia prostrata	Sa	S	2
Hoffmannseggia pumilio	Sa	S	0
Hoffmannseggia repens	Na	T	2
Hoffmannseggia tenella	Sa	T	2
Hoffmannseggia trifoliata	Sa	T	2
Hoffmannseggia viscosa	Sa	S	0
Hoffmannseggia watsonii	Na	T	2
Hoffmannseggia yaviensis	Sa	T	2
Stenodrepanum bergii	Sa	S	0
Libidibia coriaria	Sa+Na	S	0
Libidibia ferrea	Sa	S/G	0
Libidibia glabrata	Sa	S	0
Libidibia monosperma	Car	C	0
Libidibia paraguariensis	Sa	S/R	0
Libidibia punctata	Sa+Car	S	0
Libidibia sclerocarpa	Na	S	0
Denisophytum buchii	Car	S	0
Denisophytum rosei	Car	S	0
Denisophytum pauciflora	Car+Na	S	0
Denisophytum stuckertii	Sa	S	0
Denisophytum sessilifolia	Na	S	0
Denisophytum erianthera var. pubescens	Af	S	0
Denisophytum erianthera var. erianthera	Af	S	0
Denisophytum madagascariensis	Af	S	0
Gelrebia bracteata	Af	S	0
Gelrebia rubra	Af	S	0
Gelrebia dauensis	Af	S	0
Gelrebia oligophylla	Af	S	0
Gelrebia trothae subsp. trothae	Af	S	0/1
Gelrebia trothae subsp. erlangeri	Af	S	0/1
Gelrebia glandulosopedicellata	Af	G	0
Gelrebia rostrata	Af	S	0
Hultholia mimosoides	As	?	1
Caesalpinia crista	As+PA	G/R/C	1

Caesalpinia vernalis	As	R	1
Paubrasilia echinata	Sa	S	0
Pomaria autrotexana	Na	S	0
Pomaria burchellii	Af	G	2
Pomaria brachycarpa	Na	T	0
Pomaria canescens	Na	S	0
Pomaria fruticosa	Na	T	0
Pomaria glandulosa	Na	T	0
Pomaria jamesii	Na	T	2
Pomaria lactea	Af	S	0
Pomaria melanosticta	Na	S	0
Pomaria multijuga	Na	T	0
Pomaria pilosa	Sa	T	0
Pomaria rubicunda var. rubicunda	Sa	T	0
Pomaria rubicunda var. hauthalii	Sa	T	0
Pomaria sandersonii	Af	T	2
Pomaria stipularis	Sa	T	0
Pomaria wootonii	Na	S	0
Pterolobium hexapetalum	As	G	1
Pterolobium integrum	As	?	1
Pterolobium macropterum	As	G	1
Pterolobium stellatum	Af	G	1
Stuhlmannia moavi	Af	S	0
Tara cacalaco	Na	S	0
Tara vesicaria	Na+Car	S	0
Tara spinosa	Sa	S	0
Caesalpinia erythrocarpa	As+PA	R	1
Mezoneuron scortechinii	As+PA	G/R	1
Caesalpinia nitens	PA	G	1
Mezoneuron andamanicum	Af	G	1
Mezoneuron angolense	Af	G/R	1
Mezoneuron hildebrandtii	Af	S	1
Mezoneuron benthamianum	Af	G	1
Mezoneuron cucullatum	As	G	1
Mezoneuron hymenocarpum	As+PA	G	1
Mezoneuron kauaiense	PA	S	0

Mezoneuron sumatranum	As+PA	R	1
Moullava digyna	As	G	1
Moullava tortuosa	As	G/R	1
Moullava welwitschiana	Af	G/R	1
Moullava spicata	As	G/R	1
Guilandina minax	As	G	1
Caesalpinia murifructa	Car	C	1
Guilandina ciliata	Car	C	1
Guilandina major	Pantropical	G/R	1
Caesalpinia volkensii	Af	R	1
Guilandina bonduc	Pantropical	G/C	1
Haematoxylum brasiletto	Na	S	0
Haematoxylum campechianum	Na	S	0
Haematoxylum dinteri	Af	S	0
Hererolandia pearsonii	Af	S	0
Lophocarpinia aculeatifolia	Sa	S	0
Zuccagnia punctata	Sa	S	0

chapter will also include incorporating phylogenetic uncertainty in Lagrange analyses, as has been achieved by numerous studies using R scripts that allow to summarize the results of numerous Lagrange analysis performed over different tree topologies (e.g. Buerki & al., 2011).

3.3.4 Diversification rates analysis

In order to estimate rates of species diversification through time and among lineages, we used the Bayesian Analysis of Macroevolutionary Mixtures (BAMM) method (Rabosky, 2014; Rabosky & al., 2014; Shi & Rabosky, 2015), which has been shown to be more effective than other commonly used methods based on stepwise AIC-based approaches, such as MEDUSA, to estimate rates and detect rate shifts on branches across a phylogeny (Rabosky, 2014). Whereas other methods assume that rates of species diversification are constant through time within rate classes, leading to less effective detection of rate shifts, BAMM uses a reversible jump Markov Chain Monte Carlo (MCMC) to search for rate changes under a compound Poisson process and accounts for rate variation through time and among lineages. More specifically, BAMM produces posterior distribution of rate shift configurations, with each representing the likelihood of different scenarios of rate shifts occurring at different points along the phylogeny (with zero, one, two, three or more possible shifts in diversification rates) under different birth-death models. Non-random taxon sampling was accounted for by specifying the fraction of species sampled for specified clades (in this case corresponding to genera), leading to a more precise estimation of diversification rates, even in absence of a fully sampled phylogeny.

BAMM analyses for the moment do not allow to take into account phylogenetic uncertainty into their analyses, but the authors have indicated that they are planning to add documentation on how to use a bash shell to perform BAMM analyses across a set of trees from the posterior probability of a Bayesian analysis (BAMM documentation, section 12.4). The authors also discuss in their tutorials as to whether phylogenetic uncertainty always matters in diversification analyses. In the case of the Caesalpinia Group phylogeny, as previous results have suggested a rather robust inference of phylogenetic relationships within this group, with a few exceptions as to the placement of early diverging lineages of monospecific genera such as *Paubrasilia*, *Hererolandia* and *Lophocarpinia*, I predict that incorporating phylogenetic uncertainty will not impact our overall results as to whether or not there have been significant rate shifts amongst lineages within the Caesalpinia Group.

Using the Mccr tree in BAMM 2.3.0, without the outgroup taxa, rates were estimated and the results visualised using BAMMtools in R (Rabosky & al., 2014). Sampling fractions were assigned to each genus by determining the number of species in each clade. In order to account for uncertainties about species numbers posed by lack of recent monographic taxonomic accounts for several genera, we determined the maximum number of species per clade, counting all published names and varieties as valid species (Table 3.2), as well as minimum estimates, where varieties or subspecies were lumped and published names strongly suspected to be synonyms based on field and herbarium observations, removed. We found the greatest uncertainty within six genera: *Caesalpinia* s.s., *Cenostigma*, *Denisophytum*, *Gelrebia*, *Guilandina*, *Libidibia*, for which the maximum number of species was between 1.4 times and 2.3 times higher than the minimum estimates. We then ran a series of eight different analyses:

(i) with sampling fractions estimated according to the maximum estimate of species; (ii) with sampling fractions of these six genera estimated using the minimum estimates of species diversity; (iii) six other analyses with only one of the six genera being assigned a sampling fraction with the maximum estimate of species diversity and the other five with fractions corresponding to the minimum estimates. This allowed us to test for the impacts of taxonomic uncertainty on diversification rate estimates.

For each of these eight BAMM analyses (MaxAll, MaxCss, MaxCeno, MaxDeni, MaxGel, MaxGui, MaxLibi, Min6), the tree was pruned to retain only one sample per recognized taxon. This resulted in trees with different numbers of tips, depending on whether we were using the Maximum or Minimum species estimates for each of the six genera. The global sampling fraction varied between 0.74 and 0.8. In addition, for each tree we specified a different sampling prior, estimated using the function setBAMMpriors in the BAMMtools package in R (Rabosky & al., 2014). Each analysis consisted of two MCMC runs of 1,000,000 generations, sampled every 1,000 generations, for which we ensured that the MCMC runs converged on the same values and that adequate estimated sampling sizes were reached. The mean speciation and extinction rates were calculated across the phylogeny, as well as the estimate for the 90% highest posterior density (HPD) for the Caesalpinia Group and the rate-through-time curve was generated. The mean phylorate was plotted, and a Bayes Factor was calculated across different models with *K* rate shifts relative to the null model to identify the overall best shift configuration. We also computed the Bayes Factor associated with evidence for a rate shift for each branch in the phylogeny (results plotted on a phylogeny with scaling of each branch length reflecting the Bayes Factor). To determine whether the Bayes Factor values provided support or not for rate shifts, we used the interpretation of Kass & Raftery (1995): 0-3 not worth more than a bare mention; 3 to 20 is an indication of positive evidence for rate shift; 20 to 150 is strong evidence; >150 is indication of very strong evidence. Finally, we also conducted a Macroevolutionary cohort analysis (Rabosky & al., 2014), the pairwise probability that any two lineages share the same macroevolutionary rate dynamics.

3.4 Results

3.4.1 Time-calibrated phylogeny and divergence time estimates

The Mccr tree (Fig. 3.3) from the Beast analysis is consistent with previous Bayesian, Maximum likelihood and parsimony analyses carried out in the Caesalpinia Group in terms of topology and support (Gagnon & al., in prep., chapter 2; see Table 3.3 for summary statistics used to reconstruct the time-calibrated phylogeny in Beast v.1.8). All genera were strongly supported, but some inter-generic relationships and the positions of certain clades are not well resolved, notably *Hererolandia*, *Paubrasilia*, *Guilandina*, *Hultholia* and *Gelrebia*. The position of *Lophocarpinia* was also problematic, but for reasons mentioned in the Material & Methods, we constrained its monophyly with the genus *Haematoxylum*.

We report the ages estimated in the tree in Table 3.2, with the crown age estimates for genera with multiple species, whereas the stem age is specified for monospecifc genera such a *Hererolandia.* The root height of the tree was estimated to be 60.9 Ma (95% HPD [60.8-59.5]), and the age of the Caesalpinia Group to be 59.85 Ma (95% HPD [60.74-56.98]). In the Mccr tree, the earliest diverging genus is *Hererolandia*, estimated to be 58.35 Ma (95% HPD [60.43-55.49]), and the most recently diverged lineages were the Ticanto clade, estimated to be 5.51 Ma (95% HPD [11.49-1.19]), and *Coulteria,* estimated to be 5.54 Ma (95% HPD [7.86-3.29]) (see Table 3.4). The crown ages of the genera of the Caesalpinia Group are found to span the Eocene, Oligocene, Miocene and Pliocene (Table 3.4).

3.4.2 Biome shifts and the evolution of plant habit

Ancestral character state reconstruction using parsimony indicated that the root node of the Caesalpinia Group is reconstructed as a tree/shrub occurring in the Succulent Biome. The evolution of the liana and herbaceous habit are closely, albeit not precisely in all cases, associa-

Table 3.2 Estimates of number of species used to specify sampling fractions in the BAMM analysis. Min: minimum number of species estimated for each genus. Max: maximum number of species estimated for each genus. Max/Min: ratio of the max and min number of species estimated for each genus. In Mccr: number of species sampled in the Mccr tree, according to the maximum number of species estimated. Fractions with Max: sampling fractions specified in BAMM with the Max species estimate. Fractions with Min: sampling fractions specified in BAMM with the Min species estimate.

Genus	**Min**	**Max**	**Max/Min**	**In Mccr**	**Fractions with Max**	**Fractions with Min**
Balsamocarpon	1	1	1	1	1.0	...
Zuccagnia	1	1	1	1	1.0	...
Stenodrepanum	1	1	1	1	1.0	...
Hoffmannseggia	23	25	1.1	24	0.96	...
Libidibia	**7**	**10**	**1.4**	6	0.60	**0.86**
Pomaria	16	18	1.1	17	0.94	...
Arquita	5	6	1.2	6	1.0	...
Erythrostemon	31	34	1.1	30	0.88	...
Cenostigma	**14**	**21**	**1.5**	14	0.67	**0.79**
Cordeauxia	1	1	1	1	1.0	...
Stuhlmannia	1	1	1	1	1.0	...
Lophocarpinia	1	1	1	1	1.0	...
Haematoxylum	5	5	1	3	0.60	...
Hererolandia	1	1	1	1	1.0	...
Caesalpinia	**4**	**9**	**2.25**	**7**	**0.78**	**1.0**
Paubrasilia	1	3	3	2	0.67	...
Denisophytum	**5**	**9**	**1.8**	8	0.89	**1.0**
Tara	3	3	1	3	1.0	...
Coulteria	7	7	1	7	1.0	...
Gelrebia	**6**	**9**	**1.5**	8	0.89	**1.0**
Hultholia	1	1	1	1	1.0	...
Biancaea	6	6	1	6	1.0	...
Pterolobium	10	10	1	4	0.4	...
Ticanto	9	9	1	2	0.22	...
Mezoneuron	25	25	1	11	0.44	...
Guilandina	**7**	**16**	**2.28**	6	0.38	**0.86**
Moullava	3	4	1.3	4	1.0	...
Total	195	237		176	0.74	

ted with shifts into the Rainforest/Grassland and Warm Temperate Biomes, respectively (Fig. 3.4). Specifically, transitions from the tree/shrub habit to the suffrutescent/herbaceous habit have occurred multiple times: once in *Hoffmannseggia*, twice in *Pomaria* and twice in *Erythrostemon* (Fig. 3.4), and are closely, but not exclusively associated with occurrence in the Temperate Biome. Reversals to the tree/shrub habit from the herbaceous habit are not observed. In contrast, the evolution of liana habit is hypothesized to have happened only once, ca. 52 Ma, associated with the first arrival of the Caesalpinia Group in Asia, and with a shift from the Succulent to Rainforest/Grassland Biomes in that part of the world. Reversals from the liana to the tree/shrub habit occurred twice, once in *Mezoneuron kauaiense,* and once in a clade containing the Asian species *Biancaea sappan* and *B. milletii*. No transitions from the liana habit to the suffrutescent/herbaceous habit, or vice versa, were observed. BAMM with the Max species estimate. Fractions with Min: sampling fractions specified in BAMM with the Min species estimate.

Our analyses also suggest multiple shifts between or expansions into other biomes (Figs. 3.4-3.5). Firstly, we recorded multiple species as inhabiting more than one biome, including four from South America inhabiting both the Succulent and Grassland Biomes, and four in Asia and Africa inhabiting the Rainforest and Grassland Biomes. *Caesalpinia crista* and *Guilandina major* were scored as inhabiting the Grassland, Rainforest, and Coastal Biomes, and *G. bonduc* was scored as occupying the Grassland and Coastal Biomes. Based on the ancestral character state reconstruction, we hypothesize a total of 23 biome shifts. The most frequent shift or expansion occurred from the Grassland to Rainforest Biome (5 times), and from the Succulent to Temperate Biome (5 times). However, we also note several other shifts between the Succulent, Grassland, Rainforest and Coastal Biomes spanning most directions except from the Rainforest Biome for which no shifts to any of the other four biomes were observed in this analysis (Fig. 3.5).

3.4.3 Ancestral area estimates

In the DEC analyses, the AIC and likelihood ratio tests of BioGeoBEARS indicated that the DEC+J model had a better fit than the DEC model (Aikake weights ratio for DEC+J: 208.4,

Table 3.3 Sequences for the reconstruction of the time-calibrated phylogeny of the Caesalpinia Group. The number of sequences and number of characters for each locus is indicated, after the removal of ambiguous characters (original length of the matrix shown in parentheses). The % of missing characters for each matrix is indicated.

Locus	**Number Sequences**	**Number Characters**	**% missing**
ITS	225	778 (820)	28.5%
matK + *3'-trnK* intron	68	1823 (1839)	81.3%
rps16	237	989 (1081)	27.2%
trnL-trnF	136	1261 (1347)	64.6%
trnD-trnT	218	1775 (1921)	35.9%
ycf6-psbM	182	1638 (1795)	50.1%
Combined	294	8264 (8803)	52.8%

Aikake weight ratio for DEC: 0.0048). The ancestral area reconstruction analysis was ambiguous about the origin of the Caesalpinia Group as a whole, as it was reconstructed as being present in both South America and Africa on our Mccr phylogeny from the Bayesian analysis (Fig. 3.3).

The crown node ages of the genera and their corresponding ancestral ranges as reconstructed by the DEC+J unconstrained analysis suggest that the presence of members of the Caesalpinia Group in all geographic areas, except the Australian-Pacific region, dates back to the Eocene. Our analyses reconstruct the root of the Caesalpinia Group as occupying both South America and Africa, with a presence in Asia by 52.17 Ma, in the Caribbean by 44.02 Ma, and with the earliest presence in North America by 42.56 Ma (Table 3.5). In contrast, the earliest presence of the group in the Australian-Pacific region is at 28.02 Ma, in the Oligocene.

The DEC analysis also reveals the strong geographical structure of many clades within the Caesalpinia Group. For example, the majority of Asian species cluster together in a large clade containing most of the liana species (Fig. 3.3, node D37), with a few clades representing extensions into the Australian-Pacific region and Africa. Another example are the species of the genus *Erythrostemon*, that are found in two clades that almost perfectly correspond to species found in North America and species found in South America. The phylogeny of *Pomaria* also shows high geographic structure with species assigned to three geographically restricted clades in North America, South America and southern Africa.

Our DEC analyses allowed the identification of a total of 39 trans-continental crown nodes, ranging from 52.17 Ma to as recent as 1.27 Ma (Table 3.5). The large majority of these trans-continental nodes do not involve biome shifts. Of the 28 trans-continental crown nodes that span the same biome, the majority (22) are within the Succulent Biome, five representing continental disjunctions between Africa and the Neotropics between 51.97 and 25.08 Ma and the other 17 occur between the three Neotropical areas (Na, Sa, and Car), between 44.02 and 1.27 Ma (Fig. 3.6). There is also an additional Asia to Africa disjunction within the Succulent Biome at ca. 46.79 Ma, but it is difficult to interpret whether it occurred within the Succulent Biome as the subtending branches were optimized as inhabiting both the Succulent and Grassland Biomes. These trans-continental crown nodes within the Succulent Biome span the Eocene to the Pliocene (Fig. 3.6). We recovered only four dispersal events that were associated with the Grassland Biome, from Asia to Africa or to the Australian/Pacific region, and only two occurred with certainty within the Temperate Biome, between North America and South America.

In contrast, only eight trans-continental crown nodes correspond to shifts between biomes (Table 3.5). The remaining three trans-continental crown nodes are equivocal in terms of biome shifts or not, being located on nodes where two character states were optimized. The DEC analysis also allowed the identification of 15 biome shifts within geographic areas (Table 3.5). These shifts ranged from 28.02 Ma to 2.05 Ma: within North and South America, predominantly between the Succulent and Temperate Biomes, and in Asia and the Australian-Pacific region, between the Grassland and Rainforest Biomes. In Africa, we identified two shifts between the Succulent and Grassland Biomes, one of these following a dispersal event to Madagascar.

3.4.4 Diversification rate shifts analyses

The BAMM analyses found no evidence for any shift in diversification rate across the entire Caesalpinia Group. The eight analyses with varying sampling fractions assigned to *Cenostigma, Guilandina, Caesalpinia* s.s., *Denisophytum, Gelrebia* and *Libidibia,* consistently found that the 95% credible set of shift configurations contained only a single rate configuration, i.e. a model with zero rate shifts. This is reflected in the posterior distribution of shift configurations sampled during the MCMC run, which was highest for the null model with 0 shifts (e.g. numbers from the Min6 analysis: 0 shifts: 0.65; 1 shift: 0.27: 2 shifts: 0.068; 3 shifts: 0.014, 4 shifts: 0.001; 5 shifts: 0.001). This result was the same across all seven analyses with different sampling fractions assigned to different genera (an example of the mean Phyloplot rate of the min6 analysis is given in Fig. 3.7). Macroevolutionary cohort analyses also failed to find any evidence for distinct rate regimes between clades or species (Fig. 3.7). The rates through time plot recovered for all analyses shows a gradual steady decrease in speciation rate through time across the phylogeny as a whole, with a mean speciation rate of 0.0657 for the entire Caesalpinia Group for the Min6 analysis (the 90% HPD: 0.054 to 0.081). We also did not find any strong support (above 20) when looking at Bayes Factor values for rate shifts in individual branches across the phylogenies. At most, we occasionally found some positive support for rate shifts, with the highest Bayes Factor values found to be 14.15 for the branch subtending *Guilandina ciliata* in the MaxGui analysis (the second highest value for BF in that analysis was 5.5 for branches subtending the genus *Coulteria*).

3.5 Discussion

3.5.1 Origin of the Caesalpinia Group

The early and widespread distribution of Caesalpinia Group species on all continents, except the Australian-Pacific region, could be accounted for by the Tethys Seaway hypothesis of early legume diversification proposed by Schrire & al. (2005). The crown node of the Caesalpinia Group was estimated at 59.85 Ma (Fig. 3.3, Table 3.4), appearing shortly after the appearance

Table 3.4 Fossil calibrations and ages of crown nodes for each genus in the Caesalpinia Group, with and without the calibrations. "Root only" indicates the ages of the relevant clades with only the root of the phylogeny calibrated. Fossil calibrated nodes refer to Fig. 3.3.

Calibrations	**Node**	**Calibration specs.**	**Estimated Age (Ma)**	**95% HPD (Ma)**	**Root only (Ma)**	**95% HPD (Ma)**
Root	F1	UNIF [60.8-55.6]	60.35	[60.8-59.5]	58.54	Not available
Senna	F2	UNIF [60.8-45]	46.16	[48.17-45]	33.7	44.39-22.71]
Mezoneuron fossil	F3	UNIF [60.8-45]	45.44	[46.30-45]	15.98	[20.37-11.49]
Mezoneuron kauaiense	F4	EXP [offset: 4.7, mean=7, Maxcutoff=32]	10.97	[21.29-6.10]	7.46	10.64-2.54]
Clade			**Crown Age (Ma)**	**95% HPD (Ma)**	**Root only (Ma)**	**95% HPD (Ma)**
Caesalpinia Group			59.85	[60.74-56.98]	40.35	[49.42-30.45]
Arquita			24.79	[32.41-16.90]	16.45	[22.46-10.67]
Pomaria			27.46	[33.33-20.92]	18.23	[24.02-12.86]
Erythrostemon			36.28	[40.84-31.24]	24.28	[30.02-17.39]
Cenostigma			13.59	[17.58-10.07]	23.48	[31.24-15.17]
Cordeauxia			11.54	[18.19-5.54]	7.35	[11.41-3.56]
Stuhlmannia			7.08	[11.58-3.472]	4.59	[7.44-2.10]
Libidibia			22.86	[35.71-12.07]	15.29	[25.27-7.24]
Stenodrepanum			35.63	[42.16-28.59]	23.66	[29.86-16.06]
Hoffmannseggia			30.03	[35.60-24.13]	19.96	[25.46-13.86]

Zuccagnia			35.25	[43.55-25.25]	23.48	[31.24-15.17]
Balsamocarpon			35.25	[43.55-25.25]	23.48	[31.24-15.17]
Caesalpinia			44.02	[53.16-34.63]	26.09	[33.57-18.55]
Paubrasilia			22.29	[35.88-9.35]	14.41	[25.53-5.38]
Denisophytum			25.08	[33.04-18.29]	16.09	[21.78-10.89]
Tara			18.31	[27.01-10.47]	3.45	[5.09-1.93]
Coulteria			5.54	[7.86-3.29]	11.29	[16.98-6.13]
Gelrebia			12.99	[17.11-8.85]	8.13	[11.1-5.44]
Hultholia			46.79	[52.66-34.67]	24.5	[30.19-16.08]
Moullava			31.27	[41-83-18.67]	14.63	[19.93-9.23]
Biancaea			28.02	[39.81-16.69]	14.04	[18.53-9.70]
Mezoneuron			24.06	[37.15-16.13]	12.81	[16.60-8.64]
Guilandina			23.41	[34.67-12.74]	13.12	[18.57-7.94]
Pterolobium			17.45	[27.63-9.77]	10.94	[14.04-6.92]
Ticanto clade			5.51	[11.49-1.19]	3.36	[6.6-0.77]
Haematoxylum			36.72	[47.70-22.36]	24.96	[35.68-14.71]
Lophocarpinia			39.55	[55.26-26.58]		
Hererolandia			58.35	[60.43-55.49]	37.29	[46.00-27.77]

of the Leguminosae family in the Paleocene. Under the Tethys Seaway scenario, legume taxa, particularly those with a strong affinity to tropical dry ecology akin to the Succulent Biome, could have spread across a putative tropical arid belt located around the seaway and spanning the equator, which is thought to have existed during the Eocene (56-43 Ma),. This is the pattern observed in the Caesalpinia Group, where the earliest trans-continental crown nodes are estimated to be Eocene in age. Although the root node was reconstructed equivocally as either of African or South American origin, at latest by 52 Ma members of the Caesalpinia Group are estimated to have reached Asia, by 44 Ma the Caribbean and by 42 Ma North America (though fossil evidence indicates an earlier presence in North America by 45 Ma (Herendeen & Dilcher, 1991; Herendeen, 1992)). Only the Australian/Pacific region had not been reached by the Oligocene, which is not unexpected, given that New Guinea and islands west of Borneo and Sundaland did not emerge before the crashing of the Australian and Eurasian plates at the boundary of the Oligocene/Miocene era (Hall, 2009).

Trans-continental crown nodes between these five geographic areas in the Eocene is difficult to explain by any other phenomenon than long distance dispersal. The ages of these disjunctions (Fig. 3.6, Table 3.5) are too young to be accounted for by vicariance, as the geographic areas we described were separated by wide oceanic barriers for most of the Paleogene and Neogene (Scotese, 2001). These trans-continental crown nodes are also too young to be explained by some of the major continental reconfiguration events, such as the Cretaceous opening of the Southern Atlantic (Parrish, 1993), the North Atlantic land bridges of the Mid-Tertiary (Tiffney, 1985), as well as the mid-Tertiary land connection between North and South America (Iturralde-Vinent & Macphee, 1999). Later land connections do not seem to have been necessary for dispersal. For example, there is no signature of dispersal opportunity following closure of the Panama Isthmus linking South America and North America 15 - 13 Ma (Montes & al., 2015), with dispersal events occurring both before and after the formation of the isthmus (Fig. 3.3, Table 3.5), as found for many plant and animal taxa more generally (Cody & al., 2010; Hughes et al., 2013; Bacon & al., 2015). Similarly, there is evidence for dispersal between Africa and Asia before and after the definitive closing of the Tethys Seaway (Dercourt & al., 1986), which occurred at ca. 20 Ma (Fig. 3.3, Table 3.5).

Table 3.5 Ages of trans-continental crown clades within the Caesalpinia Group, as reconstructed by the unconstrained DEC model, with or without biome transitions. The dispersal column indicates changes in geographical areas; the Biomes column identifies the biomes associated with the dispersal event. Biome abbreviations: S = Succulent Biome; G = Grassland Biome; T = Temperate Biome; R= Rainforest Biome; C = Coastal Biome.

Description	**Node**	**P.P.**	**Disjunction**	**Biomes**	**Age**	**95% HPD of node age**
Dispersals without biome shifts						
Libidibia sclerocarpa stem node	D01	0.47	Sa/Na	S->S	3.07	[4.37, 0.55]
Libidibia coriaria crown node	D02	0.87	Sa/Na	S->S	5.71	[8.46, 1.66]
Cenostigma eriostachys/ C. gaumeri MRCA	D03	0.49	Sa/Na	S->S	11.55	[12.84, 6.34]
Caesalpinia pulcherrima	D04	1.0	Na/Car	S->S	20.05	[29.67, 11.67]
Hoffmmanseggia peninsularis clade	D05	1.0	Sa/Na	S->S	22.20	[27.97, 16.26]
Na *Erythrostemon* clade + E. Placida	D06	0.94	Sa/Na	S->S	36.28	[40.84, 31.24]
Haematoxylum campechianum clade	D07	0.34	Af/Na	S->S	39.55	[55.26, 26.58]
Tara-Coulteria-Denisophytum clade	D08	1.0	Sa/Na	S->S	42.56	[52.08, 33.08]
Coulteria mollis	D09	1.0	Sa/Na	S->S	1.27	[2.31, 0.40]
Denisophytum stuckertii	D10	1.0	Sa/Na	S->S	18.31	[25.64, 11.57]
Tara spinosa	D11	1.0	Sa/Na	S->S	18.31	[27.01, 10.47]

Lophocarpinia	D12	1.0	Af/Sa	S->S	39.55	[55.26, 26.58]
Dispersal Af to Sa	D13	0.73	Af/Sa	S->S	51.97	[56.90, 43.39]
Libidibia punctata	D14	0.39	Sa/Car	S->S	2.34	[3.23, 1.1679]
Cenostigma gaumeri	D15	0.72	Na/Car	S->S	5.08	[7.52, 2.23]
Tara vesicaria	D16	1.0	Na /Car	S->S	9.38	[14.62, 4.30]
Cenostigma pellucida	D17	0.23	Na/Car	S->S	9.55	[7.7601, 0.001]
Denisophytum pauciflora clade	D18	1.0	Na/Sa /Car	S->S	18.31	[25.64, 11.57]
Erythrostemon glandulosa	D19	0.71	Na/Car	S->S	33.54	[37.82, 27.31]
Caesalpinia nipensis and *C. brasiliensis clade*	D20	1.0	Sa/Car	S->S	44.02	[53.16, 34.64]
Denisophytum madagascariense clade	D21	1.0	Na/Sa/Af	S->S	25.08	[33.04, 18.29]
Gelrebia clade	D22	0.76	As/Af	S->S	46.79	[52.66, 34.67]
Pterolobium stellatum	D23	0.81	As/Af	G->G	12.13	[20.06, 3.48]
Mezoneuron angolense clade	D24	1.0	As/Af	G->G	12.75	[12.23, 4.44]
C. nitens clade	D25	1.0	As/PA	G->G	24.06	[37.15, 16.13]
Biancaeae decapetala	D26	0.99	As/PA	G->G	28.02	[39.81, 16.69]
Hoffmannseggia glauca	D27	0.85	Sa/Na	T->T	3.65	[5.95, 1.61]

Pomaria glandulosa clade + *Pomaria multijuga*	D28	0.99	Sa/Na	T->T	27.46	[33.33, 20.92]
Hoffmannseggia humilis clade	D29	0.52	Sa/Na	S/T->S/T	12.45	[16.42, 8.58]
Guilandina bonduc	D30	1.0	As/Pantropics	GC->GC	11.24	[17.05, 6.51]
Caesalpinia crista	D31	1.0	As/PA	GR->GR	5.51	[11.49, 1.19]
Dispersals with biome shifts						
Hoffamnnseggia drummondii	D32	1.0	Sa/Na	S->T	8.96	[14.21, 3.96]
Erythrostemon caudata	D33	0.99	Sa/Na	S->T	18.51	[13.58, 23.80]
Libidibia monosperma	D34	1.0	Sa/Car	S->C	22.86	[35.71, 12.07]
Moullava. welwitschiana	D35	1.0	As/Af	G->GR	17.41	[26.12, 9.12]
Pomaria lactea clade	D36	0.99	Sa/Af	T->GT	19.79	[25.95, 13.39]
Clade with Asian-African lianas	D37	0.87	As/Af	S->G	52.17	[54.45, 49.23]
M. hymenocarpum clade (sumatranum)	D38	0.80	As/PA	G->GR	14.67	[21.29, 6.10]
M. hymenocarpum clade (kauaiense)	D39	0.80	As/PA	G->GS	14.67	[21.29, 6.10]

Table 3.6 Biome shifts within continents. Node indicates the number associated with Figure 3.3. P.P. and BS. Continent indicates in which geographic area the shift occurred. Biome abbreviations are provided in table 3.5.

Description of Node	**Node**	***P.P.***	**Continent**	**Biome Shift**	**Ages**	**95% HPD of node age**
Pomaria clade	B01	1.0	Sa	S->T	40.17	[46.81, 34.44]
Pomaria fruticosa stem node	B02	1.0	Na	T->ST	17.79	[23.72, 11.73]
Pomaria burchellii stem node	B03	0.96	Af	T->G	9.25	[14.43, 3.60]
Erythrostemon exilifolia stem node	B04	0.96	Na	S->T	11.44	[15.60, 7.25]
Hoffmannseggia herbaceous clade, stem node	B05	1.0	Sa	S->T	22.74	[22.68, 17.93]
Hoffmannseggia yaviensis stem node	B06	1.0	Sa	T->ST	13.55	[17.61, 9.27]
Libidibia paraguariensis stem node	B07	1.0	Sa	S->SR	11.56	[16.97, 6.53]
Cenostigma tocantinum stem node	B08	0.87	Na	S->R	2.05	[4.45, 0.12]
MRCA of *Cenostigma marginata* and *Cenostigma pluviosa* var. *sanfranciscana*	B09	0.38	Sa	S->G	9.96	[12.10, 6.29]
Gelrebia glandulosopedicellata stem node	B10	0.47	Af	S->G	10.16	[13.78, 7.33]
Crown clade of *Guilandina*	B11	1.0	As	G->GC	23.41	[34.67, 12.74]
MRCA of *C. crista* + *C. vernalis*	B12	1.0	As	G->GR	23.45	[34.20, 13.86]
Biancaea sappan clade	B13	0.99	As	G->R	28.02	[39.82, 16.69]
Mezoneuron hildebrandtii stem node	B14	0.50	Af	G->S	6.23	[9.27, 1.39]
M. erythrocarpa + *M. scortechinii* MRCA	B15	1.0	As/PA	G->GR	6.09	[10.28, 2.51]

Certain genera of the Caesalpinia Group have fruit and seeds that are well adapted for long distance dispersal. The clearest examples are the classical drift seeds of *Guilandina* species, which are buoyant and capable of long-distance dispersal by sea, washing up on the shores of all six geographic areas (Gunn & Dennis, 1976). *Caesalpinia crista* and other members of the

Ticanto clade have coriaceous one-seeded pods that can also potentially float, which may explain its wide distribution from New Caledonia, across the Indo-Malay peninsula to China and India (Hattink, 1974; Vidal & Hul Thol, 1976). Other Asian species have winged fruits, including the samara-like fruits of *Pterolobium* and the broadly-winged pods of *Mezoneuron*, two genera which occur in both Asia and Africa. Whilst the samaras of *Pterolobium* species are most likely wind-dispersed, the broadly-winged pods of *Mezoneuron* might also be sea-dispersed, with the wing serving as a flotation device for dispersal over water. However, in all other species of the Caesalpinia Group, it is not always entirely clear how long-distance dispersal could have happened. Whilst *Coulteria* has long, tardily-dehiscent, thin papery fruits that are likely wind dispersed, other genera such as *Tara*, *Libidibia,* and *Moullava* have, thicker, heavier fruits, that are either indehiscent or dehiscent, and appear to be more likely dispersed by animals. The most common fruit type in the Caesalpinia Group is a typical explosively dehiscent pod with elastically twisting valves, and while it has been observed that these types of fruit can project seeds over several meters, they are clearly not adapted for long-dispersal over thousands of kilometers, which seems to be occurring repetitively in the Caesalpinia Group. Sea dispersal for these taxa should also not be discounted, as there is evidence from studies of colonization of emerging volcanic islands that many plant taxa can arrive via long distance dispersal, even when they bear no features suggesting adaptation to this type of dispersal (e.g. 78% of plant species colonizing the volcanic island of Surtsey, near Iceland, arrived by ocean currents, with only 25% of these taxa having morphological adaptations for dispersal by water (Higgins & al., 2003)). Other vectors could possibly explain long distance dispersal in this group, such as dispersal by birds, and extreme meteorological events (Nathan & al,, 2008; Nogales & al., 2012), which would have increased chances of arriving due to the long evolutionary time-scale of this group.

3.5.2 Global-scale phylogenetic biome conservatism

Our study provides evidence for global-scale phylogenetic niche conservatism at the level of the major global Succulent, Warm Temperate, Rainforest, and Grassland Biomes. Indeed, our study indicates that more than 92% of the nodes within the phylogeny did not represent switches, whereas the total number of overall biome shifts, within or between continents and geographic regions, represents roughly less than 8% of the phylogeny (22/284 nodes in the DEC analysis tree, . The majority of these shifts occurred within landmasses (15), and a few occurred in intercontinental disjunctions (8); in comparison, we found more than three times more intercontinental disjunctions (28) which occurred within the same biome. The total number of disjunctions between areas (within the same biome) is higher than the total number of biome shifts, whether within or between continents. This evokes the idea of trans-continental-scale biome conservatism, suggesting that it has been easier for taxa in the Caesalpinia Group to disperse to similar habitats on other continents, than for local lineages in different but geographically adjacent biomes to shift and adapt (Donoghue, 2008; Edwards & Donoghue, 2013). This idea could be tested formally using comparative phylogenetic methods by comparing whether there is phylogenetic signal or not in the evolution of the biome trait. The majority of intercontinental shifts within the same biome occur in the Succulent Biome (22), with a smaller number within the Grassland (4) and the Temperate (2) Biomes, though there are possibly more, as we were not always able to clearly classify the type of biome transition for at least three dispersal events.

We found a directional asymmetry in biome shifts across the Caesalpinia Group similar to patterns for the Leguminosae as a whole. Schrire & al. (2005) found that both rain forest and temperate clades were predominantly derived from dry clades, a pattern that we also observed, with the most frequent type of biome transitions occurring from the Succulent to Temperate Biomes and from the Grassland to Rainforest Biomes (Fig. 3.6). Both the Rainforest and Coastal Biomes were net sinks, with no reversals back to the Grassland or Succulent Biome (Fig. 3.6), suggesting that aridity or seasonal drought is a difficult ecological barrier to overcome , and/or that Succulent Biome communities are less disturbance prone than Rainforests, Savannas and Coastal Biomes and therefore potentially saturated in their species carrying capacity, hindering establishment of new mal-adapted lineages (Pennington & al., 2009; Hughes & al., 2013).

Similar repeated patterns of trans-continental disjunctions confined to the Succulent Biome have been reported in other groups with similar ecological affinities, including the legume clades *Parkinsonia* (Hawkins & al., 2007), the *Conzattia/Heteroflorum-*

Colvillea/*Delonix* clade (Haston & al. 2005; Babineau, 2013), tribe Robinieae (Lavin & al., 2004; Lavin, 2006; Särkinen & al., 2012), two clades within the dalbergioid legumes and the clade comprising the informal Leucaena and Dichrostachys groups of mimosoid legumes (Lavin & al., 2004), as well as in other plant families, including the Anacardiaceae *(Loxopterygium*), Polygalceae (*Ruprechtia*), and Cactaceae *(Pereskia*) (Pennington & al., 2004). This suggests that these intercontinental disjunctions within the Succulent Biome are even more prevalent than previously thought, and phylogenetic Succulent Biome conservatism appears to be a pervasive pattern potentially affecting the majority of taxa belonging to this biome.

In addition to strong niche conservatism across the Succulent Biome, the lineages of the Caesalpinia Group in the Succulent Biome also show many of the same patterns and features of high levels of geographical structure across the phylogeny, and reciprocal monophyly of species that are thought to be the hallmarks of evolutionary diversification of plants in this biome (Lavin, 2006; Pennington & al., 2006, 2009; Särkinen & al., 2012; Hughes & al., 2013). In the Neotropics, these features are thought to be the result of dispersal limitation across the island-like distribution in seasonally dry tropical forests (Pennington & al., 2000, 2006, 2009). This contrasts with savannahs and rainforests, which have much larger and more continuous distributions (Lavin & al., 2004.). This phenomenon of strong isolation associated with dispersal limitation is also reflected in the beta diversity of SDTFs, which tend to have high levels of endemism (Linares-Palomino, 2006), whereas the opposite trend is found in rainforest trees. For example, the number of endemic woody taxa in inter-Andean valleys varies from 16.4% to 47.1% on a par with levels of oceanic island endemism (in the Galapagos is around 48% (Tye & al., 2000)), and reaches 65.5% in the Mexican Pacific coast and 77.5% in the insular Caribbean (Linares-Palomino & al., 2011). In contrast, studies on the western Amazonian forest in Peru have found that a majority of the 825 legume trees surveyed in this area have broad distributions, with the most common species extending into Ecuador, resulting in very low beta diversity (Pitman & al., 1999; 2001). Furthermore, in the Rainforest Biome, closely related species frequently occur on the same territory, with a study reporting the presence of 19 species of *Inga* found in one hectare of rainforest in South America (Valencia & al., 1994; Richardson & al., 2001). In contrast, in the SDTF it is rarer to find more than one species from a same legume lineage co-occurring in the same area. These patterns are exemplified by the intensive studies of the robinioid legume genera *Coursetia* and *Poisonnia* (Lavin, 2006; Särkinen & al., 2012), and are also observed in almost all genera of the Caesalpinia Group present in the Neotropics and Africa. It also appears that the species from these different dry habitat geographic nuclei have been isolated for several millions of years. Perhaps the most striking examples of long-term isolation and persistence of Succulent lineages are those occupying the seasonally dry inter-Andean valleys, where divergence times of species of *Arquita*, restricted to different inter-Andean dry valleys in Ecuador, Peru, Bolivia and Argentina, range from 6-24 Ma (fig. 3.3) suggesting ancient isolation of species growing in disjunct valleys in line with other recent studies of Andean SDTF lineages (Pennington & al., 2010; Särkinen & al., 2012).

3.5.3 Timing of the trans-continental disjunction events in the Succulent Biome

In the Neotropics, it has long been debated whether the seasonally dry tropical forests, the principal component of the Succulent Biome, are very recent (Pleistocene) or of much more ancient Gondwanan origin (Prado & Gibbs, 1993; Pennington & al., 2000). Pennington & al. (2004) found evidence that diversification of the various SDTF lineages they selected for their study occurred before the Pleistocene, with the majority of lineages diversifying during the Miocene and Pliocene. For the Neotropical lineages of the Caesalpinia Group, we also find that trans-continental dispersal within the Succulent Biome occurred for the majority throughout the Pliocene and Miocene, but certain dispersal events are also estimated to have occurred during the Oligocene and Eocene (Fig. 3.3-3.4, Table 3.5). The time-calibrated phylogenetic analyses of Pennington & al. (2004) of various plants endemic to the Succulent Biome in the Neotropics showed that most of the North American lineages in the taxa they studied were somewhat younger than South American ones, but their sample size was small. While we find a few North American lineages that appear to be relatively younger, such as *Coulteria* with an estimated crown age of 5 Ma and the more recent dispersals within *Libidibia*, we also find evidence that SDTF lineages, such as *Erythrostemon* and *Tara* have been present in North America throughout the Miocene. This lack of any strong peak of ages of dispersal within the Neotropics fits with a scenario of stochastic long distance dispersal between these two continents within the context of strong niche conservatism. We predict that future studies will continue to fail to find evidence for specific time peaks of intercontinental disjunctions within the Succulent Biome in the Neotropics (e.g. such as the closure of the Isthmus of Panama, which has been suggested as a landbridge facilitating biotic exchanges between North and South America; Cody & al. 2010; Bacon & al., 2015).

While there are considerably fewer studies with dated phylogenies of lineages endemic to the Succulent Biome in Africa, Cowling & al. (2005) suggested that the African Thicket Biome (the equivalent of the Succulent Biome) was probably derived from elements of various ages, including basally-branching clades from the Upper Cretaceous and the Eocene, as well as lineages derived from adjacent biomes that diversified following the intensification of the arid period observed during the mid-Miocene onward. The African Succulent Biome lineages of the Caesalpinia Group also include both older, basally-derived clades from the Eocene and more recently-derived Miocene clades. For example, the stem ages of the two species from Namibia (*Hererolandia pearsonii* and *Haematoxlum dinteri*) from the Oligocene and Paleocene (table 3.4) are considerably older than the stem or crown ages of the lineages such as *Cordeauxia*, *Stuhlmannia*, *Gelrebia* and African *Denisophytum*, which occur predominantly in East Africa, from the Somali-Masai region of endemism (White, 1983), through Tanzania, Kenya, Mozambique, and Madagascar (although *Gelrebia* has species extending across South Africa and Namibia). The ancient origins of the first two Namibian species is possibly linked to the fact that Namibia hosts some of the oldest deserts on the continent, which are thought to have developed progressively from the late Paleocene, and remained arid to semi-arid thereafter (van Zinderen Bakker, 1975; Ward & al., 1983). This pattern of having an early diverging lineage that is endemic to arid environments in Namibia is found in a number of other plant lineages as pointed out by Schrire et al. (2009), who cited examples in the Indigoferae, in *Gazania* and the core Arctotis group in the Asteraceae, *Pelagornium,* as well as in *Monsonia* including *Sarcocaulon* in the Gesneriaceae, as well as members of the subfamily Zygophylloideae (see Schrire & al. 2009 for details and references cited therein).

In contrast, all the other African Succulent Biome lineages are younger, with the majority of crown node age estimates between 12 and 11 Ma, coinciding with the mid to late Miocene global cooling and drying and expansion of arid areas in Africa which started between 17 and 16 Ma (Senut & al., 2009). Interestingly, this predates the major expansion of the savannahs, that occurred later in the Pliocene (Strömberg, 2005; Strömberg, 2011; Maurin & al., 2014; Pennington & Hughes, 2014), and suggests that perhaps before the establishment and dominance of the savannahs, with its recurrent fire cycles, this period in Africa allowed Succulent Biome lineages to expand and diversify.

3.5.4 *Caesalpinia* in the Grassland and Rainforest Biomes: diversification in Asia, followed by expansion during the middle Miocene

With the exceptions of a few derived species in the predominantly Succulent Biome Neotropical genera *Cenostigma* and *Libidibia*, the majority of Grassland and Rainforest Biome species in the Caesalpinia Group are lianas or scrambling shrubs from Asia and Africa (Figs. 3.3-3.4). The initial biome shift to Grassland is thought to have occurred early, and coincides with evolution of the liana habit and dispersal to Asia (Fig 3.3 clade D37, Fig. 3.4, Table 3.5). This early liana clade in Asia (and then Africa), currently spans the rainforest-savannah mosaic found in these regions, and a lower number of intercontinental disjunctions are noted in these clades than in clades of the Caesalpinia Group with affinities to the Succulent Biome. If the pantropical sea-dispersed genus *Guilandina* is excluded, only eight dispersal events are noted, four to Africa and four to the Australian/Pacific region (Fig. 3.3, Table 3.5-3.6). Schrire & al. (2005) suggested that many Asian species of legumes can be considered as pioneer species, preferring transitional habitats, and we find that many of the species in this clade are described in the literature as occupying habitats that correspond to disturbed areas, such as along roadsides, river margins, and forest fringes or clearings, as would be expected for lianas which are well-adapted to these types of disturbed sites.

Within this large clade of species consisting predominantly of lianas, the majority of dispersals to Africa occurred in the middle to late Miocene, from 17.4 Ma to 8.12 Ma, a period coinciding with global late-Miocene aridification concomitant with expansion of the Antarctic ice sheet. In combination with other factors, such as the closure of the Tethys Seaway, and the gradual uplift of Eastern Africa, this led to the expansion of semi-arid conditions across Africa. This period slightly predates the global expansion of C4 grass-dominated ecosystems in the Early Pliocene (Cerling & al., 1997; Jacobs & al, 1999; Strömberg, 2005; Strömberg, 2011; Maurin & al., 2014), probably in response to lower levels of C02 in the atmosphere (Ehleringer & al., 1997; Christin & al., 2008), and fire feedback loops, which were accentuated by the diversification of bovid herbivores affecting the grass/tree balance in these habitats (Vrba, 1985). This repeated dispersal of Asian Grassland clades to Africa is the predominant pattern, and is found in *Pterolobium*, *Mezoneuron*, *Guilandina*, and *Moullava*.

In addition to these Asian and African lineages, some derived species of two New World genera, although ancestrally and predominantly occurring in the Succulent Biome, also occur in the Grassland Biome, and also diverged during the late Miocene, coinciding with the expansion of the savannas in South America (Beerling & Osborne, 2006; Simon & al., 2009; Pennington & Hughes, 2014). *Libidibia* and *Cenostigma* show classical Amazonian Arc distributions (Prado & Gibbs 1993; Pennington & al. 2000), from the Atlantic Coastal forests around the southern fringes of the Amazon to Paraguay, Bolivia, and north through the inter-Andean valleys of Bolivia and Peru. This contrasts with other Neotropical genera and species in the Caesalpinia Group, which are restricted to the Succulent Biome. In both these genera the majority of species grow in the Succulent Biome, but a number of species also clearly belong to the Grassland Biome (*Cenostigma marginata*, some elements within the widespread polymorphic *C. pluviosa* alliance*,* and *Libidibia ferrea*), one occurs in rainforests (*Cenostigma tocantinum*; Warwick & Lewis, 2009) and another species occurs in both xerophytic and wet environments (*Libidibia paraguariensis*; Ulibarri, 1996). The ages of these two genera predate the appearance and spread of the Cerrado Biome in South America, but the subclades containing the Cerrado species within these genera agree with the Pliocene age of the Cerrado estimated by Simon & al. (2009), with the majority of the Cerrado lineages less than 10 Mya.

3.5.5 Transitions to the Warm Temperate Biome – ancient and recent links with the Andes

The amphi-tropical distribution pattern of Warm Temperate plants with affinities to cooler, open grasslands and deserts is a well-known North American and South America pattern of disjunctions, and has long attracted the attention of biogeographers (Bray, 1898; Johnston, 1940; Raven, 1963; Solbrig, 1972). In contrast, the disjunction presented by *Pomaria* between North America, South America and southern Africa in the Temperate Biome is a much rarer pattern (Thorne, 1973; Simpson & al. 2006), and it is the only example known in the Caesalpinia Group. In Africa, species of *Pomaria* are found in the high, subtropical grassland plateau of the Transvaal, but also in semi-arid thicket and savannah-type habitats across Namibia, Botswana and South Africa.

Interestingly, taxa of Andean origin are closely related to all the clades and species occurring in the Warm Temperate Biome, suggesting that shifts into this biome (which can have cooler temperatures) could be linked to the early phases of Andean uplift. For example, the genus *Pomaria* is sister to *Arquita,* which is restricted to inter-Andean dry valleys from Ecuador to Argentina. This suggests a likely South American ancestral area for *Pomaria,* contradicting earlier work that suggested a North American origin with subsequent dispersals to South America and Africa (Simpson & al., 2006). Another example of possible Andean affinities of Warm Temperate Biome species is the sister group relationship between *Erythrostemon angulata,* endemic to Chile in the Atacama and Coquimbo Mountains, and the North American species *Erythrostemon caudata*, which occurs in open grassy areas and mesquite savannas of Mexico and Texas. Similarly, in the *Stenodrepanum-Hoffmannseggia* clade*,* which has multiple species found in high altitude deserts and other warm temperate environments across the Andes, at least four dispersals to North America occur, including the recent dispersal of *H. glauca* from the South American Andes to North America (Simpson & al., 2005) (Figs. 3.3-3.4; Table 3.5). The entire *Stenodrepanum-Hoffmannseggia* clade is sister to the Andean genera *Balsamocarpon* (from the Coquimbo and La Serena valleys in Chile) and *Zuccagnia* (from north-western Argentina and western Chile).

The Temperate Biome species, found for the most part in cooler arid deserts and prairie grasslands in North and South America, have diversified from the Oligocene, through the Miocene and more recent Pliocene periods, from 27.47 Ma to as recent as 3.56 Ma (Fig. 3.3-3.4). While we found no in-depth review of the timing of these more arid desert/grassland disjuncts, the dated phylogeny of *Tiquilia* shows a similar pattern of an Eocene/Oligocene boundary (~33–29 Ma) origin in South America, followed by a more recent dispersal to North America (Moore & Jansen, 2006). The family Cactaceae also has an origin in South America, in the Andes of northern Chile, north-west Argentina, Bolivia and Peru, around the Eocene-Oligocene boundary, between 32 Ma to 35 Ma (Arakaki & al., 2011; Hernández-Hernández & al. 2014).

3.5.6 Constant rates of species diversification through the Cenozoic

We found no evidence for significant variation in species diversification rates among lineages or through time across the Caesalpinia Group, suggesting a model of constant diversification throughout the Cenozoic. Speciation rates here estimated to be low, with an average speciation rate of 0.0725 for the Caesalpinia Group, and examination of the rate through time plot (Fig. 3.7D) actually suggest that speciation rates have been slowly decreasing since the Paleocene. This result is in line with the legume-wide diversification analysis of Koenen & al. (2013), which detected no rate shift associated with the Caesalpinia Group in the context of the family as a whole. Koenen & al. (2013) found that other legume lineages confined to the Succulent Biome also appear to be diversifying at a constant and relatively slow rate, as exemplified by the Indigofereae and *Mimosa* lineages, and the tribe Robinieae. For example, they found a significant diversification rate slowdown subtending the entire robinioid clade and a lack of any rate shifts among lineages within the clade (Koenen & al., 2013). Thus there appears to be growing evidence that the evolutionary dynamics of globally niche-conserved Succulent Biome clades are indeed characterised by steady, constant and relatively slow rates of species diversification. This is consistent with emerging views of the Succulent Biome as an ecologically and geographically confined, ecologically resilient and relatively stable biome little subject to natural disturbance (Pennington & al., 2006, 2009).

Whilst rate constancy across Succulent Biome lineages is in line with previous findings, perhaps more surprising is the lack of any diversification rate shifts associated with biome shifts or the evolution of contrasting plant habits in the Caesalpinia Group. Koenen & al. (2013) documented a number of diversification rate accelerations associated with biome shifts in several disparate legume clades (e.g. shifts into Grassland and Temperate Mediterranean and montane Biomes). However, in the Caesalpinia Group, shifts into Warm Temperate, Rainforest and Grassland Biomes do not appear to have resulted in altered diversification regimes. Although we hypothesized that the more recently derived clades (e.g. *Coulteria* and *Cenostigma*), where species delimitation has proved difficult and where species monophyly is not universal and clearcut (Fig. 3.3), would show evidence of accelerated species diversification rates due to a recent rapid range expansion, this was not the case. However, we observed that Grasslands/Rainforest species were for the majority lianas, whereas the suffrutescent/herbaceous habit occurred principally in clades with affinities to the Temperate Biome, such as *Hoffmannseggia*, and *Erythrostemon*.

One explanation for the lack of diversification rate shifts found in the Caesalpinia Group is that the transitions to the Grassland/Rainforest habitats are not accompanied by complete adaptations to the fundamental characteristics defining these biomes. For example, in the genus *Cenostigma*, few species are found in true rainforest or savanna-like conditions in South America, and most species are described as being able to occupy a transition area. While this has undoubtedly helped the species of *Cenostigma* spread across South America, particularly in the Amazonian Arc as defined by Prado & Gibbs (1993), it has also not translated into higher rates of diversification. Furthermore, the majority of the Asian and African liana species which inhabit the Grassland Biomes are pioneer species that often occupy disturbed or transitional habitats, such as forest fringes and river margins. These species are often moderately widespread spanning several countries even if they are not necessarily locally abundant. It is notable that several of these species apparently retain preferences for environmental conditions typical of the Succulent Biome and grow in edaphically dry local microhabitats within rainforests (e.g.

Caesalpinia nitens), or on termite mounds with richer soils in African savannas (e.g. *G. glandulosopedicellata*). It may be that none of these species are truly well-adapted to these Grassland/Rainforest conditions, and are instead tracking particular, probably marginal, niches within these biomes.

Lack of diversification in Caesalpinia Group and in other legume genera from the Succulent Biome contrasts sharply with other succulent plant lineages that have diversified so spectacularly, including the Cactaceae (Arakaki & al., 2011; Hernández-Hernández & al. 2014), the Agavaceae (Good-Avila & al., 2006), as well as the Ruschioideae in the Aizoaceae in Africa (Klak & al. 2004; Arakaki & al. 2011), as well as the genus *Euphorbia* (Horn & al. 2014).). It also constrasts with diversification patterns in the genus *Bursera,* a diverse group of trees typical of SDTF in Mesoamerica, which underwent at least two independent increased diversification shifts in the Miocene, but the exact underlying causes remain to be identified (de-Nova & al., 2012). Therefore, it would seem that the majority of the diversity of the Caesalpinia Group is the result of lineages slowly accumulating and persisting through time, but without any key innovations or climatic/geographic opportunities presenting themselves to promote speciation within these groups.

3.5.7 Niche conservatism across time

One intriguing question to ask about niche conservatism, which appears to be predominant in the Caesalpinia Group, is how far back in time are they actually conserved. While the fossil record of the Caesalpinia Group is not sufficiently rich to allow for more in-depth studies integrating niche modelling of ancestral biomes with fossils (e.g. Meseguer & al., 2015), the few fossils that are known do seem to hint at a certain amount of niche conservatism through time. For example, the *Caesalpinia* s.l. fossils, with explosively dehiscing valves found in the Clairborne group, in the Puryear and Lawrence formations, are thought to have been part of a periodically dry tropical forest, as evidenced by the floristic composition of the site and the smaller size of the fossil leaves and leaflets of the fossils at the site (Berry, 1916, 1930; Ball 1931; Dilcher 1973). With the exception of Asian lianas belonging to the genus *Biancaea*, these types of fruits are currently found in taxa that occupy the Succulent Biome, incuding *Caesalpinia* s.s., *Denisophytum*, *Tara*, *Stuhlmannia*, *Cenostigma* and *Erythrostemon*. Furthermore, niche conservatism is also hinted at in the geo-temporal distribution pattern of fossils bearing fruits attributed to *Mezoneuron*. While this genus currently occupies Asia and Africa, the fossil record of this taxon is only found in Western North America, spanning the Eocene (Clairborne formation, Warman pit in western Tennesse, *Caesalpinia clairbornensis* (Herendeen & Dilcher, 1991)) to the middle Miocene (several sites in Idaho, ranging from 13 to 17 Ma in age (Herendeen & Dilcher, 1991)). Their disappearance from the fossil record might be in part due to their inability to adapt to dramatic changes in climate that occurred late in the Miocene. While we could not find detailed paleoclimatic reconstructions of these sites, paleogeographical and paleobotanical evidence suggests that much of North America was covered by tropical and sub-tropical forests for much of the Eocene and Oligocene (Axelrod, 1992). It is quite possible that both these sites contained grasslands or rainforests, and the *Mezoneuron* fossils could have occupied these forests in the same way they do now in Africa and Asia. Persistence of *Mezoneuron* in North America until the Miocene, for about 30 Ma, and its subsequent disappearance coincides with the onset of the cooling in the Miocene, at 15-14 Ma, which resulted in the disappearance of the tropical and subtropical forests and subsequent replacement by large grasslands and a more temperate climate and flora, as evidenced by paleobotanical and geological studies (Axelrod, 1992, and references therein).

3.5.8 Conclusions

While we did not carry out a statistical, quantitative test of niche evolution (Smith & Donoghue, 2010; Wuërst & al, 2015), the analyses presented here demonstrate that at a broad ecological level, the Caesalpinia Group is highly niche conserved, particularly in lineages occupying the Succulent Biome, but also in the Warm Temperate Biome. This tendency towards biome niche conservatism leads to a strikingly large number of intercontinental disjunctions within the same biome, perhaps best exemplified by the genus *Denisophytum* and the *Lophocarpinia* + *Haematoxylum* clade. There is evidence that the last major peak in aridification in the mid- to late-Miocene is reflected in the expansion and diversification of both Succulent and Grassland lineages in Africa and in the genera *Cenostigma* and *Libidibia* in the Neotropics. The repeated dispersal to North America of lineages with affinities to the Warm Temperate Biome, is also attributed to this period. The increasing trend in aridification in North America led to the spread of desert and prairie grasslands and to the disappearance of tropical and subtropical forests in North America; this possibly explains why the genus *Mezoneuron,* which lives in habitats associated with this biome, disappeared from the fossil record in North America.

The historical biogeography of the Caesalpinia clade reconstructed here is in agreement with most of the recent studies of legumes suggesting that ecological processes and the capacity of plants to adapt to different ecological conditions have a profound impact in shaping plant diversity and distribution across globe (Lavin et al., 2004; Donoghue & Edwards, 2014). Absence of key morphological characteristics allowing this group to successfully thrive in different ecological conditions might explain the lack of high diversification rates found across the clade, even in lineages that have seemingly adapted to new ecological conditions in different biomes.

We suggest that diversity in the Caesalpinia Group is the result of stochastic long distance dispersal, or in specific cases the result of vicariance events followed by long-term isolation (e.g. species of the genus *Arquita* in the Andes (Gagnon & al., 2015, chapter 4), or the fragmentation of the Succulent Biome following the rise and expansion of savannahs in Africa (Cowling & al., 2005)). The strong geographic structuring of this group, at both species and population levels (Lira & al., 2003; Sotuyo & al., 2007; Gagnon & al., 2015, chapter 4), makes it particularly vulnerable to habitat loss. This is a notably urgent issue in the Succulent Biome: for example, Miles & al. (2006) estimated that 97% of the remaining dry tropical forests around the world are at risk from anthropogenic activities, including habitat fragmentation and conversion to agricultural land, as well as climate change.

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3.7 Authors contribution

EG, CEH and AB were involved in study conception and design; EG generated and assembled all the data, which she was also responsible for analysing and interpreting; EG drafted the manuscript, and critical revision was provided by AB, CEH and GPL, as well as from members of her PhD committee (S. Joly, C. Favret and L. Gillepsie).

Figure 3.1 Global distribution map of the biomes by Schrire & al. (2005). In Red : the Succulent Biome; in orange: the Grassland Biome; in green: the Rainforest Biome; in blue: the Temperate Biome; in beige: the Sahara and Arabian deserts; in white: Antarctica, lakes, or miscellaneous habitats.

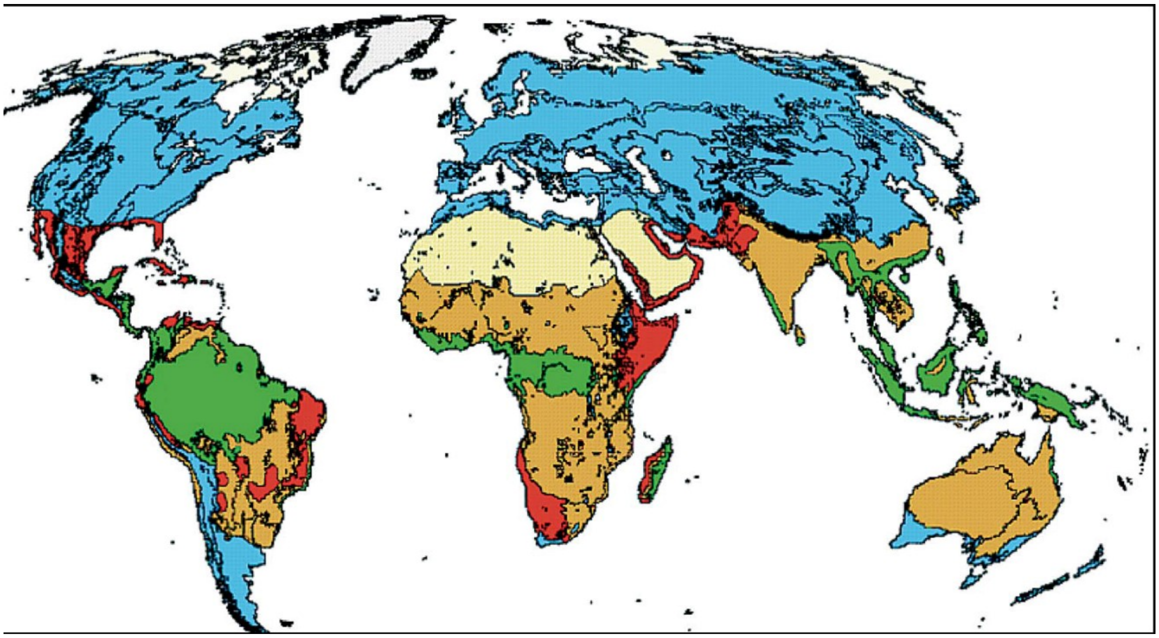


Figure 3.2 Geographic areas defined for the DEC analysis. Dark blue: Central America and warm temperate North America; Light blue: South America; Green: the Caribbean islands, including the Greater and smaller Antilles; Yellow: Africa, including Madagascar and the Arabian Peninsula; Red: Southern Asia, from India to the Indo/Malay peninsula; Lilac: Australia/Pacific region, separated from Asia by Wallace's line, between Borneo and Sundaland. Estimate of the nb of species from the Caesalpinia Group inhabiting each area is indicated.

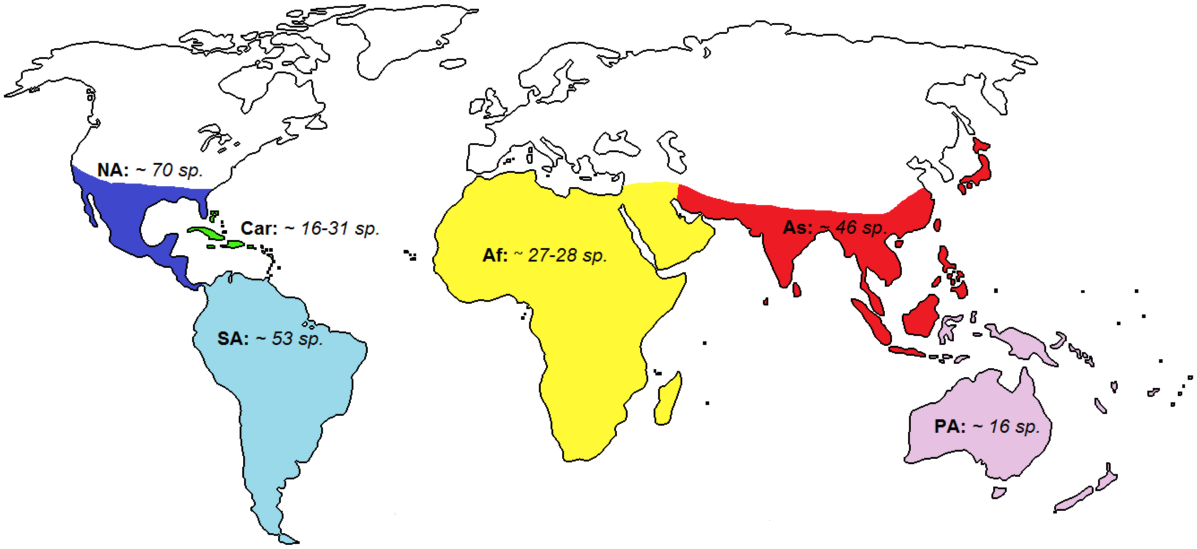
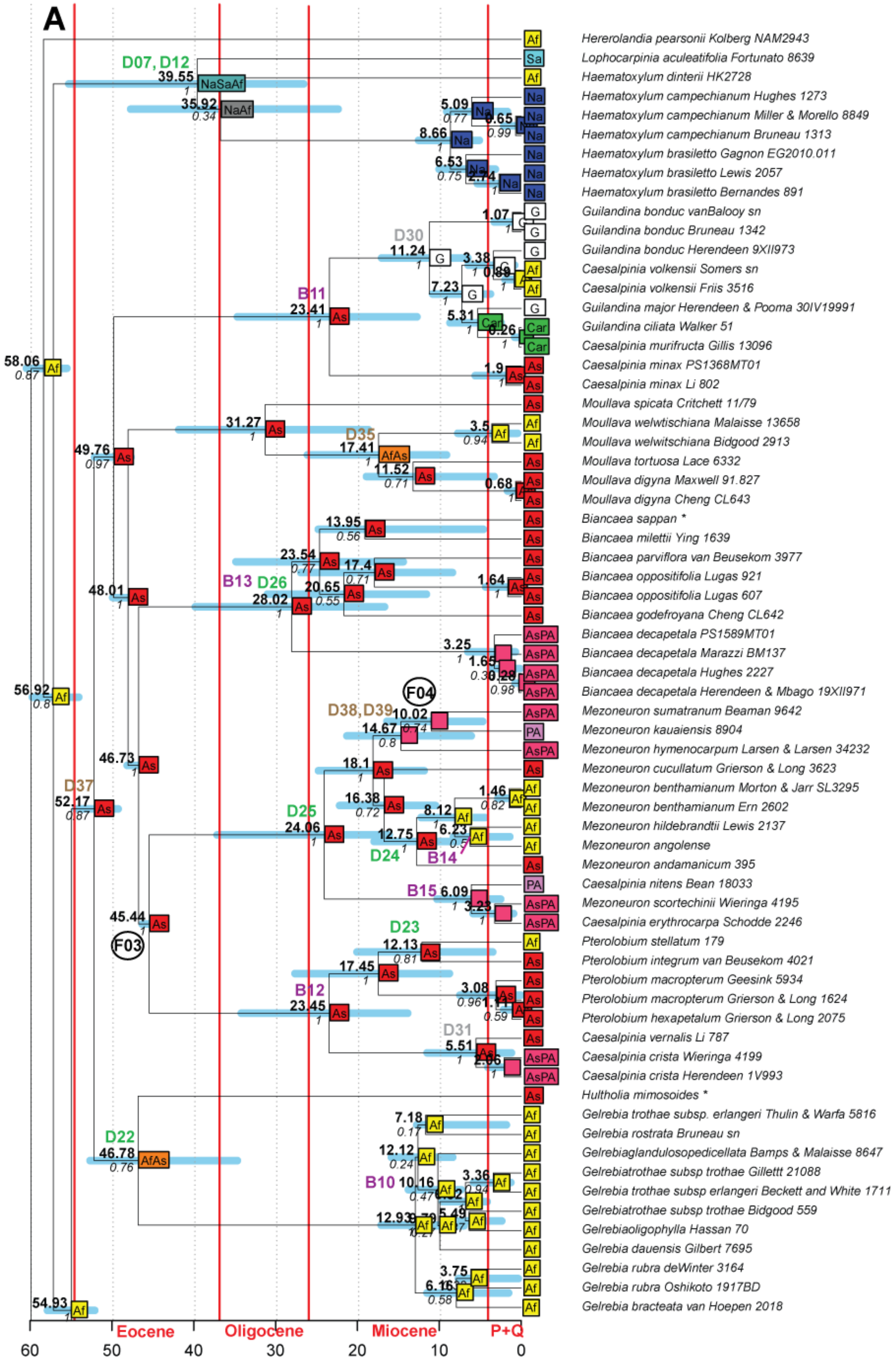


Figure 3.3 A-D (next pages) Maximum Clade credibility phylogeny from Beast 1.8.0, with results from the DEC+J unconstrained analysis in Biogeobears. Red bars indicate the boundaries of the Eocene, Oligocene, Miocene and Pliocene+Quarternary (P+Q) periods. Posterior probability of branches are indicated below, in italic; Node ages are indicated in bold above branches, with blue bars representing the 95% HPD height of the node. Node labels with the prefix D-: in Green are the trans-continental disjunction that are within the same biome; in Brown, are the trans-continental disjunctions that are accompanied by a biome shift; in Gray, are the trans-continental disjunctions where biome shift or conservation is ambiguous. Node labels with the prefix B, in Purple, are the biome shifts within the same continent. Node labels within circles and the prefix F indicate fossil calibrations (see Table 3.4). Boxes at tips represent the geographic areas occupied by the terminal taxa, indicated by the abbreviations (Af: Africa, As: Asia, Ca: Caribbean, G: Pantropical, Na: North America, Pa: Australian-Pacific, Sa: South America), and coloured by area(s) occupied; the same boxes at the nodes indicate the results of the ancestral area estimated to be occupied by the ancestors at that node.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0.97
48.01
46.73
D37
52.17
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45.44
F03
D22
46.78
0.76
AfAs
D30
11.24
B11
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13.95
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0.77
17.4
0.71
B13 D26
20.65
0.55
28.02
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F04
D38, D39
10.02
14.67
0.74
18.1
D25
24.06
16.38
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D24
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Lophocarpinia aculeatifolia Fortunato 8639
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Haematoxylum campechianum Miller & Morello 8849
Haematoxylum campechianum Bruneau 1313
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Haematoxylum brasiletto Lewis 2057
Haematoxylum brasiletto Bernandes 891
Guilandina bonduc vanBalooy sn
Guilandina bonduc Bruneau 1342
Guilandina bonduc Herendeen 9XII973
Caesalpinia volkensii Somers sn
Caesalpinia volkensii Friis 3516
Guilandina major Herendeen & Pooma 30IV19991
Guilandina ciliata Walker 51
Caesalpinia murifructa Gillis 13096
Caesalpinia minax PS1368MT01
Caesalpinia minax Li 802
Moullava spicata Critchett 11/79
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Moullava digyna Cheng CL643
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Biancaea decapetala Hughes 2227
Biancaea decapetala Herendeen & Mbago 19XII971
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Caesalpinia erythrocarpa Schodde 2246
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Caesalpinia crista Herendeen 1V993
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Gelrebia rostrata Bruneau sn
Gelrebiaglandulosopedicellata Bamps & Malaisse 8647
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Gelrebia trothae subsp erlangeri Beckett and White 1711
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Gelrebiaoligophylla Hassan 70
Gelrebia dauensis Gilbert 7695
Gelrebia rubra deWinter 3164
Gelrebia rubra Oshikoto 1917BD
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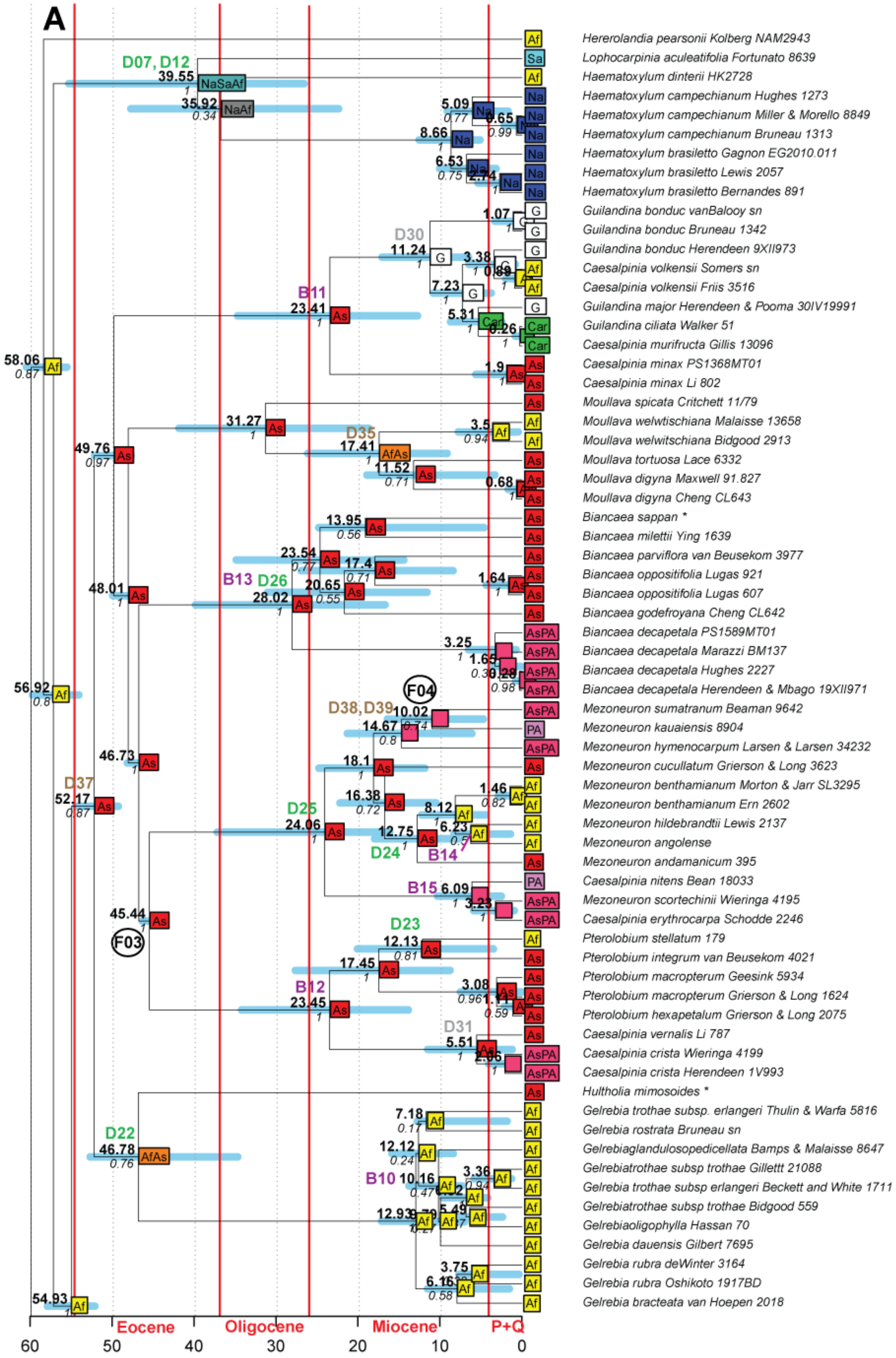
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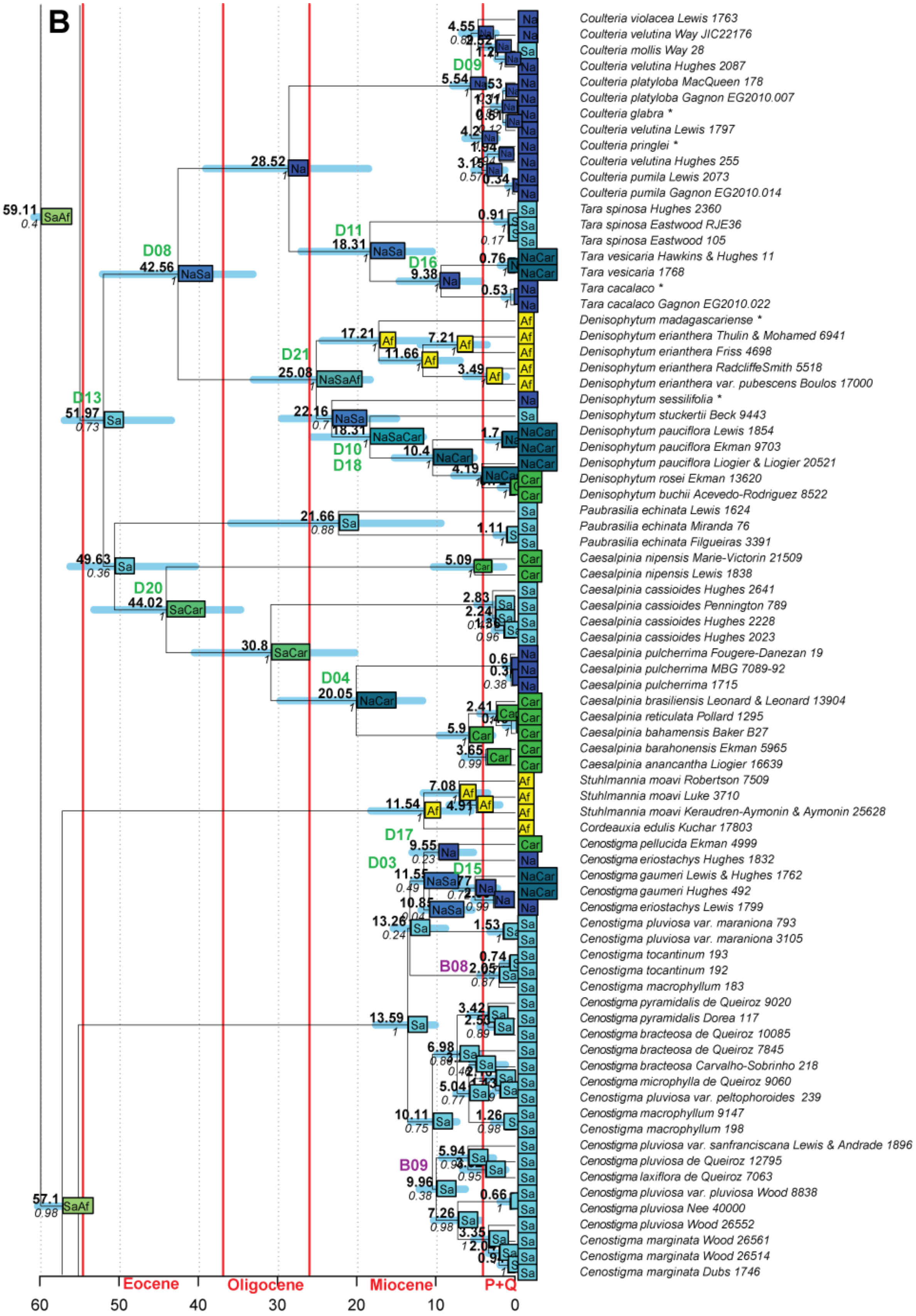
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Coulteria velutina Hughes 255
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Tara vesicaria 1768
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D15
B08
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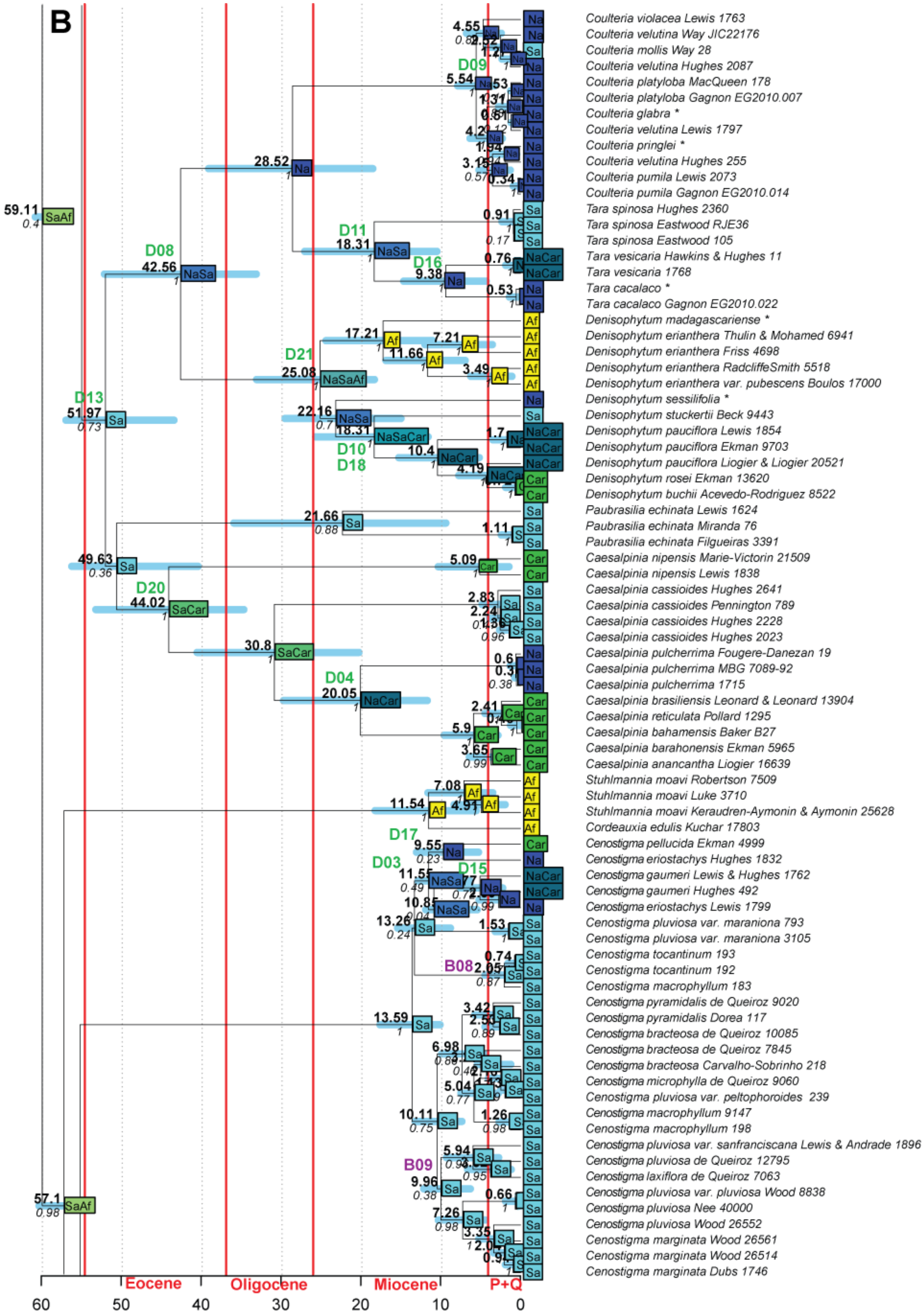
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11.54 Af
7.08 Af
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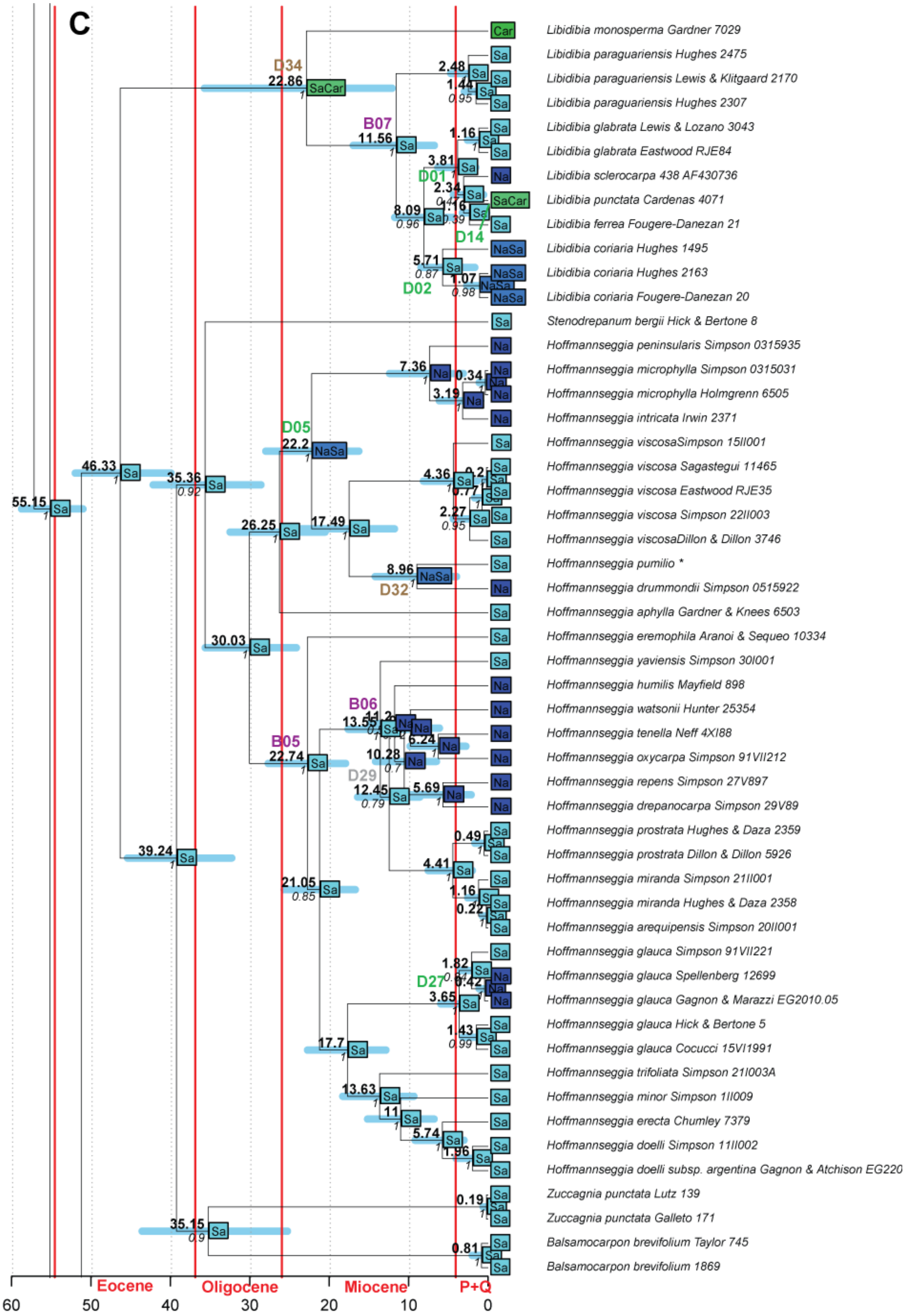
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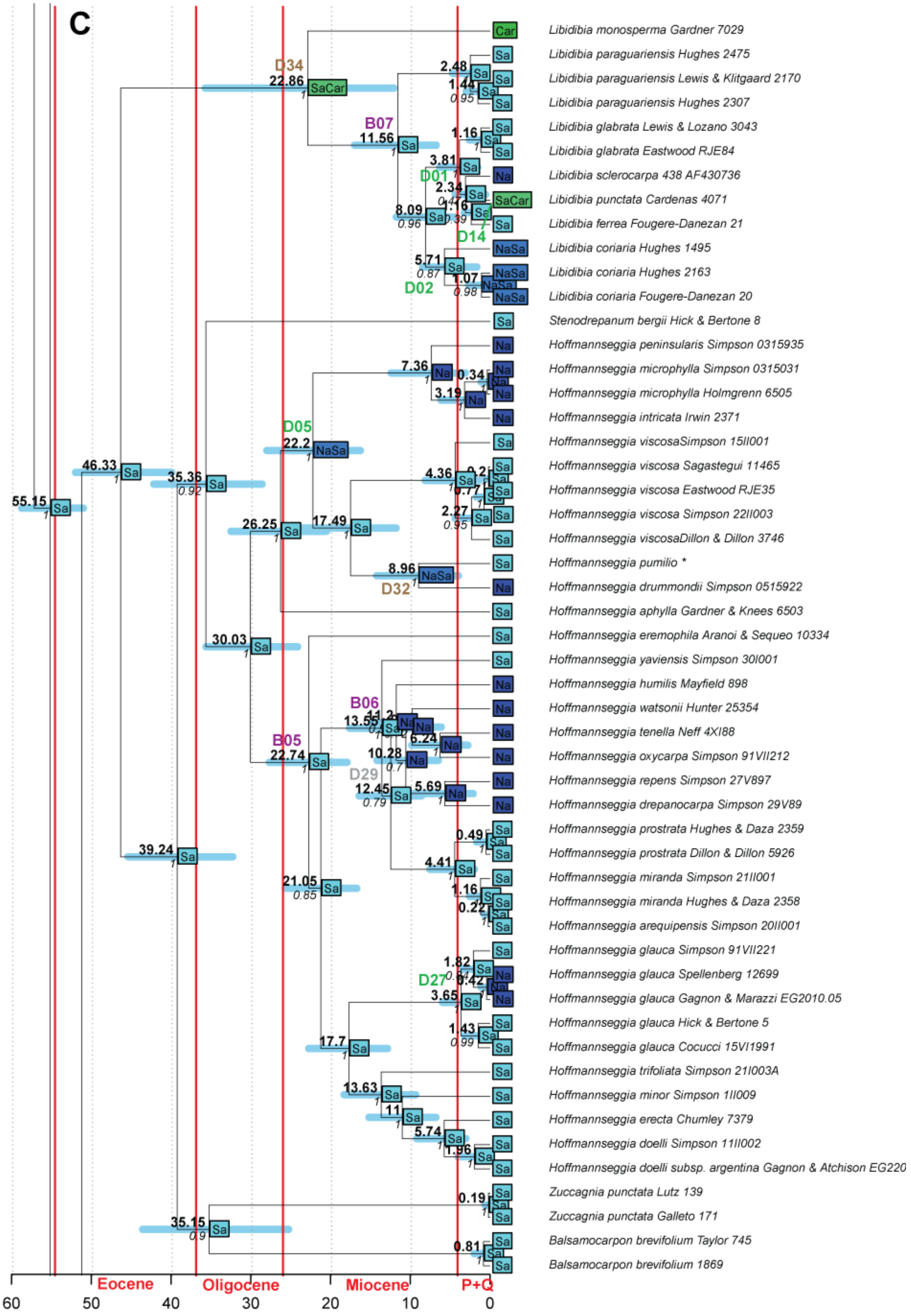
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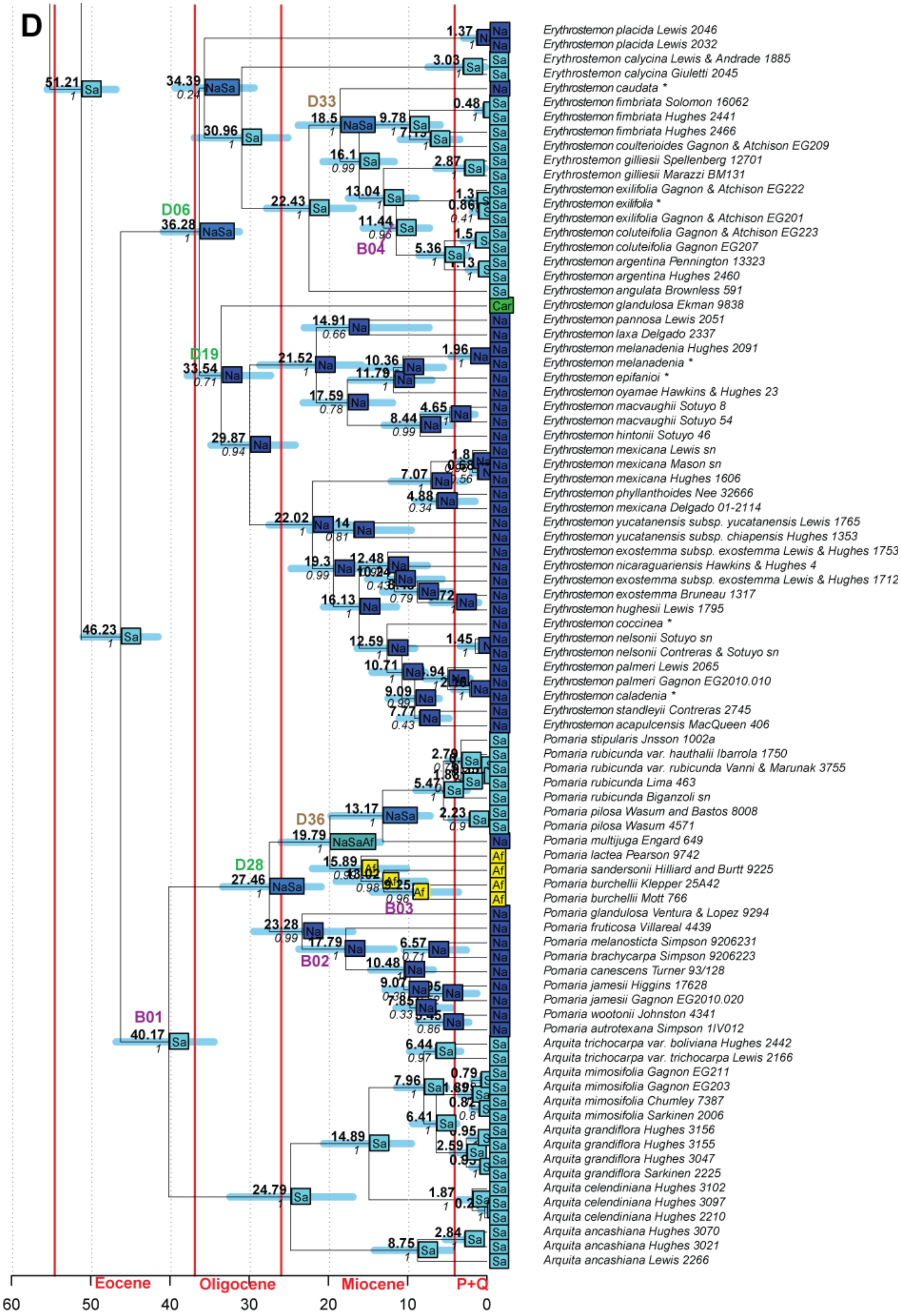
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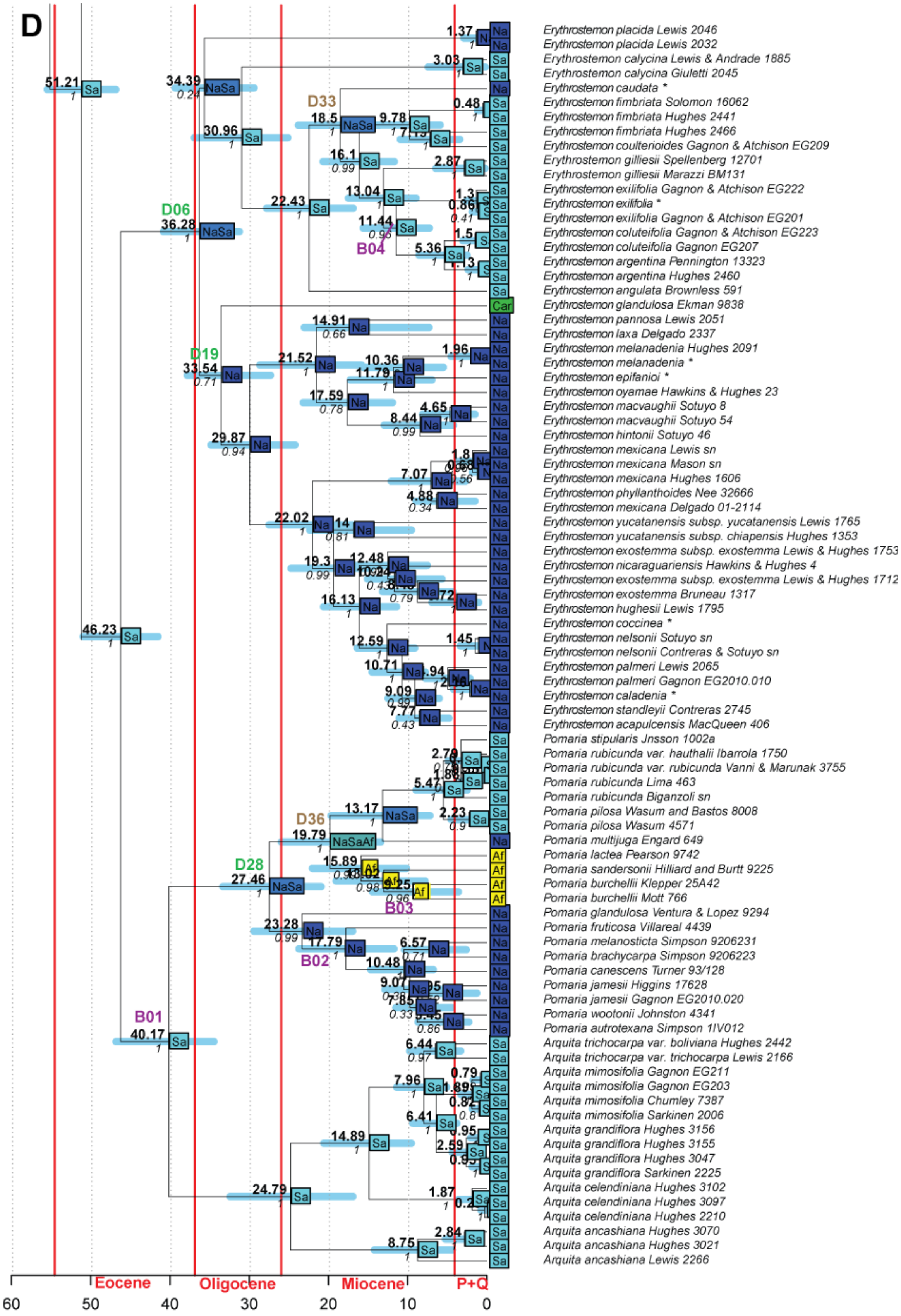
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Arquita ancashiana Hughes 3021
Arquita ancashiana Lewis 2266
Eocene
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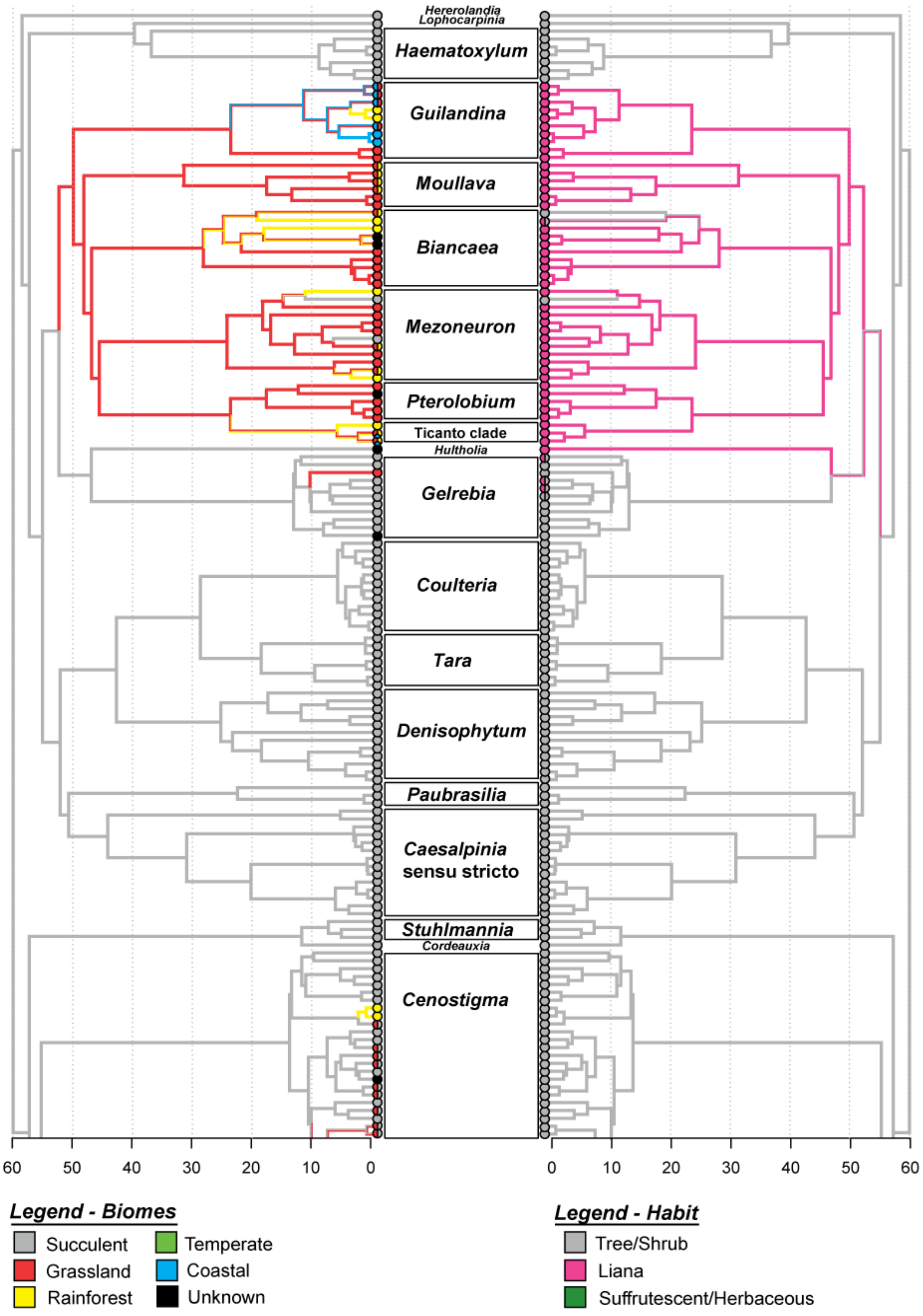
Figure 3.4 Parsimony ancestral state reconstruction in Mesquite of the biome and habit characters.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Biancaea
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Gelrebia
Coulteria
Tara
Denisophytum
Paubrasilia
Caesalpinia sensu stricto
Stuhlmannia
Cordeauxia
Cenostigma
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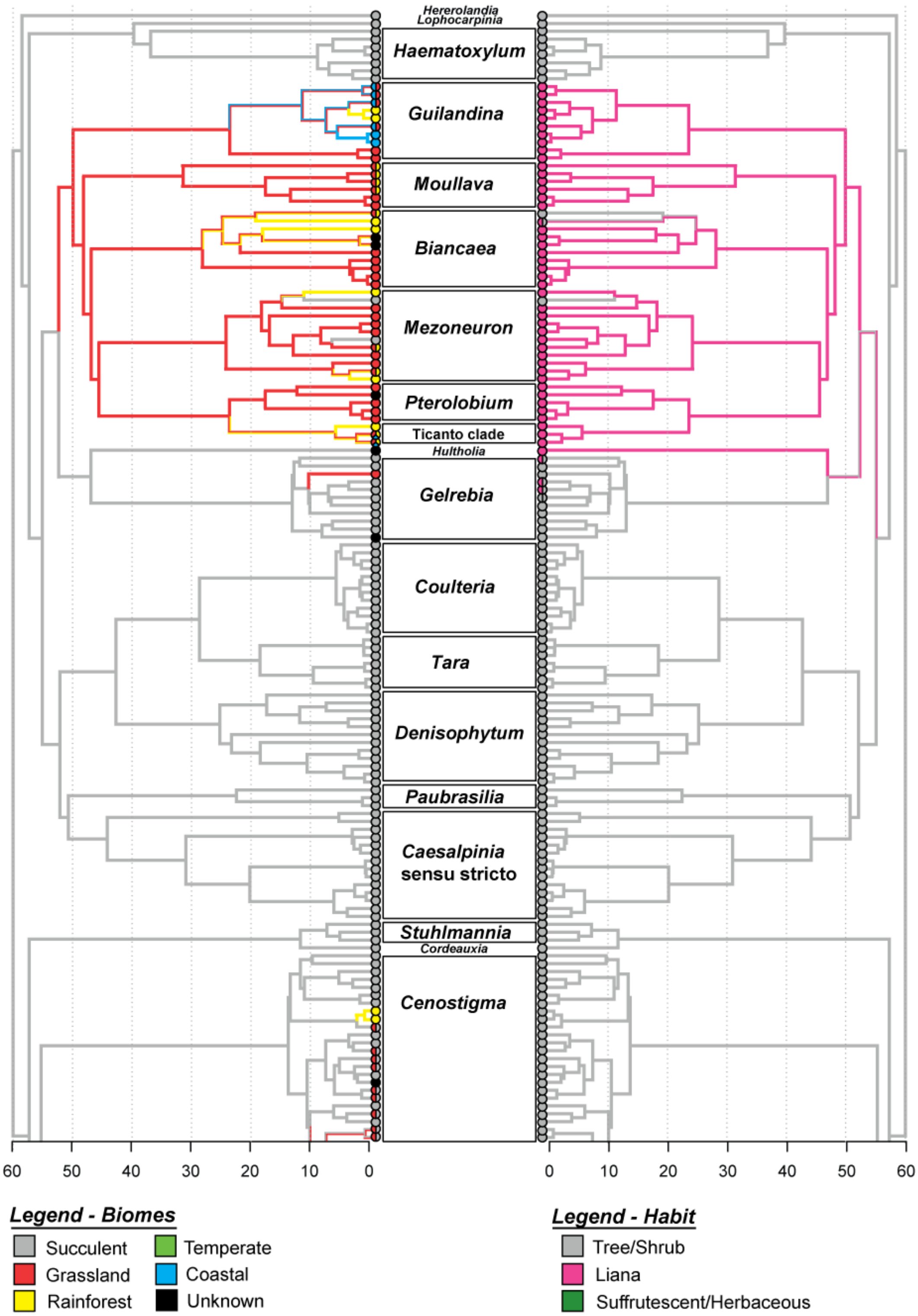
Legend - Biomes
Succulent
Grassland
Rainforest
Temperate
Coastal
Unknown
Legend - Habit
Tree/Shrub
Liana
Suffrutescent/Herbaceous



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Mezoneuron
Pterolobium
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Gelrebia
Coulteria
Tara
Denisophytum
Paubrasilia
Caesalpinia sensu stricto
Stuhlmannia
Cordeauxia
Cenostigma
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Legend - Biomes
Succulent
Grassland
Rainforest
Temperate
Coastal
Unknown
Legend - Habit
Tree/Shrub
Liana
Suffrutescent/Herbaceous

Figure 3.4 (suite)

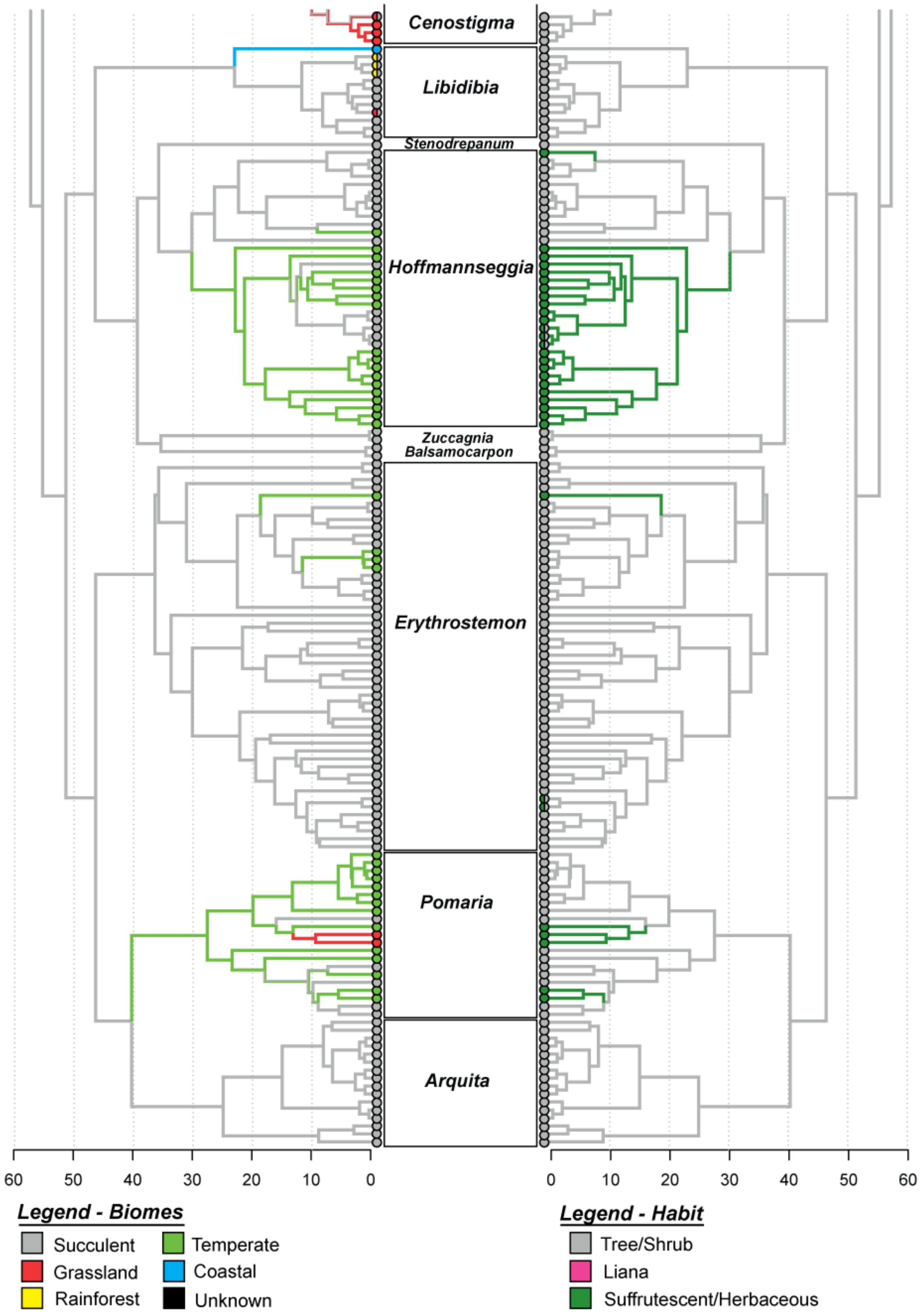


Figure 3.5 Biome shifts found in the ancestral parsimony character reconstruction on the Bayesian Mccr phylogeny of the Caesalpinia Group. S: Succulent biome, G: Grassland biome, T : Temperate biome, R: Rainforest biome, C: Coastal biome.

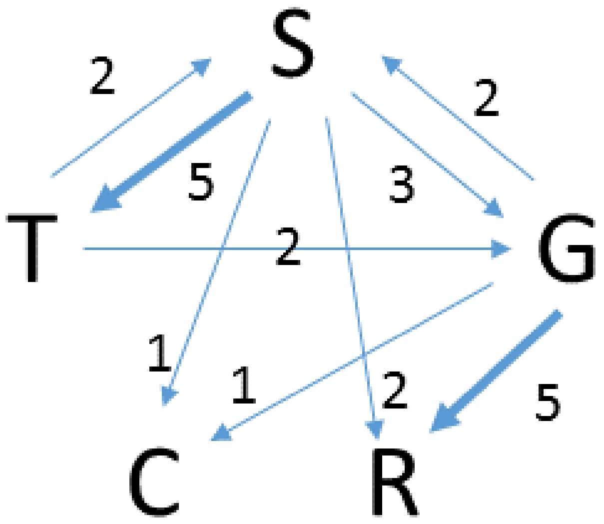


Figure 3.6 Ages of trans-continental dispersal events within the same biome: A. Scatterplot of the ages of trans-continental dispersal events within biomes, listed in Table 3.5; In Gray: trans-continental dispersal events in the Succulent biome; in Red: trans-continental dispersal events in the Grassland biome; in Green: trans-continental disjunction events in the temperate biome.; B. histogram of the ages of trans-continental dispersal events in the Succulent biome.

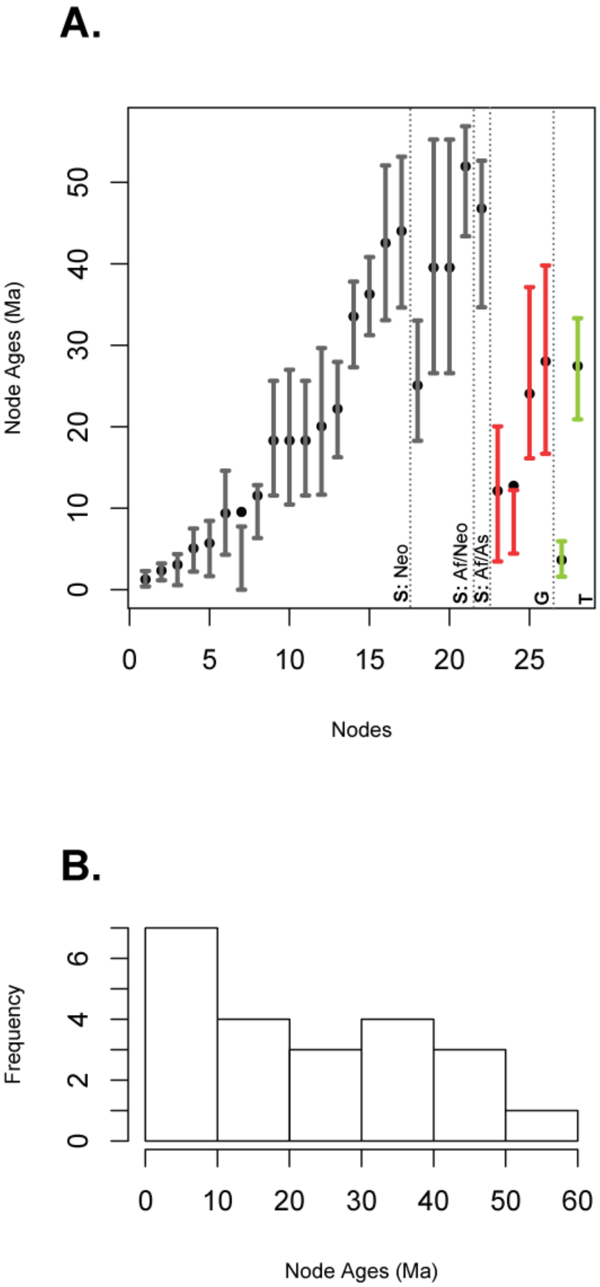
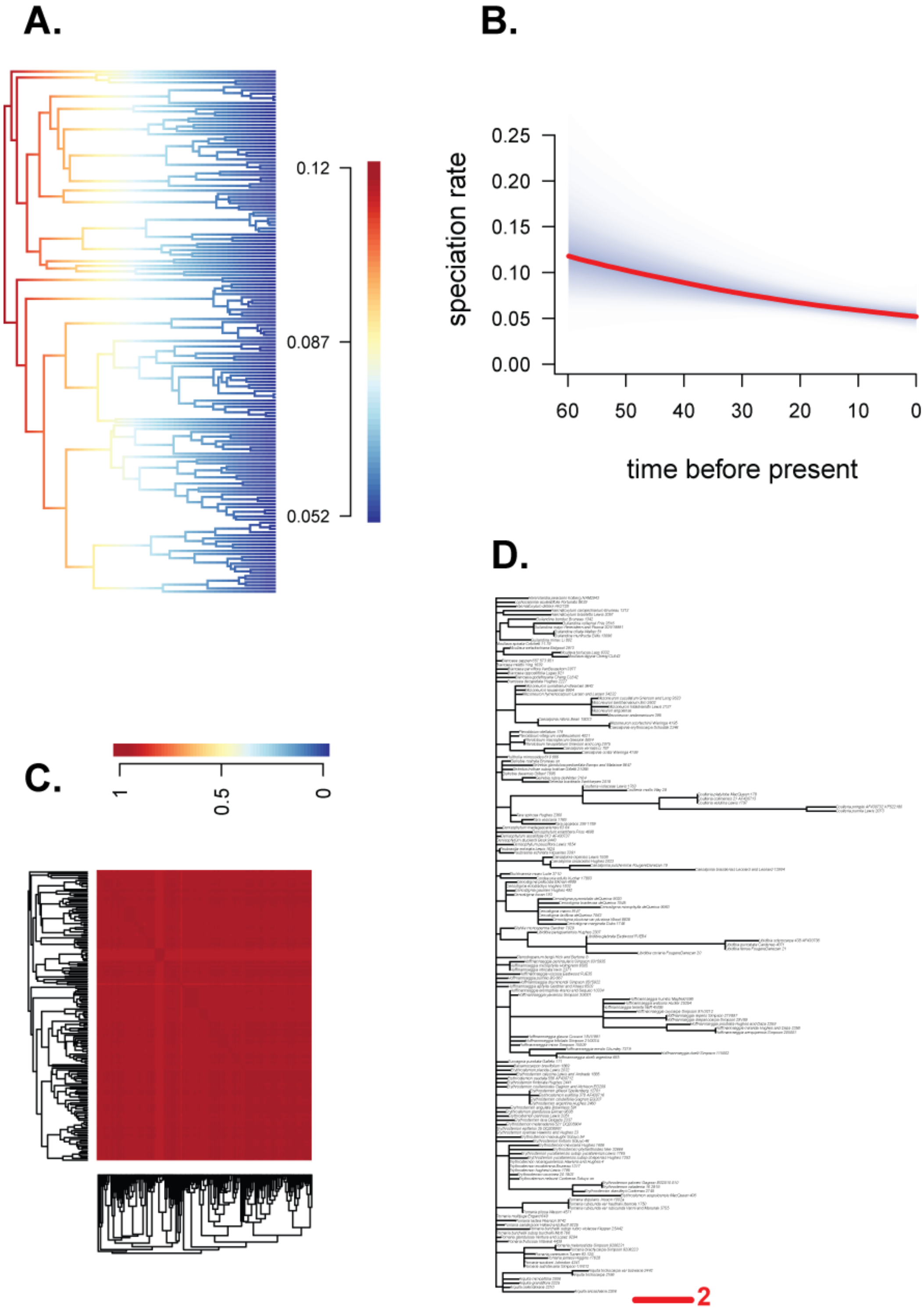


Figure 3.7 Results from the Min6 BAMM analysis (minimum species estimate used for all genera). A: Mean phylorate plot; B: Rate-through-time plot; C: Macroevolutionary cohort matrix plot; D: Phylogeny with branches scaled by the bayes factor (scale in red).



Chapitre 4: A new cryptic species in a new cryptic genus in the Caesalpinia Group (Leguminosae) from the seasonally dry inter-Andean valleys of South America

Edeline Gagnon[1], Colin E. Hughes[2], Gwilym P. Lewis[3] and Anne Bruneau[1]

1. Institut de recherche en biologie végétale and Département de sciences biologiques, Université de Montréal, H1X 2B2, Montréal, Canada;
2. Institute of Systematic Botany, University of Zürich, 8008, Zürich, Switzerland;
3. Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, United Kingdom;

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(Modifié pour les besoins de la présente thèse)

4.1 Résumé/ Abstract

Résumé

L'affiliation générique des espèces andines *Caesalpinia trichocarpa, C. mimosifolia* et de leurs espèces parentes demeure incertaine dans les études récentes de *Caesalpinia* s.l. (Leguminosae, sous-famille Caesalpinioideae). Cette étude présente des nouvelles analyses phylogénétiques basées sur quatre marqueurs génétiques (*rps16*, *trnD-trnT*, *ycf6-psbM*, et ITS), qui supportent le monophylétisme de ce clade contenant uniquement des espèces des Andes. Malgré l'absence de synapomorphies, nous présentons des arguments en faveur de reconnaître ce groupe andéen comme un nouveau genre distinct, baptisé *Arquita.* Au sein ce même groupe, il existe aussi un problème de délimitation d'espèces, concernant l'espèce *C. trichocarpa* qui se retrouve dans des aires géographiquement disjointe en Argentine, Bolivie et au Pérou. Des observations sur le terrain, ainsi que des analyses phylogénétiques préliminaires, suggèrent que les populations au Pérou, qui sont isolées par plus de 1350 km des populations les plus proches en Bolivie, pourraient former une espèce cryptique, c'est-à-dire qui présente des différences morphologiques subtiles, mais qui forme une lignée génétique distincte. La cohésion morphologique et génétique du complexe *C. trichocarpa* est étudiée en utilisant des analyses morphométriques sur des traits qualitatifs et quantitatifs des fleurs et des feuilles, et une phylogénie comprenant un échantillonnage taxonomique dense, avec plusieurs individus représentant les trois aires disjointes. Les résultats confirment que les populations du Pérou forme une lignée distincte qui représente une nouvelle espèce caractérisée par quelques synapomorphies subtiles, qui est baptisée *Arquita grandiflora.* Sa description taxonomique est présentée dans cette étude à travers une révision taxonomique du nouveau genre *Arquita,* et inclut une carte de distribution de toutes les espèces, ainsi qu'une clé d'identification des espèces de ce nouveau genre.

Mots clés: Andes, *Caesalpinia*, Caesalpinioideae-Leguminosae, espèce cryptic, delimitation générique, analyses morphologiques, analyses phylogénétiques, forêts tropicales sèches.

Abstract

The generic affiliation of the Andean species *Caesalpinia trichocarpa*, *C. mimosifolia*, and their close relatives has remained uncertain in all recent studies of *Caesalpinia* s.l. (Leguminosae, subfamily Caesalpinioideae). A new densely sampled phylogeny based on four DNA sequence regions (*rps16*, *trnD-trnT*, *ycf6-psbM*, ITS) strongly supports the monophyly of an Andean clade. We propose that despite the lack of obvious diagnostic morphological synapomorphies, this Andean group should be considered as a distinct genus, here described as the new genus *Arquita*. Phylogenetic analyses also suggest a problem with species delimitation in this group. Within *C. trichocarpa*, accessions from disjunct geographic areas in Argentina, Bolivia and Peru each form a robustly supported, unresolved clade that includes *C. mimosifolia*. The morphological and genetic cohesiveness of the *C. trichocarpa* complex is investigated using morphometric phenetic analyses of qualitative and quantitative flower and leaf traits, and reconstruction of a densely sampled phylogeny using three plastid and one nuclear ribosomal DNA sequence loci. Our results suggest that the most geographically isolated of these clades, narrowly endemic to two inter-Andean valleys in central-north Peru and separated by ~1350 km, and extensive high Andean cordilleras above 4000 m, from the nearest populations in Bolivia, represents a genetically highly distinct and morphologically cryptic lineage here described as a new species (*Arquita grandiflora*). A full taxonomic account of the new genus *Arquita* and its component species is provided, with a distribution map and a key to the species.

Keywords: Andes, *Caesalpinia*, Caesalpinioideae-Leguminosae, cryptic species, generic delimitation, morphological analysis, phylogenetic analysis, seasonally dry thorn scrub.

4.2 Introduction

Harbouring one of the largest assemblages of endemic plants and vertebrates (Myers & al., 2000; Orme & al., 2005; Brooks & al., 2006), the tropical Andes are one of the most important biodiversity hotspots on the planet. The seasonally dry tropical forests (SDTF) of the inter-Andean valleys make up one important component of the overall tropical Andes hotspot, and despite having a less diverse flora in terms of absolute number of species, these forests harbour some of the highest levels of endemism (Linares-Palomino, 2006; Wood, 2006; Linares-Palomino & al., 2010, 2011), comparable to those found on oceanic islands such as the Galapagos (Särkinen & al., 2012). Nonetheless, it is also clear that the levels of species diversity and endemism in these Andean SDTFs are still significantly underestimated (Knapp, 2002; Young & al., 2002), they remain very incompletely explored and inventoried (Knapp, 2002; Linares-Palomino & al., 2010), with many new taxa being described (e.g., Lewis & al., 2010; Särkinen & al., 2011b and references therein). Furthermore, densely sampled phylogenetic studies that include all species and sampling of intraspecific diversity for woody legume taxa of seasonally dry tropical forests of the Andes are revealing repeated examples of previously unrecognized or cryptic species (Pennington & al. 2011; Särkinen & al., 2011b), i.e., species that have been classified together due to their morphological similarity, sensu Bickford & al. (2007), as well as deeply divergent reciprocally monophyletic populations that occupy very narrow and highly disjunct ranges (Pennington & al., 2010). In order to understand these patterns of endemism, detailed taxonomic, phylogeographic and biogeographic studies of a wider range of SDTF lineages are needed (Hughes & al., 2013; Luebert & Weigend, 2014). These studies are important not only as a means of documenting species diversity and endemism, but also to establish optimal and effective conservation strategies that preserve both the total species diversity (Swenson & al., 2012), and also the potential of species to diversify by protecting diverging ecological and evolutionary lineages and populations (Moritz, 2002).

Our study addresses these issues by focusing on a small clade of legume shrubs (Leguminosae: Caesalpinioideae) with a strictly Andean distribution, the "Caesalpinia trichocarpa clade". Extensive fieldwork in Ecuador, Peru, Bolivia and Argentina by the authors and other botanists over the past decade, alongside a new and densely sampled molecular phylogeny of *Caesalpinia* s.l. and the genera of the Caesalpinia Group (Gagnon & al., 2013, chapter 1; and in prep., chapter 2) have revealed both the extent of species diversity in the "C. trichocarpa clade", as well as its phylogenetic, geographical and ecological affinities. This group of four species of suffrutescent to medium-sized shrubs is confined to mid-elevation (1000–3000 m) seasonally dry rupestral thorn scrub forest. Two of the species, *C. ancashiana* Ulibarri and *C. celendiniana* G.P.Lewis & C.E.Hughes, were only described recently from the western flanks of the Andes of Peru and southern Ecuador (Ulibarri, 1996; Lewis, 1998), and from the seasonally dry upper Marañón valley in northern Peru (Lewis & al., 2010), respectively. The other two species, *C. trichocarpa* Griseb. and *C. mimosifolia* Griseb., are more widely dispersed in inter-Andean and Piedmont seasonally dry valleys of Argentina and Bolivia. While this clade has previously been referred to as the "C. trichocarpa clade" (Gagnon & al., 2013), to avoid confusion with the C. trichocarpa species complex discussed in detail in this study, here we refer to it as the "Arquita clade", in reference to the vernacular name for *C. trichocarpa* in Argentina (Ulibarri, 1996).

While the monophyly of the Arquita clade has been clearly established, its relationships and generic status remain to be determined. This group of species was initially placed by Lewis (1998) in the informal Poincianella-Erythrostemon (P-E) group based on marked morphological affinities, particularly with *C. placida* Brandegee, found in Baja California, Mexico. However, subsequent molecular phylogenetic analyses based on trnL-trnF plastid sequences placed these species not within the P-E group, but instead in an unresolved polytomy with the genus *Pomaria* Cav. and the P-E group (Simpson & al., 2003; Nores & al., 2012). Later analyses with greater resolution found support for the Arquita clade as sister to *Pomaria* (Simpson & al., 2006; Gagnon & al., 2013, chapter 1). These results suggest that this Andean clade represents a lineage distinct from the P-E group, closely related to *Pomaria*, but stronger evidence is required to support its segregation.

In addition to the generic placement of the Arquita clade, extensive field and herbarium work have also revealed previously unrecognized cryptic morphological variants across the widely disjunct distribution of *C. trichocarpa*, questioning the delimitation of this species and suggesting the possibility that one or more additional cryptic species need to be recognized.

While this species was originally known only from Bolivia and Argentina, collections made in the late 1970s suggested that it also occurred in Peru, in the province of Ancash. These Peruvian populations are separated from the nearest populations in Bolivia by about 1350 km and by extensive Andean cordilleras exceeding 4000 m elevation, whereas the populations in Bolivia and Argentina form a more contiguous series in more narrowly disjunct valleys. Our recent fieldwork in all three countries suggests that the geographically isolated northern populations potentially represent a morphologically cryptic species, with larger flowers, and leaves with larger leaflets and fewer pairs of pinnae. To test this hypothesis, a detailed morphological and molecular analysis of this species complex is needed to serve as the basis for the delimitation of species.

In this study we address the following questions: (1) Does the Arquita clade merit recognition as a distinct genus? (2) Should more than one species be recognized to account for variation across the disjunct *C. trichocarpa* lineages? To answer these questions, we use molecular data to reconstruct a densely sampled phylogeny of the Arquita clade together with a detailed morphometric analysis of populations of the *C. trichocarpa* alliance. Finally, we bring together all available field, herbarium and taxonomic data in the form of a new taxonomic account of the Arquita clade, including detailed species descriptions, a key to the identification of species and a distribution map. This study forms part of a wider investigation of the entire Caesalpinia Group, in which we present a new generic system for the group as a whole (Gagnon & al., in prep., chapter 2)

4.3 Material and Methods

4.3.1 Molecular methods

To test the monophyly and sister- group relationships of the Arquita clade, we selected a large outgroup of 24 species from the Caesalpinia Group based on previous results (Gagnon & al., 2013, chapter 1), including from the Poincianella-Erythrostemon clade, *Pomaria* Cav., *Balsamocarpon* Clos, *Zuccagnia* Cav., *Hoffmannseggia* Cav., *Libidibia* Schltdl., *Cenostigma*

Tul. and *Caesalpinia echinata* Lam. (see Annexe 3). We sampled multiple accessions of all species from the Arquita clade across their geographic range (*C. trichocarpa* 23, *C. ancashiana* 9, *C. celendiniana* 3, *C. mimosifolia* 3 plus one sequence from GenBank; Benson & al., 2013). Samples consisted both of field-collected silica-dried leaves and herbarium material. Although sampling of the *C. trichocarpa* alliance for the molecular analyses is less extensive than in the morphometric analyses due to the poor quality of DNA available from herbarium specimens, it nonetheless includes accessions spanning the complete range of *C. trichocarpa* in the Andes, from Peru, Bolivia, and NW Argentina providing an excellent basis for re-evaluation of species limits.

Three protocols were used to extract DNA: (1) a modified CTAB protocol (Joly & Bruneau, 2006); (2) QIAGEN DNeasy Plant Mini Kit (Mississauga, Ontario, Canada), following the manufacturer's instructions; or (3) a 4% MATAB protocol (Ky & al., 2000).

Table 4.1 Primer pairs used for PCR (1) and nested-PCR (2) amplifications. Forward and reverse primers used for each locus are listed, followed by the reference, or the nucleotide sequence if it was designed for this study. TA$_{N}$: Annealing Temperature of PCR with standard TAQ; TA$_{PH}$: annealing temperature of PCR with Phire polymerase;

Locus	**TA$_{N}$**	**TA$_{PH}$**
rps16		
(1) rps16F, rps16R (Oxelman & al. 1997)	53°C	62°C
(2) F68, R851 (Babineau, 2013)	57°C	66°C
trnD-trnT		
(1) trnD, trnE (Shaw & al., 2005)	57°C	59°C
(2) trnD2 (Simons & al., 2009), trnE (Shaw & al., 2005)	57°C	64°C
(1) trnY, trnT (Shaw & al., 2005)	55°C	59°C
(2) trnY3 – CCC CAT TAA CCG CTC GGG CA trnT3 – GCC CCG TTT GAT TCA ATT CCT GA	53°C	70°C
ycf6-psbMR		
(1) ycf6F, psbMR (Shaw & al., 2005)	57°C	66°C
(2) ycf6-int2 – CCG TAT CAA TTG GGG TTC TG psbMR2 – TCG CAT TTA TTG CTA CTG CAC;	62°C	62°C
ITS		
(1) AB101, AB102 (Douzéry & al., 1999)	53°C	71°C
(2) ITS4, ITS5 (White & al., 1990)	57°C	57°C

Three plastid loci (*rps16, trnD-trnT, ycf6-psbM*) and the 5.8S subunit and internal transcribed spacers (ITS1, ITS2) of nuclear ribosomal DNA were amplified and sequenced for all accessions. Primer pairs are listed in Table 4.1. For all plastid loci, we used the same PCR protocols as previously described in Gagnon & al. (2013), but with different annealing temperatures (Table 4.1). For ITS, the PCR cycle consisted of an initial denaturing step of 5 min at 96°C, with 35 cycles of the following three steps: a denaturing step of 45 s at 96°C, an annealing step of 4 s at the optimal annealing temperature, and an elongation step of 1 min 15 s at 72°C; the final elongation step was 5 min at 72°C.

For samples that were difficult to amplify, we used a nested PCR procedure in which a second amplification was carried out, using 1:10 or 1:25 dilution of the original PCR product, in identical PCR conditions but replacing the primer pairs so that they would amplify shorter sequences within the original target. We used both previously published primers, and designed new primer pairs when needed (Table 4.1).

Finally, for the most problematic samples, including those where we had sequencing problems due to mononucleotide repeats, we used a PCR protocol with Phusion Hot Start II High-Fidelity DNA polymerase (Thermo Scientific, Waltham, Massachusetts, U.S.A.), which is more accurate and yields longer and higher-quality mononucleotide sequence reads (Fazekas & al., 2010). The Phusion protocol was used for both standard and nested-PCRs in 20 µl reaction volumes, with the following reagents: 1× Phusion HF Buffer, 200 µM of each dNTPs, 0.4 µM of each primer, 50 ng/µl BSA, and 0.02 U/µl of Phusion Hot Start II DNA polymerase. We used the 3-step cycling protocol suggested by the manufacturer, but increased the number of cycles to 40. All PCR products were submitted to Genome Quebec (Montreal, Canada), where they were purified and sequenced with Big Dye Terminator 3.1 chemistry 199 on an ABI 3730xl DNA Analyzer (Applied Biosystems, Carlsbad, California, U.S.A.). Chromatograms were assembled and visually inspected using Geneious (v.5.6–6.1.8, Biomatters, Auckland, New Zealand). All sequences were checked using BLAST (Altschul & al., 1990) and eliminated if they did not correspond to Leguminosae sequences in GenBank.

4.3.2 Phylogenetic analyses

Sequences were aligned, inspected and manually adjusted in Geneious. Gaps were coded using simple indel coding (SIC; Simmons & Ochoterena, 2000), implemented in SeqState v.1.4.1 (Müller, 2005). Only non-autapomorphic indels were retained. We also excluded ambiguous portions of the alignments, which mostly corresponded to variable mononucleotide and/or tandem repeats that were difficult to align. For the chloroplast markers, the identification of ambiguously aligned regions was done visually, and resulted in the exclusion of 40 nucleotides for *rps16*, 15 for *trnD-trnT*, and 47 for *ycf6-psbM*. Although the ITS region was by far the most variable locus studied, no ambiguously aligned regions were identified. Because there is always the possibility to amplify paralogs or different copies of the ITS region, we visually inspected the alignment to ensure that there were no significant length variations in the 5.8 subunit and the ITS toplogy was carefully screened to identify unusually long terminal branches. Finally, we carried out a recombination test with Phi-test in the software SplitsTree4 (Huson & Bryant, 2006) to test for recombinants.

Each of the four loci, with their partitioned indel characters, were initially analysed separately, through parsimony, maximum likelihood and Bayesian approaches. Because we never found bootstrap or posterior probability support (above 60%) for conflicting relationships between the topologies of the resulting gene trees, the four data partitions were concatenated for a combined analysis. All phylogenetic analyses were rooted with *C. echinata*, which is considered a more distantly related species in the analyses of Gagnon & al. (2013, chapter 1).

Maximum parsimony analyses were carried out in PAUP* (Swofford, 2003) using the procedure described in Gagnon & al. (2013, chapter 1). Maximum likelihood analyses were carried out using RAxML v.8.0.0 (Stamatakis, 2014), on the CIPRES gateway v.3.3 (Miller & al., 2010). The analyses were conducted using the GTRGAMMA model for the DNA sequences and the BINGAMMA model for the indel partitions. Branch support was calculated using the standard nonparametric bootstrap procedure, with 5000 replicates. Bayesian analyses were conducted in MrBayes v.3.2 (Ronquist & al., 2012). jModelTest v.2 (Darriba & al., 2012) was used to estimate the best evolutionary model for each DNA locus separately. Based on the

Akaike criterion, the best models identified were GTR+I+G for ITS, TPM1uf+I+G for rps16, and TVM+I+G for trnD-trnT and ycf6-psbM. We specified the GTR+I+G model for the ITS region, but because it is not possible to specify the exact models for the three other gene regions in MrBayes, we used the reversible-jump MCMC option, which allows sampling of different schemes of nucleotide substitution as part of the MCMC run (nst = mixed). The F81 model was specified for all partitions corresponding to the indel characters. The analysis was run on a high-performance computer cluster (Calcul Québec, Université de Montréal, Canada) with two parallel runs of eight Markov Chain Monte Carlo (MCMC) chains each, four swaps per swapping cycle, and trees sampled every 1000 generations. The stop criterion was set to an average standard deviation of split frequencies that dropped to below the critical value of 0.01. We observed results with Tracer v.1.5 (Rambaut & al., 2009) ensuring that effective sample sizes were sufficient and that chains had mixed appropriately; if not, we continued to run the MCMC analysis until all effective sample sizes were above 200. The "burn-in" fraction for all analyses was set to 10%.

4.3.3 Morphological analyses

A total of 50 herbarium specimens representing the entire range of *C. trichocarpa* (from Peru to Argentina) were measured and scored for the morphological analyses. These included specimens from K, MO, NY and US, and recent collections from Peru and Argentina (deposited at MT and K), including from the type locality of *C. trichocarpa* in Jujuy, Argentina. *Caesalpinia mimosifolia* was not included because it is a morphologically and geographically distinct species, and its taxonomic status is not disputed (see taxonomic account below).

A total of 31 quantitative and 9 qualitative flower and leaf characters were selected that are straightforward to measure on herbarium specimens and show variation among populations of *C. trichocarpa* (Table 4.2). The qualitative characters relate to the presence of gland-tipped trichomes on leaves (5 binary characters) and flowers (4 binary characters). Quantitative characters include both ordinal and continuous measurements (17 leaf characters, 14 flower characters). Measurements were made with a caliper (0.1 mm precision) or a dissecting microscope when necessary. Special care was taken to measure only flowers that had reached complete anthesis, and to select mature and fully expanded leaves.

When possible, all characters were measured from at least two leaves and two flowers for each herbarium specimen (e.g., either two leaves from one specimen, or one leaf from duplicates deposited in different herbaria); however, this was not possible for all specimens because of poor preservation of flowers (19 specimens) or leaves (21 specimens). In total, 53 flowers were measured from 37 herbarium specimens, and 75 leaves from 49 herbarium specimens (see Annexe 3). Thus, of the 50 specimens studied 32 were scored for both leaf and flower characters. We carried out analyses on the flower dataset, the leaf dataset, as well as on a combined dataset for 32 specimens. For the combined dataset, the analyses used mean values if more than one leaf or flower had been sampled from a specimen, and the binary characters were transformed into factors (zero: absent; one: present; two: present and absent on organs of different specimens).

Table 4.2 Quantitative and binary characters scored for the morphological analyses of *Caesalpinia trichocarpa*. All measurements in mm.

Leaf characters

1. **MAXP:** Maximum number of pairs of pinnae per leaf observed on all the leaves of a herbarium sheet
2. **MINP:** Minimum number of pairs of pinnae per leaf observed on all the leaves of a herbarium sheet
3. **Lpet:** Length of the petiole
4. **Lrac:** Length of the rachis (top of the petiole to base of petiolule of terminal pinna)
5. **Llf:** Length of the leaf (petiole+rachis+terminal pinna)
6. **TPNlf**: Number of pairs of leaflets on the terminal pinna
7. **TPLpet**: Length of the petiolule of the terminal pinna
8. **TPLpin**: Length of the petiolule and the rachis of the terminal pinna
9. **TPL2**: Leaflet length (one leaflet from the 2ndlowest pair of the terminal pinna)
10. **TPW2**: Leaflet width (one leaflet from the 2nd lowest pair of the terminal pinna)
11. **TPNG:** Number of glands on margin of one side of the lowest leaflet of the terminal pinna
12. **P1Nlf**: Number of pairs of leaflets on the lowermost pinna
13. **P1Lpet:** Length of the petiolule of the lowermost pinna
14. **P1Lpin:** Length of the petiolule and the rachis of the lowermost pinna
15. **P1L2:** Leaflet length (one leaflet from the 2ndlowest pair of the lowermost pinna)

16. **P1W2:** Leaflet width (one leaflet from the 2nd lowest pair of the lowermost pinna)
17. **P1NG:** Number of glands on margin of one side of the lower leaflets of the terminal pinna
18. **GPET**: Glandular trichomes on petiole: absent [0], present [1]
19. **GTPP:** Glandular trichomes on petiole of the terminal pinna: absent [0], present [1]
20. **GTPLM:** Glands on leaflet margins of the terminal pinna: absent [0], present [1]
21. **GP1P:** Glandular trichomes on pinna rachis of the lowest pair of pinna: absent [0], present [1]
22. **GP1LM:** Glands on leaflet margins of the lowest pair of pinna: absent [0], present [1]

Flower characters

1. **CucL:** Length of the cucullate sepal
2. **CucW:** Maximum width of the cucullate sepal
3. **CucB:** Width at the base of the cucullate sepal
4. **4SL:** Average length of all other sepals
5. **4SW:** Average of the width of all other sepals
6. **4SB:** Average of the width at the base of all other sepals
7. **SPL:** Length of the standard petal
8. **SPW:** Maximum width of the standard petal
9. **UpL:** Average length of the two upper lateral petals
10. **UpW:** Average of the maximum width of the two upper lateral petals
11. **LowL:** Average length of the two lower lateral petals
12. **LowW:** Average of the maximum width of the two lower lateral petals
13. **AFL:** Average filament length of all filaments measured
14. **AAL:** Average length of all anthers measured
15. **GCR:** Presence of glandular trichomes on the calyx ring: [0] absent, [1] present
16. **GSS:** Glandular trichomes on outer surface of sepals: [0] absent, [1] present
17. **GSM:** Glandular trichomes on margins of sepals other than the lower cucullate sepal: absent [0], present [1]
18. **GSP:** Glandular trichomes on the dorsal surface of the standard petal, above the claw: [0] absent, [1] present

To determine if the morphological traits show a pattern congruent with the molecular phylogeny, we used two statistical approaches implemented in the program R (R Core Team, 2012): an ordination analysis using principal coordinates (PCoA) and a clustering analysis based on Ward's minimum variance method. Both analyses were carried out using Gower distance matrices of our three datasets (flowers, leaves, the two combined), calculated using the "daisy" function of the package "cluster" (Maechler & al., 2014). This transformation of the data allowed us to analyze the binary, quantitative and ordinal characters together. Gower's coefficient also allowed us to handle missing values in the flower dataset (3.6%), without having to estimate new values, by down-weighting missing data to zero. This transformation has been shown to be an effective approach compared to other commonly used techniques to deal with missing data (Brown & al., 2012).

Ward's minimum variance clustering was carried out using the function "hclust" in R on all three datasets, and compared to the phylogenetic analyses to determine if similar groups were recovered. PCoA was performed with the "pcoa" function in the "ape" package (Paradis & al., 2004). As Gower's coefficient is non-Euclidean, we checked if the resulting eigenvectors had negative values. If the absolute negative values were larger than the absolute positive values, we applied the Cailliez correction (Legendre & Legendre, 2012). The broken stick model was used to assess the most significant PCoA components. Variable vectors were projected onto the PCoA plot, and we measured the goodness of fit (GOF) in three ways: (1) on the corrected eigenvalues using the Cailliez method; (2) as the ratio of the sum of the raw eigenvalues of the significant principal components (PCs) on the sum of the absolute values of all the eigenvalues; (3) as the ratio of the sum of the raw eigenvalues of the significant PCs on the sum of all the positive eigenvalues.

We also carried out classification tree analyses on the raw, untransformed data of the three morphometric datasets. The goal of this method of recursive partitioning is to evaluate if it is possible to recover groups corresponding to the clades from the phylogenetic analyses of DNA sequences, and identify specific characters that have a high diagnostic value for these groups. Classification tree analyses were carried out using 100 cross-validations (function "rpart" in package "rpart": Therneau & al., 2012), and the percentage of misclassified specimens was examined to determine how well the analyses performed. Specimens that were not sampled for molecular data were assigned to phylogenetic clades based on their geographic distributions.

Table 4.3 Sequence statistics and results of the Maximum parsimony, Maximum Likelihood and Bayesian phylogenetic analyses of the Arquita clade. N, number of nucleotide characters; SIC, number of indels; PI, phylogenetically informative characters; CI, Consistency Index, RI, retention index.

Matrix	**No. of seq**	**N**	**SIC**	**SIC characters removed**	**% missing data**	**PI/Total characters (%PI)**	**Length (No. trees retained)**	**CI RI**	**Maximum Likelihood Scores**	**Average standard deviation of split frequencies**	**Generations in Bayesian analysis**
rps16	54	870	50	42	5.3%	74/838 (8.83%)	L= 206 (1610)	CI: 0.82 RI: 0.93	-2476.05	0.009862	2,540,000
trnD-trnT	57	1458	56	36	3.1%	132/1463 (9.02%)	L= 337 (100,000)	CI: 0.80 RI: 0.91	-4196.06	0.009999	131,210,000
ycf6-psbMR	51	1481	117	84	9.1%	175/1467 (11.86%)	L=424 (100,000)	CI: 0.76 RI: 0.89	-4457.91	0.004954	3,380,000
ITS	59	696	66	37	0.2%	317/725 (43.72%)	L=1341 (3504)	CI: 0.51 RI: 0.77	-7166.81	0.009858	1,320,000
Combined	63	4505	289	199	21.8%	696/4491 (15.49 %)	L= 2347 (100,000)	CI: 0.61 RI: 0.82	-18728.46	0.00499	2,120,000

4.4 Results

4.4.1 Phylogenetic analyses

The combined matrix (4505 bp) included 696 phylogenetically informative characters (roughly half of these from ITS and the other half plastid) and 21.8% missing data (Table 4.3). Results from Phi-test indicated that no recombination was detected within the ITS matrix and no non-functional copies were detected based on length variation. In all, four gene trees with similar topologies were recovered, albeit with some variation in resolution and support, justifying concatenation of the four data partitions for combined analysis, which yielded a well-resolved and robustly supported phylogeny (Fig. 4.1). The Arquita clade (PP: 1.0, ML: 100%, BS: 100%) is strongly supported as sister (PP: 1.0, ML: 94%, BS: 98%) to *Pomaria*. Members of the P-E clade were never recovered as sister to the Arquita clade in any of these analyses, but instead the P-E clade is sister to the combined *Pomaria*+Arquita clade (Fig. 4.1).

Within the Arquita clade, multiple accessions of *C. ancashiana*, *C. celendiniana*, and *C. mimosifolia* each form clades with strong branch support (PP: 1.0, ML: 100%, BS: 100%). *Caesalpinia mimosifolia* and all accessions of *C. trichocarpa* were placed in a robustly supported clade (PP: 1.0, ML: 98%, BS: 92%) comprising four subclades—*C. mimosifolia*, plus three geographically structured lineages of *C. trichocarpa* accessions from Peru, Bolivia and Argentina (Fig. 4.1). Relationships amongst these four subclades were poorly resolved, with only weak support (PP: 0.58, ML: 72%, BS: 68%) for a sister relationship between the Argentinian and Bolivian subclades (Fig. 4.1; alignments and all trees have been deposited in TreeBase, submission ID 16354).

4.4.2 Morphological analyses of *C. trichocarpa* populations

Three main clusters, largely geographically structured as in the phylogenetic analysis of DNA sequences, were found in the analysis of the combined leaf and flower dataset using Ward's minimum variance clustering analysis (Fig. 4.2), with the exception of two Bolivian specimens nested within the Argentinian cluster, and one Peruvian specimen nested within the Bolivian cluster. In this analysis, the Bolivian and Argentinian clusters are more similar morphologically to each other than to the Peruvian group. In the flower dataset, a similar structure is recovered, with three specimens from Bolivia nested within the Peruvian cluster. In contrast, clustering analyses based on leaf characters alone did not recover clear geographic clusters, as two Peruvian and several Bolivian samples occur in the Argentinian cluster, one Bolivian sample occurs in the Peruvian cluster, and one Peruvian individual is nested within the Bolivian cluster.

Results from the PCoA analysis mirror the results found in the clustering analysis (Fig. 4.3). Results from the Broken stick model indicated that the first three principal components (PCs) were important for the leaves and flowers (flowers GOF of three PCs: 63.3%; leaves GOF of three PCs: 69.3%), whereas the first four PCs were important in the combined morphometric data (GOF of four PCs: 72.8%). Projection of the flowers and combined datasets on the first two PCs resulted in clustering of individuals based on geographic origin, with slight overlap of the Bolivian and Peruvian taxa for the flower dataset, and an overlap between Bolivian and Argentinian taxa for the combined morphological dataset. In the PCoA ordination plot for flowers, projection of variable vectors indicated that Argentinian individuals can be characterized by the presence of glands on the surface and margins of all sepals, whereas the cluster of Peruvian taxa had larger flower parts. Finally, for the PCoA analysis of leaf characters, it is possible to visually identify a cluster of individuals from Argentina that are characterized by the tendency to have larger values of the number of maximum pinnae and minimum pinnae observed on the associated herbarium sheet (MaxP, MinP) and smaller values for quantitative leaf measurements such as the size of leaflets and length of pinna. In contrast, leaves for specimens from Peru overlapped significantly with specimens from Bolivia (Fig. 4.3).

Cross-validation analyses for the classification trees of the three datasets all suggested that the optimal partitioning was in three groups. In all cases, taxa were generally partitioned into these three groups based on their geographical area, with only one or two misclassified individuals (Fig. 4.4). For the flowers dataset, the presence of glands on the sepal margin (GSM) and average filament length (AFL) helped distinguish the three groups, while length of the petiole (Lpet) and maximum number of pinnae observed on a leaf on the associated herbarium specimen (MaxP) were the key characters for classifying the leaves. Two floral characters were selected in the classification tree of the combined morphometric dataset, the presence of glands on the sepal margin (GSM) and width of the lower cucullate sepal (CucW). Boxplots and barplots show the range of variation for each geographical area (Fig. 4.4).

4.5 Discussion

4.5.1 Generic delimitation

Our analyses show that the Arquita clade does not nest within the P-E group, as suggested by Lewis (1998). It is shown here, and in other studies, that the P-E group is polyphyletic, and the generic status of the clades previously attributed to this group requires reconsideration (Gagnon & al., 2013, chapter 1; and in prep., chapter 2). While a core P-E group composed of North and South American taxa is resolved in all recent phylogenetic analyses, several other P-E species (referred to as the Poincianella B group; Lewis & Schrire, 1995; Gagnon & al., 2013, chapter 1) do not group with the core P-E group but instead with the genus Cenostigma. The Arquita clade represents a third strongly supported lineage, that is recovered here as sister to a monophyletic *Pomaria*, and together both clades are sister to the core P-E group.

The robustly supported sister-group relationship of the Arquita clade to Pomaria, rather than to the core P-E group, strongly suggests that the Arquita clade should be recognized as a distinct genus. Although this leads to a stable classification that best reflects the phylogenetic history of these species, we have yet to identify any reliable and consistent diagnostic synapomorphies for the Arquita clade, despite a complete taxonomic treatment of the original P-E Group (Lewis, 1998) and careful examination of specimens in several herbaria. This lack of morphological diagnosability and the morphological similarity of the Arquita clade to one of the P-E Group species, *Caesalpinia placida* from Baja California in Mexico, could argue in favour of recognising a paraphyletic genus comprising the Arquita clade and the core P-E Group. However, this would go against the principles of a Linnaean phylogenetic classification system, and of the current general consensus and practices of systematists in generic-level classifications of plants (Humphreys & Linder, 2009). Alternative options would be to include

Pomaria, the Arquita clade, and the core P-E group in a single large genus, or to expand the genus Pomaria to include the Arquita clade. In both cases, this has the notable disadvantages of abolishing *Pomaria* and undermining its morphological diagnosability, one of the most distinctive and oldest genera recognized in the Caesalpinia Group (see Table 4.4, and studies by Simpson, 1998; Simpson & Lewis, 2003; Simpson & al., 2006).

Issues of morphological homoplasy and convergence have plagued previous attempts to provide a satisfactory generic system for the informal Caesalpinia Group, and other clades, such as the polyphyletic lineages of *Caesalpinia* s.s., also appear to lack diagnostic synapomorphies or combinations of characters (Gagnon & al., 2013). A recent review of phylogenetic studies focusing on generic delimitation in plants has shown that robust monophyly in molecular phylogenies is the principal and most important criterion for delimiting genera (Humphreys & Linder, 2009). While morphological synapomorphies are desirable to communicate about taxonomic groups, such diagnostic characters are not always present due to the varied evolutionary histories of different groups (e.g., the process of hybridisation, reticulation, etc., Linder & al., 2010). At another extreme, morphology can be misleading for identifying all of the taxa derived from a common ancestor (e.g., Albach, 2008; Dillenberger & Kadereit, 2014). While it is rare to find generic-level clades that lack any morphological synapomorphy, there is at least one precedent in legumes where a morphologically cryptic genus from the SDTF is recognised based on phylogenetic evidence in the Robinioid legumes (*Gliricidia*, sensu Lavin & al., 2003, subfamily Papilionoideae). Despite the lack of morphological diagnosibility, we argue that the Arquita clade forms a distinct, morphologically and ecologically coherent group of shrubs of medium height with slender branches, restricted to steep mid-elevation slopes of loose soil in valleys dominated by seasonally dry rupestral thorn scrub forest of the Andes (Table 4.4). These mid- elevation rupestral dry habitats, which are always above 1000 m, are notable as they occur at higher elevations than typical SDTF in the Andes and elsewhere in the Neotropics (Pennington & al., 2000; Hughes & al., 2013). They are more similar to those occupied by species of *Pomaria*, which occur in rupestral habitats consisting of subtropical or warm temperate thorn scrub, desert and grassland/savannah, and occur in disjunct patches in North America, southern Brazil, the Misiones province of Argentina, and southern Africa (Simpson, 1998; Simpson & Lewis, 2003; Simpson & al., 2006). While we accept that delimiting the Arquita clade creates a genus that will not be easy to identify in the field or the herbarium, recognizing it as a distinct genus in our classification adds information about the phylogenetic relationships with two other distinct and ecologically important groups (Table 4.4) and is a better reflection of the evolutionary history and diversity of the Caesalpinia Group.

4.5.2 Species delimitation

In the molecular phylogenetic analysis, all accessions of the *C. trichocarpa* alliance were placed in a robustly supported but poorly resolved clade with *C. mimosifolia*. Within this clade four distinct lineages, corresponding to *C. mimosifolia* and three geographically disjunct subclades of *C. trichocarpa* accessions from Peru, Bolivia and Argentina are well supported (Fig. 4.1). Each of these subclades is subtended by significant branch lengths, indicating the genetic distinctiveness of these three lineages. Weak support for a sister relationship was found between the Argentinian and Bolivian accessions, which are geographically relatively close (~200 km), but still separated by mountains over 4000 m in altitude (Fig. 4.5). Although the relationships of the much more geographically isolated Peruvian lineage are unresolved, it forms a highly supported monophyletic group subtended by a long branch. In recent analyses that include the plastid locus matK (Gagnon & al., in prep., chapter 2), the Peruvian lineage appears as more closely related to *C. mimosifolia* than to the Bolivian and Argentinian lineages of *C. trichocarpa*, supporting the idea that this lineage be recognised as a distinct species.

It is notable that the clusters uncovered in the morphological analyses for the combined and flower datasets in all three statistical analyses correspond closely to the clades uncovered in the phylogenetic analyses, with very few misclassified individuals (Fig. 4.3). Although the Ward clustering and PCoA analyses of the leaves-only dataset do not recover clusters corresponding to the phylogenetic clades, the classification tree analysis segregates the accessions into three geographically structured groups based on length of the petiole and number of pairs of pinnae, with only 6 of the total 75 individuals misclassified. These patterns of morphological variation (Figs. 4.3, 4.4) suggest that the Argentinian and Peruvian lineages are distinct and easily differentiated from each other by the presence of smaller flowers with a glandular margin on all five sepals and more pairs of pinnae (2–5) in the Argentinian populations compared to the larger flower parts (including filaments, anthers, calyx and corolla), eglandular sepal margins (apart from the lower cucullate sepal), and fewer pairs of pinnae per leaf (1–2) in the Peruvian populations. While the Bolivian specimens can be distinguished by their longer petioles and their eglandular sepal margins (except for the lower cucullate sepal), they are still more variable morphologically and tend to overlap with the other two clades to some extent (e.g., small flowers with eglandular sepal margins), potentially suggesting a more continuous pattern of morphological variation.

Despite the morphological variation of the Bolivian accessions, the flowers of the Peruvian lineage are markedly larger and in combination with the aforementioned suite of characters, the Peruvian populations can be reliably distinguished from those in Bolivia and Argentina. We also observed certain characteristics unique to the Peruvian lineages, but which vary within Peru. For example, distinctive flowers with red markings on all five petals, resulting in orange flowers, are common in Peru (Fig. 4.6B), but never observed in the field in Bolivia or Argentina. Finally, differences in habit that were not possible to score for the morphometric analysis were also observed: while specimens in Argentina generally form upright shrubs to 2 m in height, Peruvian specimens tend to be decumbent shrubs, with long trailing branches, rarely over 1 m in height (Fig. 4.6A).

The geographical isolation of the Peruvian lineage, separated by the high altiplano of south-central Peru from the closest occurrence of C. trichocarpa in Bolivia more than 1350 km away, combined with the clear floral differentiation and the robustly supported genetic distinctiveness strongly suggest that it represents a cryptic species, below described as Arquita grandiflora. In contrast, we choose to recognize the other two subclades as varieties of Arquita trichocarpa, which although genetically distinct, are morphologically, geographically and genetically (albeit this with only weak support) closer, distinguished from each other only by lack of glandular trichomes on the margins of the sepals, and a generally longer petiole (though these characters can be variable). Denser sampling from Bolivia and more sequence data facilitating application of coalescent methods would be desirable both to resolve relationships among the four subclades and to further test whether the Bolivian lineage also represents a second cryptic species within this complex.

Similar studies in recent years have revealed several cases of cryptic, undescribed or improperly circumscribed legume species from the Succulent Biome (sensu Schrire & al., 2005, a collection of semi-arid, fire-intolerant, succulent-rich dry tropical forests, thickets and bushlands) based on the coalescence of genetic loci from geographically localized individuals (e.g., *Caesalpinia oyamae* Sotuyo & G.P.Lewis, Sotuyo & al., 2007; *Leucaena cruziana* Britton & Rose and *L. zacapana* (C.E.Hughes) R.Govindarajulu & C.E.Hughes, Govindarajulu & al., 2011; *Mimosa jaenensis* Särkinen & al., Särkinen & al., 2011b; *Poissonia eriantha* (Benth.) Hauman, Pennington & al., 2011; *Coursetia greenmanii* (Millsp.) R.Duno & Carnevali, Stefano & al., 2010; and *Coursetia caatingicola* L.P.Queiroz, Queiroz & Lavin, 2011). In many of these genera similar patterns of robustly supported reciprocally monophyletic species clades subtended by long stem branches are evident, a pattern reflecting the narrowly restricted endemic distributions, but often local abundance of these Succulent Biome woody legumes (Pennington & al., 2010, 2011). Phylogenies of all these taxa also show high levels of geographic structure (Pennington & al., 2009), as observed here, not only in the C. trichocarpa alliance, but also across the Arquita clade as a whole, both between and within species. For example, accessions of *C. ancashiana* from the provinces of Cajamarca (coll. no. 3065, 3070, Fig. 4.1) and Ancash (coll. no. 3021, 3025–27, Fig. 4.1) are placed in robustly supported reciprocally monophyletic subclades, subtended by accessions from Ecuador (coll. no. 2266, 3073, 3815, Fig. 1). Similarly, the Peruvian lineage of *C. trichocarpa* comprises two reciprocally monophyletic geographical subclades on either side of the Cordillera Blanca in the Callejon de Huaylas (coll. no. 3056–57, 3041–42, 3047, 3063, Fig. 1), and the Upper Rio Marañón Valley (coll. no. 3155–3156, Fig. 1). The three other species of the Arquita clade also correspond to robust clades occupying allopatric distributions in disjunct inter-Andean valleys (Fig. 4.5).

Strong geographical phylogenetic structure, as seen here in the Arquita clade, is the hallmark of the Succulent Biome (Lavin & al., 2004; Schrire & al., 2005; Pennington & al., 2009; Hughes & al., 2013) and clearly apparent in many other Succulent Biome legume and other plant lineages, e.g., several segregates of *Caesalpinia* s.l. (Gagnon & al., 2013, chapter 1), including *Hoffmannseggia* (Simpson & al., 2005) and *Pomaria* (Simpson & al., 2006), as well as other genera such as *Parkinsonia* (Haston & al., 2005; Hawkins & al., 2007), sections of *Indigofera* (Schrire & al., 2009), *Bursera* (De-Nova & al., 2012), *Tiquilia* (Moore & al., 2006), etc., but not in lineages occupying neighbouring biomes such as tropical wet forests (Lavin, 2006). While not as species-rich as tropical wet forests, the Succulent Biome is well-known for its high levels of beta diversity: the narrowly restricted occurrence of the Peruvian *C. trichocarpa* lineage in two small inter-Andean valleys in the province of Ancash in central-north Peru, and the similarly narrow endemism of *C. celendiniana* restricted to the Marañón valley reflects the high levels of narrow endemism that are often prevalent in the Succulent Biome, and especially in the inter-Andean dry valleys (e.g., endemism of woody taxa between 16.4% and 47.1% in the Equatorial Pacific, Peruvian eastern Andean nuclei and inter-Andean valleys of Colombia, Peru and Bolivia; Linares-Palomino & al., 2011; Pennington & al., 2011). In addition, succulent vegetation of the inter-Andean valleys is considered to be older than other Andean biomes, probably dating back to at least 10 Ma (Pennington & al., 2010; Särkinen & al., 2012) in line with fossil evidence (Burnham, 1995; Burnham & Carranco, 2004). Although no time-calibrated tree for the Arquita clade has yet been reconstructed, the deeply divergent species clades subtended by long branches (Fig. 4.1), suggest lack of gene flow and long isolation of these inter-Andean valley species and populations, as found for other species (Pennington & al., 2004, 2010).

We suggest that this large number of cryptic legume species recently revealed in Succulent Biome lineages is likely to be a function of isolation accompanied by low levels of adaptive divergence constrained by strong climatic niche conservatism, such that morphological changes occurred mainly through drift. This model of speciation has been widely invoked in studies of cryptic speciation in both plants and animals (Britton & al., 2014; Kozak & al., 2006; McDaniel & Shaw, 2003; Smith & al., 2011). This also suggests that additional, as yet overlooked, cryptic species will be revealed by detailed studies evaluating the status of disjunct populations in this biome as potentially distinct species (e.g., Baranzelli & al., 2014).

Based on robust phylogenetic support and explicit criteria for generic delimitation, the Arquita clade is here recognized as the new genus, *Arquita*. We also demonstrate that the Peruvian populations of *C. trichocarpa* represent a genetically distinct independent evolutionary lineage that is geographically isolated and which can be identified by a combination of morphological characters, meriting recognition as a new species. These new taxa are formally described as part of a complete taxonomic account of the genus *Arquita* presented here.

Table 4.4 Comparison of morphological and habitat differences between *Arquita, Pomaria,* and the core P-E group

	***Arquita* gen. nov.**	***Pomaria* Cav.**	***Core P-E group***
Habit	Shrubs and subshrubs with slender, often decumbent branches	Small shrubs, subshrubs or herbaceous perennials	Shrubs to small and medium-sized trees
Stipules	Caducous;	Persistent;	Caducous (except for *C. caudata (*A.Gray) Fisher and *C. argentina* Burkart);
	Chartaceous, ovate, obovate to deltoid, with a fringed margin and covered in stalked glands	Linear, sometimes pinnatifid, with a fringed to laciniate margin	Chartaceous, ovate, obovate to deltoid in shape
Leaflets	Eglandular, or with maroon/black glandular dots sunk in the depressions of crenate margins, or with a few sub-marginal glands on lower surface	Conspicuously dotted on lower surface with sessile, orange glands that dry black, sometimes with a sub-marginal pattern	Eglandular, or with maroon/black glandular dots sunk in the depressions of crenate margins, or with a few sub-marginal glands on lower surface
Sepals	Lower cucullate sepal equal or slightly longer in length than other four; Margin fimbriate, with gland-tipped trichomes	Lower cucullate sepal significantly longer than other four; Margin entire and eglandular	Lower cucullate sepal equal or slightly longer than other four; Margin entire or fimbriate, eglandular or with gland-tipped trichomes
Petals	Deflexed;	Two lower lateral petals forming a horizontal platform above the lower cucullate sepal;	Deflexed, or laterally compressed;
	Yellow, sometimes streaked with red markings	Yellow, white or red-pink	Yellow, pink, red or orange
Androecium	Free and deflexed	Cupped in the lowermost cucullate sepal	Free and deflexed
Gynoecium	Covered in gland-tipped trichomes, which are sometimes dendritic	Eglandular plumose/stellate trichomes, with orange sessile glands (drying black)	Eglandular or covered in gland-tipped trichomes
Habitat/Distribution	Dry, montane, rupestral habitats in inter-Andean valleys of Argentina, Bolivia, Ecuador and Peru.	Dry montane, rupestral habitats of Mexico; Subtropical and warm temperate arid or semi-arid desert matorral and grasslands in North and South America, and southern Africa.	Low-elevation SDTFs across Mexico, Central America, the Caribbean, and in Caatinga in Brazil; Patches of dry forests, deserts, yungas-puna transition zones, and chaco-transition forests in Argentina, Bolivia, Chile and Paraguay.

4.6 Taxonomic treatment of *Arquita*

This account is based on fieldwork and revision of 200 herbarium specimens (CORD, CTES, K, MO, NY, SI, US, USM) and past taxonomic treatments (Ulibarri, 1996; Lewis, 1998; Lewis & al., 2010) including a key for the identification of species, a detailed distribution map, a diagnosis and description of the new genus (*Arquita*), new nomenclatural combinations for four species transferred to *Arquita*, and formal description and illustration of the new species (*Arquita grandiflora*) as well as an updated description of *A. trichocarpa* including a new variety *boliviana*.

Arquita E.Gagnon, G.P.Lewis and C.E.Hughes, **gen. nov. – TYPE:** *Arquita mimosifolia* (Griseb.) E.Gagnon, G.P.Lewis & C.E.Hughes (≡ *Caesalpinia mimosifolia Griseb.*)

Description: Small to medium-sized often decumbent shrubs, 0.3 – 2.5 m in height, slender in stature. Usually glandular, often with glandular trichomes on various parts of the plant. Young stems and inflorescence rachises red-orange to maroon. *Stipules* caducous, ovate-obovate to deltoid in shape, chartaceous, 2.5 – 5.5 mm long, usually with a fimbriate glandular margin and short-stalked glands (with the exception of some species of *A. ancashiana*). *Leaves* bipinnate, with 1 to 5 pairs of pinnae, usually with a single terminal pinna. Petiole (0.3 –) 0.5 – 6 cm, rachis 0.5 – 6 cm (but sometimes absent). Leaflets usually in 4 to 12 opposite pairs per pinna, oblong-obovate in shape, 2.5 – 10(– 14) × 1 – 3.5(– 6) mm, often with maroon/black glands sunken in depressions of the crenulated leaflet margins, and sometimes with occasional sessile black glands on the leaflet blades (an exception is *Arquita ancashiana*, where the glands appear on the basal leaflets of the pinnae, and are in a submarginal position, on the lower half of the leaflet (Fig. 4.6P)). *Inflorescences* are leaf-opposed indeterminate racemes of yellow to orange flowers, with only 1 to 2 flowers open at a time, (5–) 7 – 21 (– 41.5) cm long. Bracts lanceolate and acuminate, either eglandular or covered in gland-tipped trichomes, caducous (2.75 – 7 mm long). Pedicels 5 – 12 mm, articulated 1 – 2.5mm below the calyx. *Calyx* varying from green tinged red to carmine, eglandular to covered in gland-tipped trichomes, sepals 6 – 11 mm long, the lower sepal cucullate, reflexing at anthesis, and slightly longer than the other four sepals; margins fimbriate with glandular trichomes, either only on the lower cucullate sepal or on all five sepals (with exception of some specimens of *A. ancashiana,* where the sepals are all eglandular and the margins are all entire). The standard petal 6 – 17 × 4 – 12 mm, claw pubescent at the base, either flat or inrolled, sometimes with stipitate-glandular trichomes on the dorsal surface. Upper and lower lateral petals 6 – 17 × 3 – 12 mm. Stamen filaments free, 5 – 13 mm long, anthers 0.75 – 2.3 mm, the stamens deflexed and loosely grouped around the gynoecium, the ovary usually covered with gland-tipped trichomes, the hypanthium persisting as a small ring as pod matures. *Pods* flat, lunate-falcate with a marcescent style, the valves coriaceous, and covered sparsely to densely with gland-tipped trichomes, these sometimes dendritic at maturity, 2 – 4.7 × (0.7 –) 0.9 – 1 cm. Seeds laterally compressed, ovate-orbicular, 4.5 – 6 × 3.5 – 4.5× 1 mm, the testa shiny olive-grey, sometimes mottled or streaked black.

Etymology: The genus name *Arquita* is the vernacular name of *Caesalpinia trichocarpa* in Argentina (Ulibarri, 1996).

Notes: *Arquita mimosifolia* is designated here as the type species, because it is the oldest name associated with the taxa included in the genus, and also the most abundant and widespread species in the genus. *Arquita* comprises five species all of them restricted to the Andes in South America, on mid-elevation slopes in inter-Andean valleys, extending from Ecuador south to Argentina. Species of *Arquita* are also morphologically similar to members of the core P-E group, but molecular phylogenetic analyses have conclusively shown that *Arquita* is not nested within the core P-E group and forms a robust clade sister to *Pomaria* (Fig. 4.1) (Gagnon & al., 2013, chapter 1). While *Arquita* species are similar in habit to species of *Pomaria*, they are morphologically similar to the P-E clade, and difficult to distinguish because of the close resemblance to a species from the P-E clade in Baja California, *C. placida* Brandegee. Morphological, geographical and habitat differences amongst these three groups are listed in Table 4.4.

4.6.1 Key to species of *Arquita*

1a. Stems green, strongly angular to tetragonal; erect shrub, 0.7– 2m in height, with long slender, wand-like branches; inflorescence c. 24 – 41.5 cm long, standard petal c. 6 mm long; pods covered in a mixture of white hairs and simple gland-tipped trichomes; 2 – 3 pairs of pinnae per leaf, leaf rachis 3 – 6 cm long; Peru, endemic to the upper Rio Marañón Valley (depts. Cajamarca and La Libertad)..***1. Arquita celendiniana***

1b. Stems grey, brown or maroon, terete; usually rather low, compact or decumbent shrubs, from 0.3 – 2.5m tall; inflorescence 3 – 21 cm long, standard petals 8 – 16.5 mm long; pods either with simple or dendritic gland-tipped trichomes, and sometimes also finely puberulous; 1 – 5 (– 7) pairs of pinnae per leaf, if a leaf rachis present this c. 0.5 – 5 cm long; dry inter-Andean valleys of Ecuador, Peru and Bolivia and the eastern flanks of the Andes in southern Bolivia and NW Argentina... ***2.***

2a. 1–2 pairs of pinnae, plus a terminal pinna, per leaf; plants from Ecuador or Peru.. ***3.***

3a. Pod densely covered with dendritic, gland-tipped trichomes, up to 1mm in length; standard petal 11 – 17× 7 – 12 mm, the dorsal surface eglandular and the claw flat; stamen filaments 9 – 13 mm long; all five petals sometimes with red markings, or alternating yellow and red markings only on the standard petal; endemic to Peru, in the Rio Santa Valley and the upper Rio Marañón (Depts. Ancash and Huanuco)................................ ***2. Arquita grandiflora***

3b. Pod sparsely covered with simple, gland-tipped trichomes, less than 0.5 mm in length, sometimes nearly sessile; standard petal 10 × 6 mm, the dorsal surface covered with stipitate glands, the claw inrolled; stamen filaments 7.5 – 9 mm long; only the standard petal with red markings; Peru and Ecuador on the west flanks of the Andean Cordillera ....***3. Arquita ancashiana***

2b. 2 – 5 (– 7) pairs of pinnae, plus a terminal pinna, per leaf; plants from Bolivia and Argentina...***4.***

4a. Pods densely covered with dendritic, gland-tipped trichomes, up to 1 mm in length; claw of the standard petal not inrolled; leaf rachis 0.5 – 2.8 cm long, with 2 – 5 opposite pairs of pinnae, plus a terminal pinna; Bolivia and Northern Argentina (Provs. Jujuy, Salta, Catamarca, Tucumán)…...***5.***

4b. Pods sparsely covered with simple, gland-tipped trichomes, less than 0.5 mm in length, nearly sessile; claw of the standard petal inrolled; leaf rachis 2– 5 cm long, with 3– 5 (–7) opposite pairs of pinnae, plus a terminal pinna; Argentina (Salta, Catamarca, Cordoba, La Rioja, San Juan, San Luis)..***4. Arquita mimosifolia***

5a. Plants from Argentina; petiole 3.5 – 10.5 mm long; always with glandular trichomes on the margins of all five sepal.......***5a. Arquita trichocarpa* var. *trichocarpa***

5b. Plants from Bolivia; petiole 8 – 35 mm long; generally only the lower cucullate sepal with glandular trichomes along the margin (but exceptions have been noted)…………….. ***5b. Arquita trichocarpa* var. *boliviana***

4.6.2 Species description

1. Arquita celendiniana (G.P.Lewis & C.E.Hughes) E.Gagnon, G.P.Lewis & C.E.Hughes, **comb. nov**. ≡ Caesalpinia celendiniana G.P.Lewis & C.E.Hughes in Kew Bull. 65: 210, fig. 1. 2010 – Holotype: PERU. Dept. Cajamarca, Celendín, Río Marañón Valley, km 47 rd Celendín to Balsas on slopes on W side of the valley (6°51′28″ S, 78°02′33″ W), 22 Apr 2002, fl. & fr., Hughes & al. 2210 (K!; isotypes: FHO! [Brahms specimen ID: 98138], MOL!).

Description: Erect, brittle, multi-stemmed, sometimes scrambling, shrub, 0.7 – 2m tall, woody at the base from which arise slender, green, strongly angular to tetragonal shoots that die back and resprout annually, bark of older stems smooth, grey-brown, slash greenish, stems densely covered in maroon glandular hairs and a fine puberulous, white indumentum. *Stipules* ovate-obovate, fimbriate, both the surface and the margin covered in white pubescence mixed with maroon, dendritic, gland-tipped trichomes. *Leaves* bipinnate, spirally arranged, petiole 1.8 – 3.5

cm long, leaf rachis 3 – 6 cm long, covered in maroon glandular hairs, pinnae in 2 – 3 pairs per leaf, usually ending in a single pinna, but this sometimes lacking, leaflets in 4 – 7 pairs per pinna (usually only 3 – 4 pairs on the terminal pinnae), distal leaflets of the terminal pinnae obovate, 5 – 11 × 3 – 5 mm, their apices shallowly emarginate, median leaflets of the median pinnae oblong-elliptic, 6 – 12 × 3 – 6.5 mm, all leaflets somewhat fleshy, upper surface glabrous, lower surface glabrous or with a sparse pubescence at the base of the midvein to half way along it, the margins sometimes sparsely ciliate with white hairs, only the midvein evident; some leaflets, usually the basal ones on each pinna, with a crenate, or partially crenate margin, with sessile maroon (drying black) glands (of varying number per leaflet) in the shallow marginal sinuses between the crenations, either along the basal third of the margin or all way round the leaflet circumference, together with the occasional sessile gland in shallow depressions on the leaflet blade lower surface, and usually a single gland at the apex of the midvein. *Inflorescence* a long, lax, terminal or axillary, erect, many-flowered raceme, c. 24 – 41.5 cm long, the axis with a fine puberulous indumentum of patent white hairs intermixed with stipitate maroon glandular trichomes. Flower buds globose, the lower sepal ± cucullate and slightly longer than the other four, all sepals densely pubescent with white patent hairs; pedicel of open flower 8 mm long, articulated 1.5 mm below the calyx, pubescent with white patent hairs along its whole length, with maroon stipitate glandular trichomes intermixed, or these restricted to the point of articulation (where they are especially dense) and below; bracts lanceolate, acuminate, 3.5 – 4 × 1 – 1.5 mm, the margin fimbriate-dentate, the fimbriae gland-tipped or not, the outer surface densely pubescent with white patent hairs and maroon stipitate glands intermixed. *Calyx* pale green flushed pinkish red, pubescent, with or without glandular trichomes intermixed, calyx lobes 6 – 6.5 mm long, very slightly fimbriate and glandular near the apex, the margin with white hairs, the inner surface glabrous, the outer surface moderately puberulous with white hairs and short-stalked to almost sessile maroon glands intermixed. *Corolla* orange-yellow with red markings, the standard petal fringed brilliant red along the upper part of the margin, the blade broadly ovate with an acute apex, 6 × 4 mm (including a 1 mm long broad open claw), inner surface of claw moderately to densely pubescent, outer surface of whole petal glabrous and eglandular except for a pubescent claw base; upper lateral petals yellowish orange at base, reddish orange at apex, obovate, 6 × 4 mm, glabrous, eglandular, tapering towards a very short, < 0.5 mm pubescent claw; lower lateral petals slightly smaller than the upper laterals, 6 × 3 mm, otherwise identical. Stamen filaments green tinged pink, c. 5 mm long, pubescent along the lower ½ to ⅔, especially so near the base, anthers 1 × 0.5 mm. Ovary and base of style densely covered in stipitate glandular trichomes, these mostly maroon in colour, but those of the central portion of the ovary white to ochre, a few transparent to whitish simple hairs intermixed with the glands; style 1.5 – 2 mm long, the apex curved upwards, pubescent almost to its apex, the stigma sublateral, chambered, without evident fringing papillae. *Fruit* a lunate pod, 25 × 9 mm, coriaceous, dehiscent, the apex acute (or with a persistent style forming a 5 – 6 mm long apiculum), no calyx lobes persist around the fruit base, the valves densely covered in a mixture of simple patent white hairs and gland-tipped maroon trichomes, 3 – 4-seeded. Seeds olive-green to brownish, smooth, ovate to sub-elliptic, c. 4.5 – 5 × 3.5 – 4 × 1 mm. (Fig. 4.6Q-T)

Distribution and Habitat: Endemic to Peru and currently only known from two localities on either side of the Rio Marañón Valley in Prov. Celendín, Dept. Cajamarca, and on the E side of the valley, Dept. La Libertad (Fig. 4.5). Locally common on steep loose freely-drained rocky scree slopes in dry thorn scrub and tropical dry forest with *Coursetia cajamarcana*, *Maraniona lavinii*, *Tecoma rosifolia*, *Eriotheca* and *Loxopterigium*, 1250–1600 m.

Additional specimens examined: PERU: Depto. Cajamarca: Celendín to Balsas, descent to Balsas (6°50′S, 78°1′W), 28 Nov 2003, *Pennington et al. 17567* (K, MOL); Celendín, Balsas-Celendín rd, 7 – 13 km from Balsas, Rio Marañon Valley (6°50′S, 78°3′W), 24 Feb 1984, *Smith 6182* (NY, K [photo]); Road from Celendín to Balsas, west bank of Rio Marañón (6°51′30.4″S, 78°2′36.1″W), 12 May 2011, *Hughes & al. 3097* (K, MT, USM, Z). **Depto. La Libertad:** Road from Balsas to Bolivar, on the southern side of the valley of the Rio Pusac, tributary on the eastern flanks of the Rio Marañón (6°58′40.3″S, 77°57′15.6″W), 12 May 2011, *Hughes & al. 3102* (K, MT, USM, Z);

Phenology: Flowering and fruiting from November to May.

Conservation status: *Arquita celendiniana* is known from just two populations on either side of the Rio Marañon above Balsas and, as currently known, is undoubtedly globally rare and is provisionally assigned a conservation rating of Critically Endangered (CR b1), with the current extent of occurrence just below 1 km^2 in a Geocat analysis (Bachman & al., 2011), and with an area of occupancy of 5.6 km^2 when using the default 2km cell width value. However, given the inaccessibility of the Rio Marañon valley slopes upstream and downstream of the bridge at Balsas, it remains unclear just how widespread and abundant this plant is and a more precise assessment of its conservation status must await a more thorough field survey.

2. Arquita grandiflora E.Gagnon, C.E.Hughes & G.P.Lewis, **sp. nov.** – Holotype: PERU. Dept. Ancash, Distrito de Mato, road from Caraz to Huaylas, deviation to Huaylas (ca. 15 km; 9°55′ S, 77°51′27.6″ W), 5 May 2011, Hughes & al. 3056 (K!; isotypes: FHO!, MOL!, MT No. MT00182121!, USM!).

Diagnosis: This species is very similar to *Arquita trichocarpa*, but differs in having larger floral parts, most notably the petals (standard petal 1.1 – 1.7 × 0.7 – 1.2 cm vs. 0.8 – 1.3 × 0.5 – 0.7 cm) and stamen filaments (9 – 13 mm versus 7 – 10 mm), fewer pairs of pinnae per leaf (1–2 pairs of pinnae plus a terminal pinna, versus 2 – 5 pairs of pinnae plus a terminal pinna) and a generally smaller (to 1 m), compact or decumbent habit (compared to taller, more erect shrubs to 1 to 2.5 m).

Description: Unarmed, glandular, decumbent to prostrate, suffrutescent shrub, up to 1 m, the trailing branches up to 2.5 m long. Young stems and fertile new growth dark red to maroon, covered in glandular trichomes. *Stipules* ca. 3mm long, obovate to deltoid, chartaceous (papyraceous), tinged red, margin fimbriate, covered in glandular trichomes and white hairs, caducous. *Leaves* bipinnate, pinnae reduced to one or two opposite pairs of pinnae plus a terminal pinna; petiole 4.8 – 9.6 mm long; petiole and rachis (when present) glandular, dark maroon, very finely puberulent. *Leaflets* in (5 –) 6 – 8 (– 10) opposite pairs per pinna, oblong-obovate, 3.8 – 5.5 × 1.2 – 2.6 mm, primary vein visible on underside of leaflets, excentric, leaflet margins crenulated with sunken glands in the concave indentations, proximal leaflets of each pinna generally more glandular than more distal ones. *Inflorescence* a leaf-opposed, (7 –) 16 – 21 laxly-flowered, pedunculate, indeterminate raceme, 1 – 2 flowers opening at the same time on any one inflorescence, rachis covered in glandular trichomes and finely puberulent, (4.5 –) 6.5 – 7 cm long. *Bracts* c. 7 mm long, with an acute tip, papery in appearance, tinged red, with a glandular margin, covered in glandular trichomes, puberulent, caducous. *Pedicels* sparsely glandular and puberulous, 6.0 – 6.5 mm long, articulated at 1.5mm below the calyx, lower sepal cucullate and overlapping all other sepals in bud, carmine red, pubescent, hypanthium and sepals usually eglandular or sparsely glandular and entire, except for the lower cucullate sepal which always has a fimbriate, glandular margin, sepals oblong-lanceolate, overlapping margins often thinner and more papery in appearance, 7 – 11 × 2.6 – 4.9 mm. *Corolla* orange to yellow with prominent red streaks on all petals, fading darker orange with age. Standard petal oblong-obovate (oblanceolate), 1.1 – 1.7 × 0.7 – 1.2 cm, with a tuft of white hairs at the base of the claw. Upper lateral petals 1.0 – 1.7 × 0.6 – 1.2 cm, pubescent on side of claws. Lower lateral petals 0.9 – 1.6 × 0.6 – 1.2 cm, claws glabrous. Stamen filaments pale green or red, 0.9 – 1.3 cm long, pubescent with white trichomes on the lower third, anthers 1.9 – 2.3 mm long. Ovary with a dense indumentum of gland-tipped dendritic trichomes up to the base of the style, stigma with a slightly bulbous, trichome fringed chamber. *Pod* lunate-falcate, 2.5 – 3.5 × 0.9 – 1.0 cm, young green pods covered in red-magenta dendritic gland-tipped trichomes, sepals abscise but a calyx ring is persistent at fruit maturity; older pods brown, chartaceous, elastically dehiscent with twisting valves. Seeds, laterally compressed, dark brown streaked black, ovate-orbicular, c. 6 × 4.5 × 0.5 mm. (Fig. 4.6A-D; Fig. 4.7)

Distribution and Habitat: Peru, known only from the Callejon de Huaylas in the upper Rio Santa Ana valley, mainly on the lower east flanks of the Cordillera Negra in the province of Ancash, and the upper Rio Marañon valley, on either side of the river in the districts of Llamellín (Dept. Ancash) and Huacaybamba (Dept. Huanuco), these two areas separated by the high ranges of the Cordillera Blanca (Fig. 4.5). Growing on steep, freely-drained dry, rocky or sandy slopes in open, often degraded, dry mattoral and spiny cactus scrub, with shrubby legumes including *Caesalpinia cassioides*, *Chamaecrista*, *Calliandra*, *Mimosa montana*, *Dalea* and *Senna*, other common shrubs including *Dodonaea viscosa* and *Croton*, scattered trees of *Tara spinosa* and *Schinus mole*, abundant Cactaceae and naturalized *Spartium junceum*. At 2165–2790 m altitude (very rarely above 3000 m).

Additional specimens examined: PERU: without exact locality or date, *Haenke s.n.* (M); **Depto. Ancash: prov. Huaylas:** Callejón de Huaylas, 9 Apr 1970, *Smith & Blas 4891* (F, SI);

Incapaman, 3 May 1978, *Carillo et al. 635* (SI); Incapaman, 7 May 1979, *Carillo 718* (SI); North of Caraz, main road to Huallanca (9°00′09.8″S, 77°49′08.2″W), 5 May 2011, *Hughes et al. 3063*, (K, MT, USM, Z); dirt road from Huallanca to Huaylas, 26 Apr 2007, *Särkinen et al. 2225* (FHO, K, MOL, NY); no precise locality, 27 May 2001, *Leon et al. 4887* (USM); Subida a Punta Chacay (Pueblo Libre), 10 Jan 1995, *Cano et al. 6389* (USM); Pueblo Libre (Cerro Huantar), 9 Oct 1999, *Cano et al. 9632* (USM); Distrito de Pueblo Libre, road to Punta Chacay (9°6′34.3″S, 77°49′10.1″W), 3 May 2011, *Hughes et al. 3041* (K, MT, USM, Z); Distrito de Pueblo Libre, in gullies next to road to Punta Chacay (9°6′19.28″S, 77°49′7.8″W), 3 May 2011, *Hughes et al. 3042* (K, MT, USM, Z); Distrito de Shupluy, road to Cueva Guerritera, (9°12′29.3″S, 77°41′58.9″W), 4 May 2011, *Hughes et al. 3047* (K, MT, USM, Z); Distrito de Mato, road from Caraz to Huaylas, deviation to Huaylas (c. 7 km, 8°56′0.9″S, 77°51′7.4″W), 5 May 2011, *Hughes et al. 3057* (K, MT, USM, Z); **Prov. Antonio Raymondi:** Distrito Llamellín, west flanks of the Rio Marañón (9°2′55.9″S, 76°59′31.9″W), 27 May 2011, *Hughes et al. 3156* (K, MT, USM); [prov. Huacaybamba:] Margen derecha del Rio Marañón, 25 Aug 2003, *A. Cano 13839* (USM); **Depto. Huanuco:** Distrito de Huacaybamba, east flanks of the Rio Marañón, near Puente Chochian (9°3′10.37″S, 76°59′5.67″W), 27 May 2011, *Hughes et al. 3155* (K, MT, USM, Z).

Phenology: Flowering and fruiting from January to May, occasionally in August and October.

Conservation status: As currently known, *A. grandiflora* is globally rare, restricted to just two small areas in adjacent inter-Andean valleys and a small number of localities in the Rio Santa Valley, all of them in the Prov. of Huaylas, and two nearby localities in the adjacent uppnumber ofarañón valley. Analysis of known localities in GeoCAT (Bachman & al., 2011) suggests that with a cell width of 10km, the species has an area of occupancy of 700 km^2, and a preliminary conservation assessment of Vulnerable is recorded based on IUCN criteria. Furthermore, the dry scrubland habitats where it is found are heavily disturbed, and often heavily grazed, especially in relatively densely populated Callejon de Huaylas, suggesting potential threats to this species from habitat alteration and disturbance. Few, if any, undisturbed populations have so far been found, although the species remains locally common at a few sites. The true extent of the distribution of *A. grandiflora* remains uncertain given the low number of collections.

Notes: Material of *A. grandiflora* was previously assigned to *C. trichocarpa* (Lewis, 1998). This new species is closely related to *A. trichocarpa*, and can appear almost identical on pressed herbarium sheets. Nevertheless, accessions of *A. grandiflora* from all known populations from both sides of the Cordillera Blanca form a robustly supported clade that is separate from the remaining accessions of *A. trichocarpa* (Fig. 4.1). Furthermore, *A. grandiflora* is geographically isolated from *A. trichocarpa* by the high Andes of southern Peru (Fig. 4.5). These geographically isolated, and phylogenetically and phenotypically distinct clades appear to bear the hallmarks of a significant history as independent evolutionary lineages, or independently evolving metapopulations (sensu Pennington & al., 2011), amply justifying recognition of *A. grandiflora* as a distinct species.

In addition to larger floral parts (but note that flower size can be affected by stress, with the largest flowers found in the least disturbed habitats, often with an abundant presence of cacti and other succulents, whereas in localities subjected to grazing, flowers tend to be smaller, as in accessions *CEH 3041 (K)* and *CEH 3047 (K)*), and fewer pairs of pinna per leaf, we also note that *A. grandiflora* is consistently eglandular to sparsely glandular on the calyx and pedicel, whereas in *A. trichocarpa* this character is variable. It is also not uncommon to find plants of *A. grandiflora* with an orange corolla or all five petals streaked with red, whereas in *A. trichocarpa* the petals are always yellow, with red markings only on the standard petal (Fig. 4.6B-C, F-G). Both *A. trichocarpa* and *A. grandiflora* are easily distinguished from the other three species in the genus as their fruits are densely covered in gland-tipped dendritic trichomes that are up to 1 mm in length, whereas in *A. ancashiana*, *A. mimosifolia* and *A. celendiniana* these gland-tipped trichomes are less than 0.5 mm long.

3. Arquita ancashiana (Ulibarri) E.Gagnon, G.P.Lewis & C.E. Hughes, **comb. nov.** ≡ Caesalpinia ancashiana Ulibarri in Darwiniana 30: 231. 1991 – Holotype: PERU. Dept. Ancash, prov. Recuay, Distr. De Marca (Jarrer Jamanan), 9 Aug 1963, Gomez 94 (USM barcode 21670!, SI barcode 001808!). à

Description: Unarmed subshrub, up to c. 30 cm tall, young stems with shiny white or yellowish orange bark, glabrous. *Stipules* ovate-obovate, eglandular to sparsely glandular, caducous. *Leaves* bipinnate; stipules ovate-deltoid, foliaceous, 4.5 – 5.5 mm long, scarious, subpersistent; petiole 1.2 – 6 cm long, glabrous, very sparsely glandular, grooved along the upper edge; rachis lacking, leaf reduced to one opposite pair of pinnae plus a terminal pinna, a corona of gland-tipped, lanceolate-triangular appendages encircling the insertion of the three pinnae; leaflets in (4 –) 8 – 10 (– 11) opposite pairs, oblong to elliptic-obovate, apex rounded to shallowly emarginate, base asymmetric, terminal leaflets 4 – 10 × 2 – 4 mm, medians 7 – 14 × 2.5 – 4.5 mm, both surfaces glabrous, main vein prominent below, secondaries brochidodromous, obscure, most leaflets eglandular but a few of the proximal ones on each pinna of some leaves with a few sessile, discoid glands near the leaflet base, especially near the margin, occasionally over the blade surface, leaflet margin sometimes obscurely, shallowly crenulated; tiny gland-tipped stipel-like appendages at the base of each leaflet pulvinule. *Inflorescence* a 10 – 20 flowered terminal or axillary raceme, the rachis, pedicels and calyces very finely puberulous (glabrous to the naked eye); bracts ovate-lanceolate, acute, c. 3 mm long, caducous; pedicels (5 –) 8 – 10 (– 15) mm long, articulated c. 2.2 mm below calyx. *Calyx* lobes c. 7 mm long, margins either entire and eglandular or fimbriate and glandular, finely tomentulose on inner surface. *Corolla* orange-yellow; standard petal blade ovate, 10 × 6 mm (including a 2 mm claw), dorsal surface of blade densely stipitate-glandular with pixie-cup glands, claw lacking an appendage, a few hairs on the margin basally; upper lateral petals elliptic, c. 8.5 × 5.5 mm (including a 0.75 mm claw), blade eglandular, claw very sparsely pubescent, eglandular. Stamen filaments 7.5 – 9 mm long, basal third to half with transparent hairs, basal two-thirds to three quarters with stipitate, club-shaped glands. Ovary sparsely pubescent along upper margin, stipitate, club-shaped glands moderately dense over most of the surface, especially on the suture; style sparsely to moderately glandular; stigma a terminal fringed chamber. *Fruit* a thinly woody, dehiscent pod, 3.5 × 1.05 cm, sparsely puberulous, glabrescent, sparsely glandular with short-stalked glands, the hairs and glands most evident on the suture, 1 –3-seeded. (Fig. 4.6M-P)

Distribution and Habitat: *Arquita ancashiana* occurs disjunctly along the western Pacific slopes of the Andes from northern Peru and southern Ecuador (Fig. 4.5), on either side of the Amotape-Huancabamba Zone, the lowest depression in the Andes (Weigend, 2002; Weigend &

al., 2010). It typically grows in seasonally dry mid-elevation thorn scrub and secondary low montane scrub forest with other shrubby genera including *Calceolaria*, *Dodonaea*, *Aeschynomene*, *Dalea*, *Zapoteca caracasana*, *Salvia* and other Lamiaceae, numerous Asteraceae and scattered trees of *Schinus* and *Tara spinosa*. 1700 –2750 m.

Additional specimens examined: ECUADOR: Prov. Loja: dirt road to Montaña Tarapo, NE of Catacocha, (4°3′14″S, 79°35′28″ W), 15 Apr 1996, *Lewis & al. 2266* (K, MO, NY); Catacocha-Catamayo, km11, track to Montaña Tarapo NE of Catacocha, km 3 along track (4°3′14″S, 79°35′28.4″W), 8 Mar 1997, *Lewis & Lozano 3073* (K, MO, NY); Loja-Catamayo, km 7 at Villonaco, 30 km along track to Cera and Chantaco and onwards to La Toma (3°54′S, 79°20′W), 9 Mar 1997, *Lewis & Klitgaard 3083* (K, MO, NY); **Prov. Azuay:** Road Saraguro-Cuenca, 5 km N of Oña (3°25′S, 79°8′W), 17 Jan 1990, *Lewis & al. 3815* (K, MO, NY); **PERU: Depto. Ancash: Prov. Recuay:** road Pativilca-Conococha, 27 May 1970, *Lopez & al. 7614* (SI); Distrito de Marca, on side road to pueblo Marca, 6 km off the main road (10°6′32.4″S, 77°29′31.4″W), 1 May 2011, *Hughes & al. 3021* (K, MT, USM, Z); Distrito de Marca, on side road to pueblo Marca (10°6′54.3″S, 77°30′0.3″W), 1 May 2011, *Hughes & al. 3025* (K, MT, USM, Z); Distrito de Cajacay, Highway 14, from Pativilca towards Huaraz, 5 km past the village of Cajacay (10°8′42.6″S, 77°25′27.2″W), 2 May 2011, *Hughes & al. 3026* (K, MT, USM, Z); Distrito de Cajacay, Highway 14, from Pativilca towards Huaraz, 5 km past the village of Cajacay (10°8′41.6″S, 77°25′20.5″W), 2 May 2011, *Hughes & al. 3027* (K, MT, USM, Z); **Depto. Cajamarca: Prov. Contumazá**: Rio Contumazá, 25 May 1981, *Sagastegui 9893* (K, MO); Andaloy (San Benito – Yeton), 28 Mar 1985, *Sagastegui & al. 12544* (K, MO, NY); El Molino (Cascas-Contumazá), 17 Apr 1992, *Sagastegui & al. 14590* (K, MO); Alrededores de Comtumazá (salida a Chilete), 5 Ap 1996, *Sagastegui & al. 15869* (NY, USM); Distrito de Contumazá, road from Chilete to Contumazá (7°20′11.7″S, 78°48′25.3″W), 7 May 2011, *Hughes & al. 3065* (K, MT, USM, Z); Distrito de Contumazá, road from Contumazá to Cascas (7°25′28.6″S, 78°47′11.3″W), 7 May 2011, *Hughes & al. 3070* (K, MT, USM, Z); **Prov. San Miguel:** between Lives and Payac, 11 May 1977, *Sagastegui & al. 8785* (F, MO, NY, US, SI).

Phenology: Flowering January – May (also in August), fruiting March – May.

Conservation status: *Arquita ancashiana* is known from only a few disjunct localities in Peru and Ecuador, on the Western slopes of the Andean Cordillera. In Peru, we observed it to occur mainly in secondary vegetation, on roadside cuttings and occasionally in cultivated fields, suggesting that this species is more or less resilient. Nonetheless, given how this rare species seems to be isolated in a few disjunct localities, known populations should be closely monitored. It also may be that the species is more widespread along the Western slopes of the Andean Cordillera, but more fieldwork is needed to validate this possibility. Based on a GeoCAT (Bachman & al., 2011) analysis of the Area of Occupancy of this species with a 15 km cell width, the species is considered Near Threatened (NT) according to IUCN's red list criteria, and we believe this to be an appropriate preliminary assessment.

Notes: Named after the Department of Ancash, in Peru, where it was thought to be endemic, until collections were made in Ecuador by Lewis & al. in 1996-97. The species is most similar to *A. mimosifolia*, with which it shares an in-rolled standard petal dorsally covered with glandular trichomes. However, the leaves of *A. ancashiana* have only a single pair of pinnae plus a terminal pinna (as opposed to *A. mimosifolia* with 3 – 5(– 7) pairs of pinnae, plus a terminal pinna). All specimens from Peru have pedicels and calyces covered in gland-tipped trichomes, whereas specimens from Ecuador are eglandular.

4. Arquita mimosifolia (Griseb.) E.Gagnon, G.P.Lewis & C.E. Hughes, **comb. nov.** ≡ Caesalpinia mimosifolia Griseb., Pl. Lorentz: 80. 1874) (= in Abh. Königl. Ges. Wiss. Göttingen 19: 128. 1874) – Holotype: ARGENTINA. Prov. Catamarca: Cuesta de Chilca, Lorentz 515 (GOET!; isotype: CORD!, SI!).

Description: Unarmed shrub, 0.5 – 1.5 m, young stems red, glabrous, densely glandular with short-stipitate sticky glands, occasionally some parts finely puberulous, older stems glabrous and eglandular. *Leaves* bipinnate; stipules ± foliaceous, ovate to obovate, apex rounded to acute, 2.5 –4 × 1.5 – 2.5 mm, margin dentate-fimbriate, covered in short stipitate-glands, caducous; petiole (0.8 –)2.5 – 3.7 cm long, stipitate-glandular; rachis (0.9 –)2 – 5 cm long, short-stalked-glandular, slightly articulated at pinnae insertions; pinnae in 3 – 5 opposite pairs plus a terminal pinna. *Leaflets* in 6 – 12 opposite pairs per pinna, oblong-obovate to oblong-elliptic, slightly falcate, apex obtuse, the basal ones on each pinna deeply crenulate, the terminal leaflets 2.5 – 4.5 × 1 – 2 mm, median ones 3 – 8 × 1.25 – 2 mm, both surfaces glabrous; venation obscure, only the main vein visible on the lower surface (flush with leaflet surface), excentric, dividing the blade 2:1 or 1.5:1; leaflet margin variable, usually crenate with red glands in deep sulcate depressions (especially on proximal leaflets of each pinna), sometimes only glandular on one side or glands lacking and leaflet margin entire (especially on distal leafets of pinnae). *Inflorescence* a terminal or leaf-opposed, 5 – 21 cm long, c. 8 – 25-flowered raceme, rachis glabrous or obscurely puberulous, eglandular distally, stipitate-glandular proximally, sometimes densely so; bracts ovate or ovate-lanceolate, apiculate, 2.75 – 4 mm long, finely pubescent, stipitate-glandular, margin fimbriate; pedicels (7 –) 9 – 12 (– 15) mm long, finely pubescent or glabrous, stipitate-glandular, especially below calyx, articulated 1–1.5 mm below calyx. *Calyx* lobes 7 – 9 mm long, sparsely to densely puberulous, sparsely glandular, the lower lobe ± cucullate, obscurely fimbriate at apex. *Corolla* yellow or orange; standard petal blade obovate, 10.5 – 11.5 × 4.5 mm, basal half inrolled, claw pubescent; upper lateral petals obovate, 11 × 5 – 8.5 mm, lower laterals obovate, 11 × 4.5 – 6.5 mm, laterals with claw sparsely pubescent. Stamen filaments red, spreading pubescent on basal third to two-thirds, sometimes very sparsely so on upper third; anthers 0.75 – 1.5 × 0.6 mm. Ovary glabrous or almost so, densely glandular with sessile and/or short-stipitate glands; style c. 9 mm long, basal half with short-stipitate glands; stigma a terminal, fringed chamber, somewhat curved upwards. *Pod* coarsely chartaceous, elastically dehiscent from apex, falcate in upper half, 3 – 4.7 × 0.7 – 0.9 cm, glabrous, a few scattered glands near base but these rub off with age, 3 – 5(– 6)-seeded. Seeds obliquely ovate, 5 × 4.5 × 0.75 mm, dark brown, or orange mottled dark brown, shiny. (Fig. 4.6I-K)

Distribution and Habitat: Found in north-western Argentina, from the mountainous zone of the Sierras of San Luis and Cordoba, extending through those of San Juan, La Rioja, Catamarca, Tucumán, Salta and Jujuy (Fig. 4.5), 1000 – 1950 m. Typically grows on sub-humid, steep slopes, either with rocky, gravelly or loose, sandy soils, with Cactaceae and other woody and shrubby species, such as *Acacia furcatispina, A. praecox, Aspidosperma*, *Bulnesia*, *Condalia* *microphylla, Ceiba, Celtis, Larrea divaricata, Prosopis chilensis, P. alba, Ramorinoa girolae*, and *Schinopsis haenkaena*.

Additional specimens examined: ARGENTINA: PROV. Catamarca: Balcones (S. Ambato), Feb 1941, *Parodi 14059* (SI); **Depto. Ambato**: La Juntas, Inmediaciones del Rio de las Trancas, 17 Dec 1971, *Ariza 2687* (CORD); Los Castillos, base W de la Sierra de Graciana, 21 Mar 1995, *Saravia Toledo & al. 12746* (CTES); **Depto. Andalgalá:** Cuesta de Muschaca, Nov 1872-1873, *Schickendantz 65* (CORD); Más arriba de la Aguada, cerca del Fuerte de Andalgalá, Jan 1876*, Schickendantz 156* (CORD, K); **Depto. Belén:** Belén, 27 Feb 1929, *Cabrera 1140* (NY, SI); La Puerta de San José to La Estancia. Mar 1939, *Schreiter 68526* (F, K, SI); Quebrada de Belén, 26 Jan 1974, *Ulibarri 588* (CORD, CTES); Los Nacimientos. 8 Feb 1992, *Lutz 147* (CTES, NY); 7 km W of Andalgalá, at the edge of a wash, 22 Mar 1973, *Cantino 759* (ARIZ); **Depto. Capayán**: Sierra de Ambato (Falda E.): Subiendo por la cuesta entre Miraflores y Los Angeles, 27 Nov 1965, *Hunziker et al. 18325* (CORD); Cuesta de la Cebila, 2 Mar 1985, *Kiesling et al. 5922* (NY, SI); **Depto. Capital**: La Brea, Jun 1910, *Castillon 1589* (SI); **Dpto. Paclín:** Cuesta del Totoral. 26 Sep 1995, *Saravia Toledo 13633* (CTES); **Depto. Pomán:** On a steep rocky slope along the road between Pomán and Colana, 2 Feb 1973, *Cantino 607* (ARIZ, CORD); **Depto. Tinogasta**: 79 km on Ruta 11 from Famatina (La Rioja) towards Tinogasta (Catamarca), 18 km N of turnoff to El Poterrillo, i.e. just near turnoff to Costa de Reyes (28°16′31″S, 67°38′89″W), 17 Feb 1994, *Leuenberger & al. 4229* (CORD); **Depto. Valle Viejo:** Sierra de Ancasti: Cuesta del Portezuelo, 20 Dec 1963, *Ragonese & Piccinini 9816* (CTES); Valle Viejo, Cuesta del Porte Zuelo, El Mirador (28°28′56″S, 65°37′14″W), 3 Mar 2007, *Särkinen et al. 2006* (K); **Prov. Salta:** La Candelaria, Muguillo, Jan 1933, *Schreiter 9224* (SI); **Depto. Chicoana**: Ruta Prov. 33, de Pulares a San Fdo. De Escoipe (25°9′54″S, 65°44′1″W), 15 Feb 2007, *Zuloaga & al. 9387* (CTES, SI); Ruta 33, de Salta a Cachi, antes del parque nacional de los Cardónes, entre el km 34 y 36, un poco antes de llegar a San Frederico del Obisco, (25°10′38.″S, 65°44′28.01″W), 28 Feb 2012, *Gagnon & al. EG211* (CTES, K, MT); **Depto. Guachipas :** Alemania. 9 Nov 1978, *Cabrera & al. 29720* (MO, SI); Perilago de Cabra Coral, 15 Jan 1989, *Saravia Toledo 1818* (CTES); **Depto. La Viña**: 20 km E de Coronel Moldes, 6 Jan 1974, *Krapovickas & Cristobal 24524* (CTES); Ruta 68, proxima del km 85, al Norte del cruce del puente a Alemania. Borde de camino (25°37′8.63″S, 65°36′42.66″W), 15 Feb 2012, *Gagnon & al. EG203* (CTES, K, MT); **Depto. Metán**: Sierra de Metán, Proyecto de Prospeccion Minera « Leon », Finca Cachari, 18-20 km al W de Lumbreras (25°12′57.3″S, 65°06′44″W). 10 Apr 2006, *Tolaba & al. 4099* (CTES); **Prov. La Rioja:** Cuesta de la Puerta de Piedra (Cuesta de Ligu), Sierra Velasco, 8-11 Jan 1879, *Hieronymus & Nierdelein 82* (CORD); Quebrada Totoral, 1895-1896*, Bodenbender 8966* (CORD); Alrededores de La Rioja, 1 Mar 1941, *Covas 1121* (NY); **Depto. Capital:** Sierra de Velasco : Ruta 75, entre Sanagasta (=V. Bustos) y Agua Blanca, 29 Jan 1965, *Hunziker & Cocucci 18151* (CORD); Faldeo oriental de la Sierra de Velasco frente a la cuidad de La Rioja, entre Villa Luisa y Las Canas, rumbo a El Cantadero, a 2 km del primero, 24 Jan 1997, *Biurrun & Pagliari 4698* (CORD, CTES); Along Ruta Nacional 75 ca. 18 km W of Sanagasta at entrance to tunnel, between Dique Los Sauces and Las Perditas, (29°33′12″S, 66°58′15″W). *Chumley et al. 7387* (TEX); **Depto. Chilecito:** Sierra de Famatina, Cuesta de Miranda, 20 Mar 1950, *Hunziker & Caso 4339* (CORD); Ruta Nac. No 40, entre Chilecito, Famatina, a 500 m del Rio Capayán, 13 Mar 1989, *Aguite 689* (CTES); **Depto. Coronel Felipe Varela:** Cuesta de la Trancas, 12 Jan 1976, *Cabrera & al. 27108* (CTES, SI); **Depto. Famatina:** Las Gredas, 22 February 1907, *Kurtz 14413* (CORD); Guanchin. 20 Dec 1928, *Venturi 7845* (MO, NY, SI); Famatina, 9 Jan 1949, *Krapovickas & Hunziker 5070* (CORD); Angulos, 3 Feb 1954, *Arehangelsky s.n.* (CTES); **Depto. General Lavalle:** Cuesta entre Las Trancas y Tambillo, 18 January 1906, *Kurtz 13202a* (CORD); Cuesta de Miranda, 2 Feb 1907, *Kurtz 14309* (CORD); **Depto. General Ocampo:** Ruta Prov. No 31, entre Catuna y Malanzán, entrando por Casangate, unos 5 km al norte, 26 May 1990, *Biurrun & Leiva 5348* (SI); **Depto. General San Martín:** Minas. 12 Mar 1907, *Stuckert 17176* (CORD); La Diana, 1 Mar 1908, *Stuckert 18642* (CORD); **Depto. General Sarmiento:** Valle del Rio Bonete, entre Junta y Cienaguita, 5 Mar 1950, *Hunziker & Caso 4219*, (CORD); La Rioja: Cienaguita, Quebrada rio Bonete, 9 Feb 1947, *Hunziker 2232* (CORD); **Depto. Independencia:** La Rioja, Sierra de Vilgo: Cuesta de Amanao, Feb 1896, *Bodenbender 9038* (CORD); Ruta Nac. 150, entre los Baldecitos (SJ) y La Torre, a 3 km de esta, 8 Nov 1995, *Biurrun & al. 4193* (MO); **Depto. Sanagasta:** Camino al dique Los Sauces (entre La Rioja y Villa Sanagasta), 17 Feb 1944, *Hunziker 4857* (CORD, SI); **Prov. Córdoba:** En la sierra cerca de Cruz del Eje, 11 Mar 1877, *Hieronymus 684* (CORD, F [photo], NY); Entre Quilpo y Rio Pinto, 30 Jan 1883, *Kurtz 273* (CORD); **Depto. Cruz del Eje**: Pichana, 20 Nov 1904, *Stuckert 14487* (CORD); **Depto. Punilla:** Capilla del Monte (Sierra Chica), 21 Dec 1889, *Kurtz 6645* (CORD, NY); Sierra Chica:

Cerro Uritorco (frente a Capilla del Monte), 19 November 1950, *Hunziker 8517* (CORD); Los Terrones, cerca de Capilla del Monte, 9 Apr 1991, *Coccuci & Vogel 486* (CORD); **Depto. Ischilín:** Copacabana, siguiendo el camino hacia el SO del pueblo, 28 Nov 1956, *Sayago 2601* (MO); Sierra de Copacabana, Faldeos del NE. 5 Feb 1960, *Hunziker 14798* (CORD); Copacabana, 15 Jan 1986, *Diaz 6892* (CTES); **Depto. Pocho:** Cerro Volcan Velis, Cañada de Sales, 2 May 1968, *Luti 4437* (CORD); **Depto. Santa María:** Alrededores del Lago San Roque, 5 Nov 1949, *Hunziker 7918* (CORD); **Prov. San Juan: Depto. Angaco:** sierra de Pie de Palo: subiendo por el camino al Mogote Los Corralitos, en la Quebrada del Molle, 19/20 Dec 1980, *Hunziker & al. 23831* (CORD); Sierra de Pie de Palo, Filo, Mogote de los Corralitos, 18 Feb 1986, *Kiesling & al. 6330* (CTES); **Depto. Jachál:** Rio de Los Piojos, 9 Dec 1957, *Leal-Roig 18873* (MO, SI); **Depto.Valle Fértil:** Los Bretes, 28 Nov 1984, *Kiesling & al. 4990* (NY, SI); de Sa. de Elizondo a Sa. De Chavez, 27 January 1987, *Kiesling & Meglioli 6622* (SI); Sierra de Elizondo, 16 Dec 1987, *Mulgura & al. 786* (SI); Sierra de Valle Fertil, subiendo por la quebrada de USNO, entre la Yerba Buena y la Mina Loma Blanco, 4 Dec 1991, *Biurrun 3633* (CORD); 5 km de Los Bretes en dirreción a San A. del Valle Fértil (30°45′S 67°27′W), 9 Mar 1998, *Fortunato & al. 5932* (CTES); N de Balde del Rosario, 8 Mar 1998, *Kiesling 8959* (SI); **Prov. San Luís:** without exact locality, 6 Nov 1940, *Burkart 10718* (K, MO); **Depto. Ayacucho:** entre San Francisco y Balde de Retamo, 28 Dec 1885, *Kurtz 3240* (CORD); **Depto. Belgrano:** Sierra de las Quijadas: Quebrada del Alambre, al Oeste de San Antonio (Ruta Nac. 147), 6 Mar 1963, *Hunziker & Coccuci* 16378 (MO, K [photo]); La Calera, 8 km hasta la cantera de extraccion de cemento, 10 Oct 1992, *Vitto & al. 7467* (CTES); **Prov. Tucumán: Depto. Burruyacú:** Sierra Nogalito, km. 4, 2 Feb 1963, *Krapovickas & Legname 10893* (CTES).

Phenology: Flowering November – March, fruiting January – March.

Vernacular name: “Pishcalilla” (given in Burkart (1936), fide Spegazzini).

Conservation status: *Arquita mimosifolia* has a conservation status of Least Concern (LC); it is the most widespread and abundant species of *Arquita* (Fig. 4.5), and is known from seven provinces in Argentina. Its distribution closely matches the lower-elevation, southern ranges of the Andes, from the provinces of Salta to San Juan.

Notes: There is robust molecular evidence to suggest that *A. mimosifolia* is closely related to *A. trichocarpa* and *A. grandiflora*, but its relationship with these species remain unresolved (Fig. 4.1). *Arquita mimosifolia* is the most southerly species of *Arquita*. Although its distribution closely mirrors that of *A. trichocarpa,* with populations sometimes separated by only a few kilometres (e.g. Dept. Andalgalá, Prov. Catamarca, Depts. Cachi and Chicoana, Prov. Salta), it grows at consistently lower elevations (below 2000 m), and there are no reports of *A. mimosifolia* growing in true sympatry with *A. trichocarpa,* or of hybridisation between the two species. *Arquita mimosifolia* is readily distinguished morphologically from *A. trichocarpa* and *A. grandiflora*: the mature pods lack dendritic trichomes and are only occasionally and sparsely covered with sessile gland-tipped trichomes, the standard petal claw is inrolled and the leaf rachises are longer (2 – 5 (– 7) cm). While *A. mimosifolia* was previously recorded from Bolivia, this was based on misidentified specimens of *A. trichocarpa*.

5. *Arquita trichocarpa* (Griseb.) E.Gagnon, G.P.Lewis & C .E. Hughes, **comb. nov.** ≡ Caesalpinia trichocarpa Griseb., Symb. Fl. Argent.: 112. 1879 (= in Abh. Königl. Ges. Wiss. Göttingen 24: 112. 1879) – Holotype: ARGENTINA. Prov. Jujuy: San José de Tilcara, May 1873, Lorentz & Hieronymus 848 (fide Burkart in Revista Argent. Agron. 3(2): 92. 1936) (GOET!; isotypes: B† [photos in: F, neg. 1791!, K!, MO barcode MO-1731776!, NY neg. 1791!], CORD!, SI!).

Description: Unarmed, glandular, prostrate to erect shrub, from 0.3 – 2.5 m. Young stems and fertile new growth dark reddish maroon, covered in gland-tipped trichomes. *Stipules* orbicular to ovate, chartaceous (papyraceous), margin fimbriate, covered in glandular trichomes and white hairs, c. 3mm long, caducous. *Leaves* bipinnate, pinnae (1 –) 2 – 5 pairs plus a terminal pinna; petiole (0.3 –) 0.6 – 2.6 cm long, rachis 0.5 – 2.8 cm long; both petiole and rachis glandular, dark maroon, very finely puberulent. *Leaflets* (4 –) 5 – 7 opposite pairs per pinna, oblong-obovate, (2.5 –) 3 – 6 (– 7) × 1 – 2 (– 3.5) mm, puberulent to glabrous. Primary vein visible on underside of leaflets, excentric, margins crenulate with sunken glands in the concave indentations, either all leaflets equally glandular or the leaflets closer to the petiole of each pinna generally more glandular than the distal leaflets, and also occasionally lower surface of leaflet blade with dark sessile glands. *Inflorescence* a lax, leaf-opposed, 9 – 20-flowered, pedunculate, indeterminate raceme, with only one to two flowers opening at the same time on any one inflorescence, rachis finely puberulent, sometimes covered in glandular trichomes, (5 –) 7 – 11 cm long. Floral bracts 4 – 5 mm long, ovate-lanceolate with an acute tip, papery in appearance, tinged red, margin fimbriate, glandular or sometimes eglandular, puberulent, caducous. *Flower buds and pedicels* puberulous, pedicels vary from eglandular to densely glandular, 5– 10 mm long, articulated c. 1.0 – 2.5 mm below the calyx. *Calyx* carmine red, puberulent, hypanthium and sepals eglandular to densely glandular, lower sepal somewhat cucullate and overlapping all other sepals in bud, the margin always fimbriate and glandular, margins of the four other sepals fimbriate and glandular or entire and eglandular, oblong-lanceolate, overlapping margins often thinner and more papery in appearance, 6 – 10 × 2.5 – 4 mm. *Corolla* yellow, the standard petal with red veins, standard oblong-obovate (oblanceolate), (7 –) 8– 13 × (4 –) 5 – 7 (– 8) mm, the claw with a tuft of white hairs, and the dorsal surface very occasionally covered with gland-tipped trichomes. Upper lateral petals 7 – 12.5 × (4 –) 5 – 7.5 mm, pubescent on the side of the claws. Lower lateral petals 7 – 12 (– 13) × 4 – 7 mm, claws glabrous. *Stamen filaments* pale green or red, 7 – 10 mm long, pubescent with white trichomes on the lower third, anthers 1.5 – 1.8(– 2.1) mm long. Ovary with a dense indumentum of gland-tipped plumose trichomes up to the base of the style, stigma with a slightly bulbous, fringed chamber. *Pod* flat, lunate-falcate, 2 – 3 × 1 cm, subtended by a persistent calyx ring, young unripe pod valves covered in red-magenta plumose gland-tipped trichomes, becoming brown, chartaceous, and elastically dehiscent, the valves twisting. Seeds laterally compressed, dark brown streaked black, ovate-orbicular, c. 6.5 × 4.5 × 0.5 mm.

a. var. ***trichocarpa***

Description: Leaf petiole 3.5–10.5 mm long, pinnae in 2 to 5 pairs plus a terminal pinnae. Inflorescence a raceme with yellow flowers, and all five sepals have glandular trichomes along the margin.

Distribution and Habitat: Growing in inter-Andean dry valleys of the Piedmont region in Argentina (Fig. 4.5). On dry slopes of rocky or sandy soil, between (1500 –) 2300 – 3100 m, amidst open, arid scrublands, dominated by spiny shrubs and small trees (such as *Senna* sp. *Hoffmannseggia pumilio,* and *Parkinsonia aculeata)* and various cacti.

Additional specimens examined: ARGENTINA: Prov. Jujuy: Depto. Tilcara: Tilcara, Feb 1936, *Schulz 1709* (SI, CTES)*;* Tilcara (Cerro pena alta), 9 Feb 1927, *Venturi 4881* (F, GH, NY, SI, US); no precise locality, 19 Feb 1927, *Venturi 7485* (US); no precise locality, 10 Mar 1935, *Schreiter 68567* (SI); Alfarsita, nr. Tilcara, 9 Feb 1939, *Balls B6058* (E, F, K, US); Tilcara, 26 Jan 1943, *Cabrera 7629* (SI); Tilcara, 2 Apr 1943, *Zabala 556* (CORD, SI); without locality, 2 Mar 1953, *Hunziker & Caso 6226* (CTES, SI); Maimará, en *cono de deyección*, 8 Jan 1971, *Krapovickas & Cristobal 17592* (CTES); Laderas al N de Tilcara, 24 Jan 1971, *Boelcke 7408* (MO); Quebrada de Huasamayo, 13 Feb 1980, *Cabrera et al. 31594* (SI); Maimará, frente a la Paleta de Pintor, por ruta 9, 2 May 1992, *Fortunato et al. 3803* (CTES); Entre Maimará y Tilcara, 28 Mar 1993, *Deginani & Cialdella 275* (SI); Route 9 from San Salvador de Jujuy to Tilcara, Maimará, just below cemetery on outskirts of town (c. 23°36′S, 65°25′W), 15 Oct 1994, *Lewis & Klitgaard 2168* (K); Around the city of Tilcara, rocky hillsides, ca. 700 m above city, 27 Feb 1973, *Dillon & Rodriguez 586* (MO); 2 km S de Tilcara, ruta 9 (23° 18′54″S 65°24′30″W), 27 Feb 2003, *Marazzi et al. BM126* (CTES); 10 km al S de Tilcara por ruta Nac. 9 en direcc. a Jujuy (24°20′S, 64°35′W), 28 Mar 2003, *Fortunato et al. 8295* (CTES); Huacalera, Finca Nacetti al otro lado del Rio Grande (23°26′40″S, 65°20′34″W), 10 Feb 2007, *Zuloaga & al. 9122* (CTES, SI); Ruta 9, N de Huacalera – Uquia, entre el km 1803 y 1804 (23°24′36.76″S, 65°20′59.96″W), 16 Feb 2012, *Gagnon & al. EG204* (CTES, K, MT); 2 km S de Tilcara, Alrededores de Maimará, ruta 9 (23°35′59.03″S, 65°24′33.29″W), 16 Feb 2012, *Gagnon & al. EG205* (CTES, K, MT); **Depto. Humahuaca:** Usquia. 20 Feb 1901, *Claren 11725* (CORD); Humahuaca, ceros, 29 Feb 1940, *Burkart & Troncoso 11935* (K, SI); 2 km al Oeste de Humahuaca, camino a Cianzo, 25 Feb 1999, *Saravia Toledo 15118* (CTES); 4.5 km, al este de Humahuaca, camino a Cianzo, 17 Mar 1999, *Saravia Toledo & Day 15185* (CTES, NY); Quebrada Colorada, 9 km North of Huacalera, 10 Feb 1991, *Clarke 109-03* (MO); 1 km al W de San Jose por la cuenca del rio Yacoraite, 20 Nov 2001, *Fortunato & al. 7421* (MO); **Depto. Tumbaya:** Volcan, 19 Feb 1926, *Venturi 6615* (US); Route 52, 9 km W of Pumamarca, 1 km W of Quisquiri, 15 Oct 1994, *Lewis & Klitgaard 2166* (K); **Prov. Salta:** Between Cachi and Cafayate, 3 Mar 1996, *Planchuelo 993* (US); **Depto. Cachi:** Cachipampa, Mar 1951, *Martinez*

Corveto 6254 (CTES); Cachipampa: recta del Tin Tin, 7 Mar 1989, *Cocucci 384* (CORD); La Paya, 4 km al W de Ruta Nac. 40, y 8 km al S de Cachi, 30 Mar 2001, *Novara 11535* (CTES); Quebrada Las Arcas, pasando Cachi Adentro, 15 km al NNW de Cachi, 3 km antes de la escuela de Las Arcas, laderas al sur de la quebrada (25°2′56″S, 65°12′35″W), 29 Mar 2003, *Novara & al. 11943* (CTES); Cachi Adentro: along the road to the village of Las Pailas (25°04′0.7″S, 66°11′57.8″W), 28 Feb 2012, *Gagnon & Atchison EG216* (CTES, K, MT); **Depto. Cafayate:** Cafayate. 22 Feb 1951, *Hayward 2155* (US); Cafayate at Yacochuyo (26°2.541′S, 66°1.29′W), 5 Feb 2001, *Simpson 5-II-00-1* (MO); **Depto. La Poma:** Road 40, km 4528 road from Cachi to La Poma,Valley Calchaquies, just before arriving at Pueblo Viejo (24°55′7.7″S, 66°8′32″W), 28 Feb 2012, *Gagnon & Atchison EG213* (CTES, K, MT); **Depto. Molinos:** Luracatao, Lag. Brealito, 9 Apr 1982, *Novara 2584* (CORD, MO, K); Road to Laguna Brealita/Luracatoa (entrance on road 40 from Cachi to Molinos, about 15 km before Molinos; 25°19′42.9″S, 66°18′41.2″W), 29 Feb 2012, *Gagnon & Atchison EG218* (CTES, K, MT); **Depto. Rosario de Lerma:** Camino a Nevada Castillo, 9 Jan 1929, *Venturi 8542* (US); **Prov. Tucumán: Depto. Tafí del Valle**: Rio Managua, 1 May 1926, *Venturi 4275* (NY, SI); El Molle. 3 Feb 1933, *Burkart 5357* (GH, K, SI); Valle de Amaicha, 3 Feb 1933, *Burkart 5358* (GH, K); Ruta 307, Amaicha del Valle, N de El Molle (26°38′6.66″S, 65°49′20.2″W), 14 Feb 2012*, Gagnon et al. EG200* (CTES, K, MT); **Prov. Catamarca: Depto. Andalgalá:** Canyon del Chenal, 20 Apr 1917, *Jörgensen 1745* (MO, SI, US); **Depto. Santa María:** Cerro Colorado. 10 Apr 1948, *Reales 1209* (CTES); Los Quesos. 29 Feb 1949, *Reales 1739a* (CTES); Los Pabellones, 16 Mar 1949, *Reales 1934* (CTES);

b. var. ***boliviana*** E. E.Gagnon, C.E.Hughes & G.P.Lewis, **var. nov.** – Holotype: BOLIVIA. Dept. La Paz: prov. Murillo, 1 km S of Mecapaca, valley of the Rio La Paz (16°40′11″ S, 68°00′54″ W), 18 Jan 2004, Hughes & al. 2442 (K barcode K000724169!; isotypes: FHO! [Brahms specimen ID: 99088], LPB!).

   = Caesalpinia fisheriana Rusby in Mem. Torrey Bot. Club 3(3): 23. 1893 – Holotype: BOLIVIA. 1891, Bang 756 (in part, perhaps distributed as 756a) (NY barcodes 00003563! and 00022748!; isotypes: E barcode E00296838!, F!, GH barcode 00059887!, K barcode K000264569!, SI!).

= *Caesalpinia rosulata* Rusby in Mem. Torrey Bot. Club 3(3): 23. 1893 – Holotype: Bolivia. 1891, Bang 756 (in part) (NY barcode 00431801!; isotypes: F!, GH barcode 00059891, K barcode K000264569, SI barcode 001818).

Diagnosis: Variety *boliviana* can be distinguished from var. *trichocarpa* by the combination of longer petioles (8 – 35mm vs. 3.5 – 10.5 mm) and the presence of glandular trichomes on the margins of the sepals only on the lower, cucullate sepal. In addition the two varieties each form robustly supported reciprocally monophyletic clades subtended by long branches (Fig. 4.1) and occupy allopatric ranges in Bolivia and Argentina.

Description: Petiole 8– 35 mm long, pinnae in 1 to 4 pairs plus a terminal pinna. Inflorescence a raceme with yellow flowers, and only the lower cucullate sepal has glandular trichomes along the margin.

Distribution and Habitat: Growing in inter-Andean dry valleys of Bolivia (Fig. 4.5), on steep, open slopes with rocky or sandy soil, or sometimes also in thin shale. Typically found in xerophitic habitats, such as dry thorn scrub, growing next to trees and shrubs such as *Schinus sp.*, *Tara spinosa*, *Tecoma sp.*, *Dodonaea sp.*, *Prosopis sp.*, and *Adesmia sp.,* as well as shrubby Asteraceae and Cactaceae. 2300 – 3000 m.

Additional specimens examined : BOLIVIA. La Granja. Dec 1923, *Brother Julio 152* (US); **Depto. La Paz, Prov. Loayza**: Valle de Luribay (17°4′S, 67°40′W), 5 April 1994, *Beck 114PG94* (K); Camino de Tacobamba a Caracato, 28 February 2003, *Ortuño 244* (K); **Prov. Murillo :** La Paz to Calacoto, Mecapaca, 3 February 1980, *Beck 3014* (MOL, NY); 2 km SE of Mecapaca (16°40′S, 68°1′W), 24 Feb 1980, *Solomon 5090* (MO); La Florida, Stadtteil La Florida, Kurz nach dem Stadtrand am Beginn des Strasse Richtung Mecapaca, Trockental, Veg.-Aufn. 702, 4 Mar 1982*, Feueurer & Menhofer 10140a* (K); 2 km E (below) Mecapaca (16°40′S, 68°1′W). 28 Mar 1982, *Solomon 7412* (MO); Hacienda Huajchilla, 18 km SE of La Paz (16°38′S, 68°3′W), 14 Feb 1987, *Solomon & Nee 16058* (K, MO); Rio La Paz (‘Rio Abajo’) on both sides below Mecapaca, 8 January 1995, *Wood 9151* (K); 1 km S of Mecapaca, valley of the Rio La Paz (16°40′11″S, 68°0′54″W), 18 Jan 2004, *Hughes & al. 2442* (K); **Depto. Potosi:** Rencillo nr. Tupiza, 28 Feb 1904, *Fiebrig 3112* (E, K); *Fiebrig 3112a* (BM, K, M); **Prov. José**

Maria Linares: valle de Oronkhota, 4 Apr 1993, *Torrico & Peca 306* (K); **Depto. Tarija: Prov. Eustaquio Méndez:** Condor, nr. Tarija, 6 Feb 1904, *Fiebrig 2983* (E); Condor-Huasi. 6 Feb 1904, *Fiebrig 2983* (P); *Fiebrig 2983a* (M); Tojo. 12 Feb 1960, *Meyer & al. 26621* (CTES); Tojo, sobre quebrada del Río Honda (21°48′S 64°18′W), 8 Nov 1997, *Beck 23114* (SI); **Prov. José María Avilés:** subiendo de Tojo a Yunchara (21°49′S, 65°17′W), 17 Apr 2000, *Beck & Paniagua 27049* (K, MO); **Depto. Chuquisaca: Prov. Nor Cinti**: Camargo, nr. Tarija, 13 Feb 1904, *Fiebrig 2981* (BM, K); **Prov. Oropeza:** In the valley below Yotala towards Nucchu. 29 Oct 1994, *Wood 8742* (K); **Prov. Sud Cinti**: c. 2 km before Impora on road from Tupiza to Las Carreras. 5 Dec 1967, *Vuilleumier 409* (NY); Tajsara Kette, W-Exp, Neigung 15 degree, Strauch. 22 Jan 1982, *Gerold 39* (NY); c. 5km S. of Villa Abecia towards El Puente. 28 Feb 1995, *Wood 9556* (K); **Depto. Cochabamba: Prov. Capinota:** Playa ancha, c. 3 km N of Capinota towards Cochabamba, 4 Mar 2002, *Wood 17692* (K); Comunidad de Apillapampa (17°50.441′S 66°14.709′), 19 Feb 2003, *Thomas ET244* (K); **Prov. Esteban Arce:** Puento Caine, al borde del camino Torotoro – Anzaldo, en la curva pared rocosa roja (17°52′95″S, 65°54′21″W), 28 Feb 2003, *Wood & al. 19278* (K); Camino Anzaldo hacia Torotoro, en la bajada hacia Rio Caine antes de la zona de roca roja (17°40′S 65°56′W), 5 Jan 2005, *Wood & al. 21342* (K).

Phenology: Flowering and fruiting from January – May, as well as in October and November.

Conservation status: *Arquita trichocarpa* is much more common and widespread than the closely related species *A. grandiflora*. It has a disjunct distribution across the dry valleys of the Bolivian Andes (Depts. La Paz, Potosi, Tarija, Cochabamba and Chuquisaca), to Argentina (Provs. Salta, Jujuy, Tucumán and Catamarca). As we observed numerous healthy populations during fieldwork in Argentina, we consider this species to belong to the category of Least Concern according to the IUCN red list criteria. However, we did notice that the species is sensitive to grazing and some populations appear to be in decline, particularly in the department of Tafí del Valle, in the province of Tucumán.

Vernacular name: The common name of *A. trichocarpa* in Argentina is “Arquita” (Ulibarri, 1996).

Notes: *Arquita trichocarpa* is closely related to the newly described *A. grandiflora*, but has smaller flower parts and a tendency to have a larger number of pinnae per leaf. Furthermore, flowers are always yellow with red markings only on the standard petal, a character that is more variable in *A. grandiflora*. The species is often confused with *A. mimosifolia*, but that species is easily distinguished by the reduced number of pinnae per leaf, the inrolled standard petal, and the almost eglandular fruits. *Arquita trichocarpa* has also often been confused with *Hoffmannseggia pumilio* (Griseb.) B.B. Simpson, a shrub with similar pods, also covered in plumose trichomes. *Arquita trichocarpa* grows together with *H. pumilio*, but the latter can be easily distinguished by its smaller stature (up to 20 cm in height) and more pronounced decumbent, tortuous habit, short-stalked glands along leaflet margins versus a crenulated leaflet margin with sunken sessile glands in *A. trichocarpa,* and sepals persistent on mature fruit which are typical of the genus *Hoffmannseggia*, and unlike the caducous sepals of *A. trichocarpa*.

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4.8 Authors contribution

EG, AB, CEH and GPL were involved in study conception and design; EG and CEH collected herbarium and field samples for analysis; EG generated and assembled all the data, for which she was also responsible for analysing and interpreting; EG drafted the manuscript, and critical revision was provided by AB, CEH and GPL; EG also wrote the key and taxonomic revision of the genus and species, which were all critically revised by GPL and CEH.

Figure 4.1 Bayesian phylogeny of Arquita and allied genera of the Caesalpinia Group. Phylogeny based on a combined matrix of *rps16*, *trnD-trnT*, *ycf6-psbmR* and *ITS*. Branches with maximum support for Bayesian, Maximum Likelihood and parsimony analyses are in bold. Posterior probabilities are indicated above branches, in bold. Bootstrap support for the maximum likelihood and parsimony analyses are indicated below, separated by a slash. Absence of branch support (--) indicate that the nodes are not supported in either the parsimony, Maximum Likelihood or Bayesian consensus topologies.

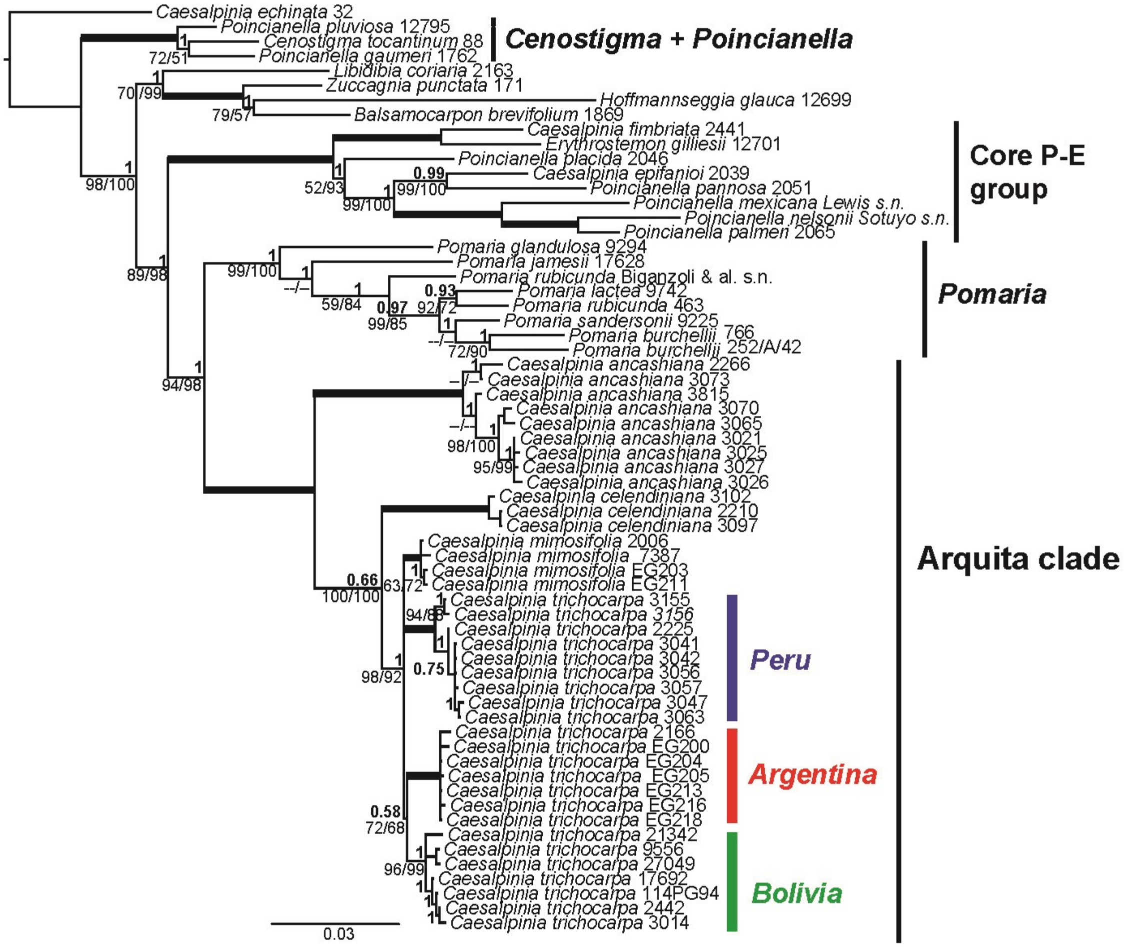

Figure 4.2 Morphometric analysis of the *Caesalpinia trichocarpa* alliance. Dendrograms of Ward's minimum variance clustering on Gower's distance matrices for flower, leaf, and combined morphological traits. Terminal names are composed of a prefix indicating country of origin (A- Argentina, B- Bolivia, P- Peru), followed by the collection number of the specimen and herbarium where it is deposited, and are coloured according to region (Red- Argentina, Green- Bolivia, Blue- Peru).

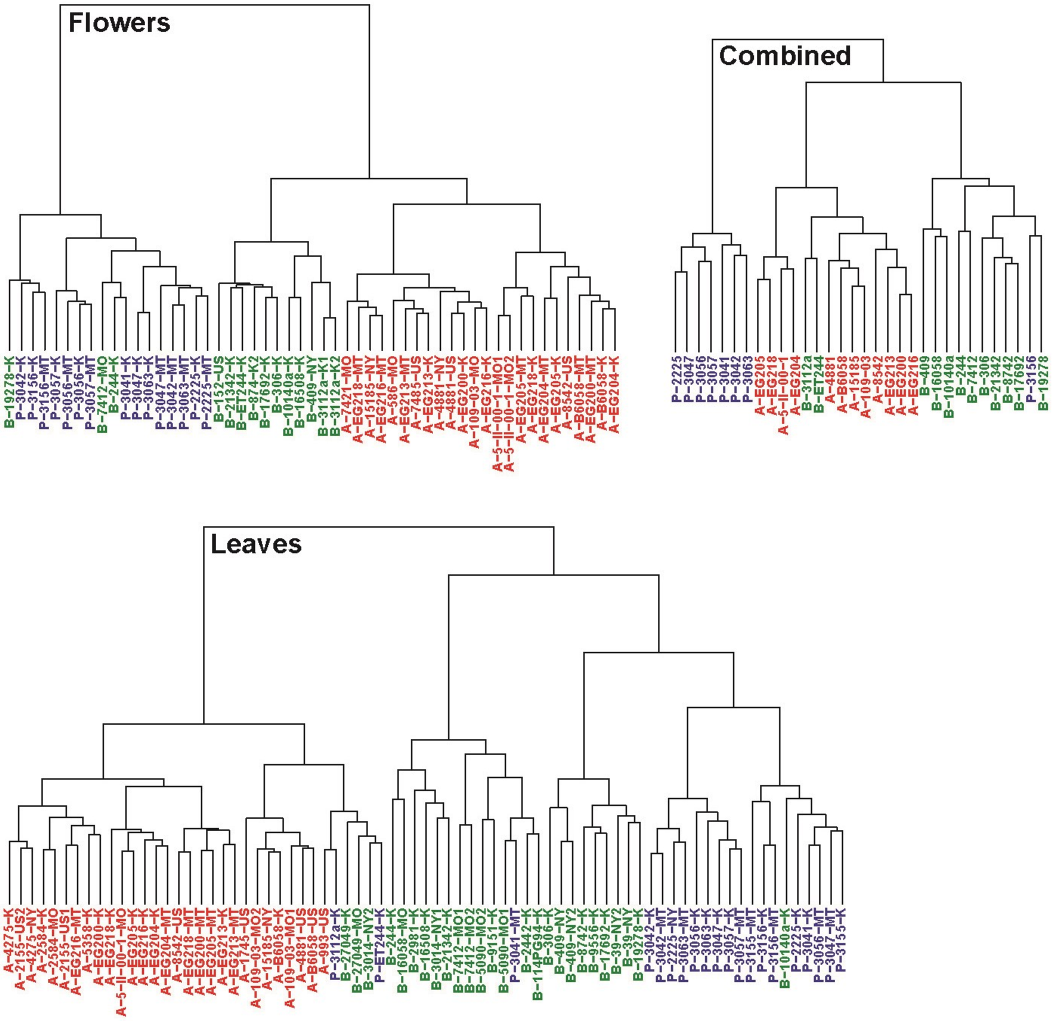

Figure 4.3 Morphometric analysis of the *Caesalpinia trichocarpa* alliance. Principal coordinate analyses of the Gower's distance matrices for flower, leaf and combined morphometric traits. Goodness of fit (GOF) measured in three ways (see Materials and Methods) are presented on the axes. Red circles- Argentina; Green squares- Bolivia; Blue triangles- Peru. Arrows represent variable vectors projected in ordination space in scaling 1, and are identified with the acronyms of the morphological characters, listed in Table 4.2.

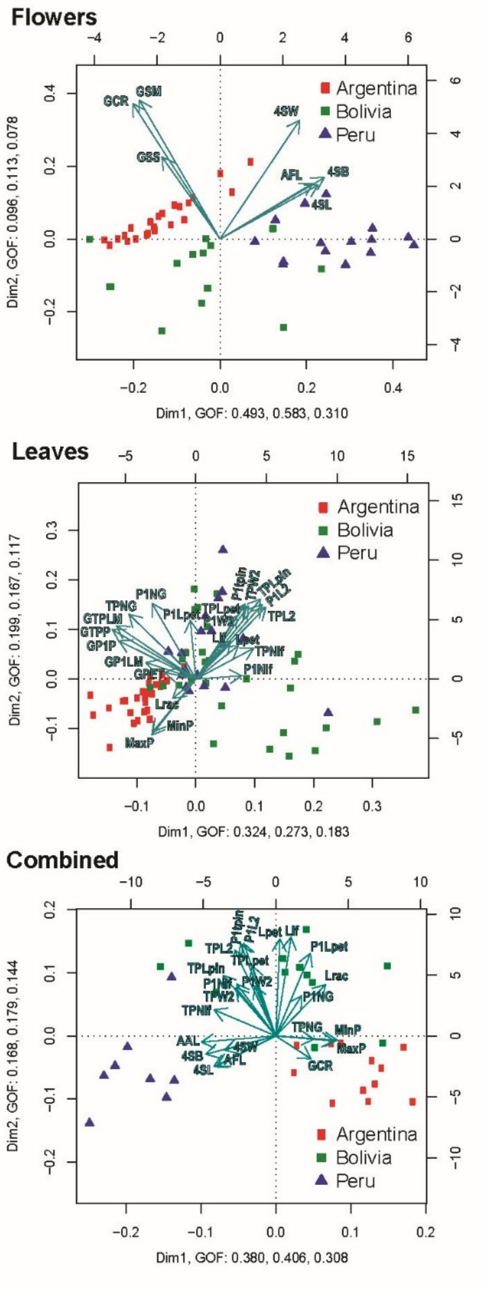

Figure 4.4 Morphometric analysis of the *Caesalpinia trichocarpa* alliance. Classification trees of the flowers, leaves and combined morphological matrices. For each character selected to partition the individuals in the classification tree analyses, the distribution of the values of the character was represented either with a boxplot (quantitative characters) or with a barplot (for binary characters). The morphological characters are indicated by their acronyms, listed in Table 4.2.

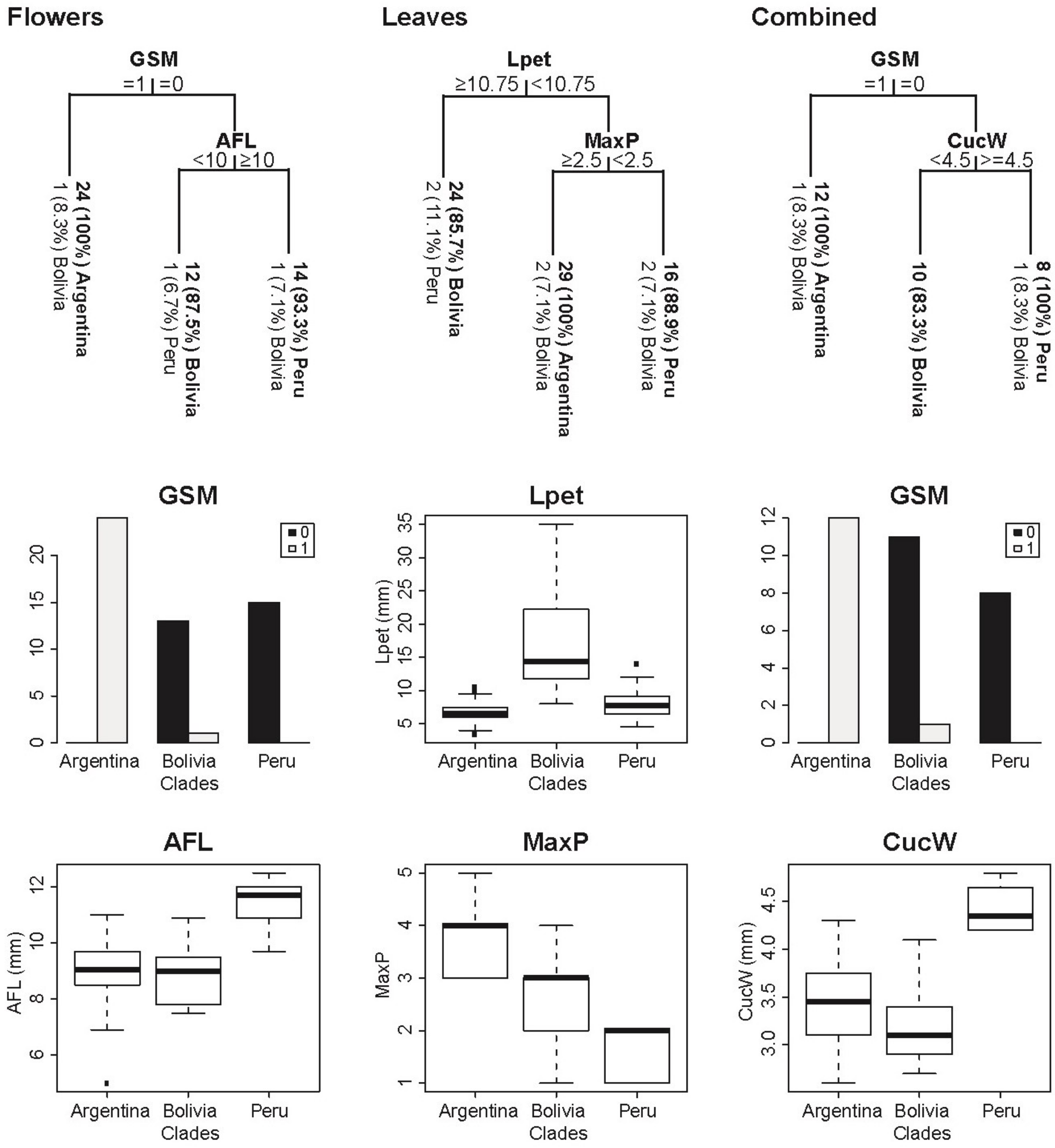

Figure 4.5 Distribution of species of *Arquita* in the Andes, South America. Hexagon: *Arquita ancashiana*; Black star: *Arquita celendiniana*; Triangle: *Arquita grandiflora*; Circle: *Arquita trichocarpa* var. *trichocarpa*; Square: *Arquita trichocarpa* var. *boliviana*; Yellow star: *Arquita mimosifolia.* Map generated using SimpleMappr (Shorthouse, 2010).

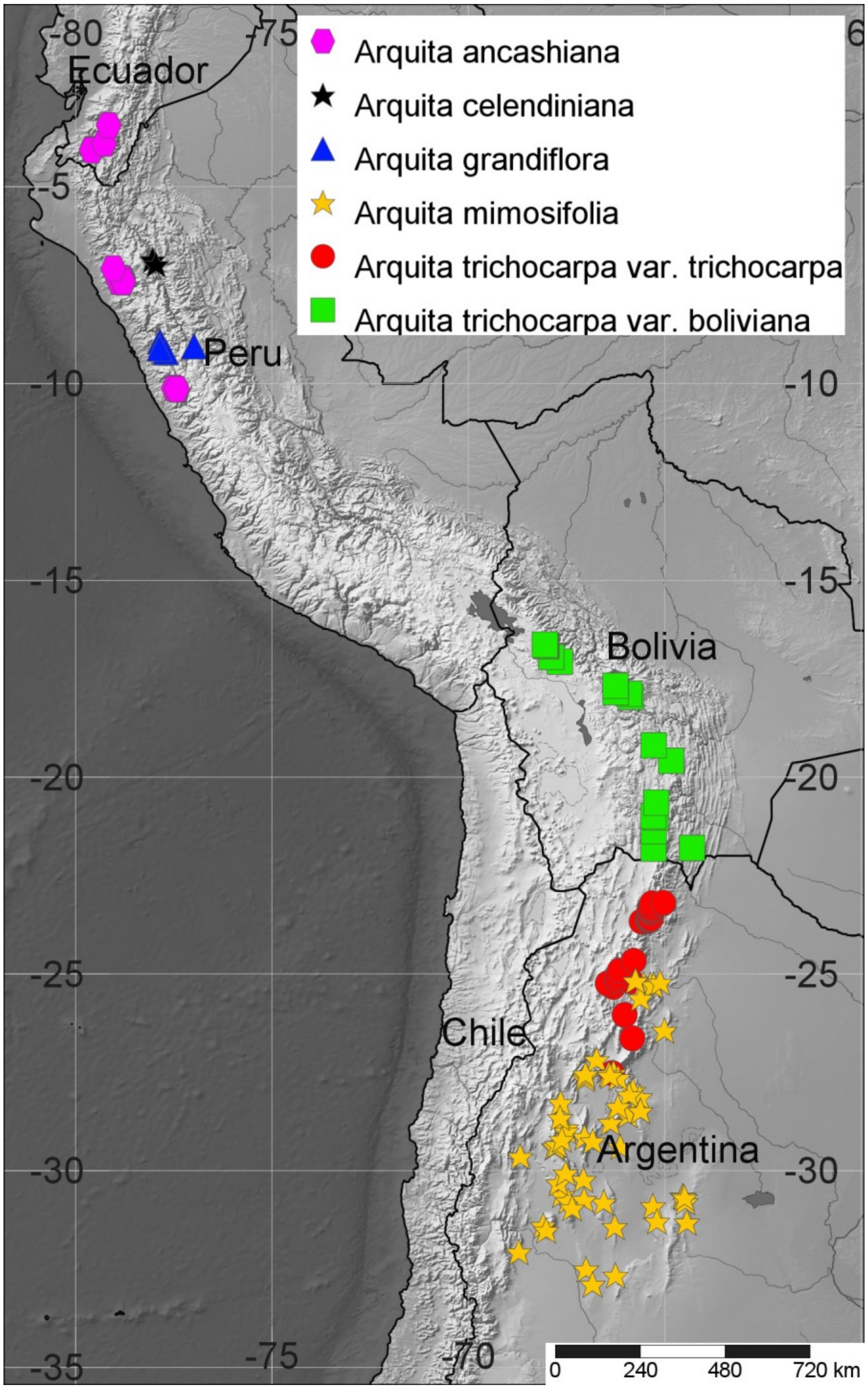

Figure 4.6 Photos of the species of *Arquita* (next page) A- Habit of *Arquita grandiflora* (Hughes & al. 3047); B,C- Color variation of the flower of *A. grandiflora* (B: Särkinen et al. 2225, C: Hughes & al. 3156); D- Pod of *A. grandiflora* (Hughes & al. 3155); E- Habit of *A. trichocarpa* var. *trichocarpa* (Gagnon & Atchison EG213); F-Inflorescence of *A. trichocarpa* var. *trichocarpa* (Gagnon & Atchison EG218, prov. Salta, Argentina); G- Inflorescence of *A. trichocarpa* var. *boliviana* (Hughes & al. 2442); H- Pod of *A. trichocarpa* var. *trichocarpa* (Gagnon & Atchison EG218); I- Habit of *A. mimosifolia* (Gagnon & al. EG203); J- Flower of *A. mimosifolia* (Gagnon & al. EG203); K- Pod of *A. mimosifolia* (Gagnon & al. EG203); L- Glands sunken on the crenulate Flower off a leaflet of *A. trichocarpa* var. *trichocarpa* (Gagnon & Atchison EG218); M- Habit of *A. ancashiana* (Hughes & al. 3026); N- Flower of *A. ancashiana* (Hughes & al. 3070); O- Pod of *A. ancashiana* (Hughes & al. 3056); P- Glands on the undersurface of a leaflet of *A. ancashiana*; Q- Habit of *A. celendiniana* (Hughes & al. 3097); R- Flower of *A. celendiniana* (Hughes & al. 3097); S- Pod of *A. celendiniana* (Hughes & al. 2010); T-Stipule of *A. celendiniana* (Hughes & al. 3097); U- Flower of *Pomaria jamesii* (credits: Patrick Alexander, http://swbiodiversity.org/seinet/imagelib/imgdetails.php?imgid=253946); V- Pod of *P. jamesii* (credits: Patrick Alexander, http://swbiodiversity.org/seinet/imagelib/imgdetails.php?imgid=253949); W- Orange sessile glands on the undersurface of leaflets of *P. lactea* (credits: A.A. Dreyer, http://www.kyffhauser.co.za/Plants1/Pomaria_lactea/Image2.htm); X- Stipules of *P. jamesii* (Gagnon & Marazzi EG2010.020);


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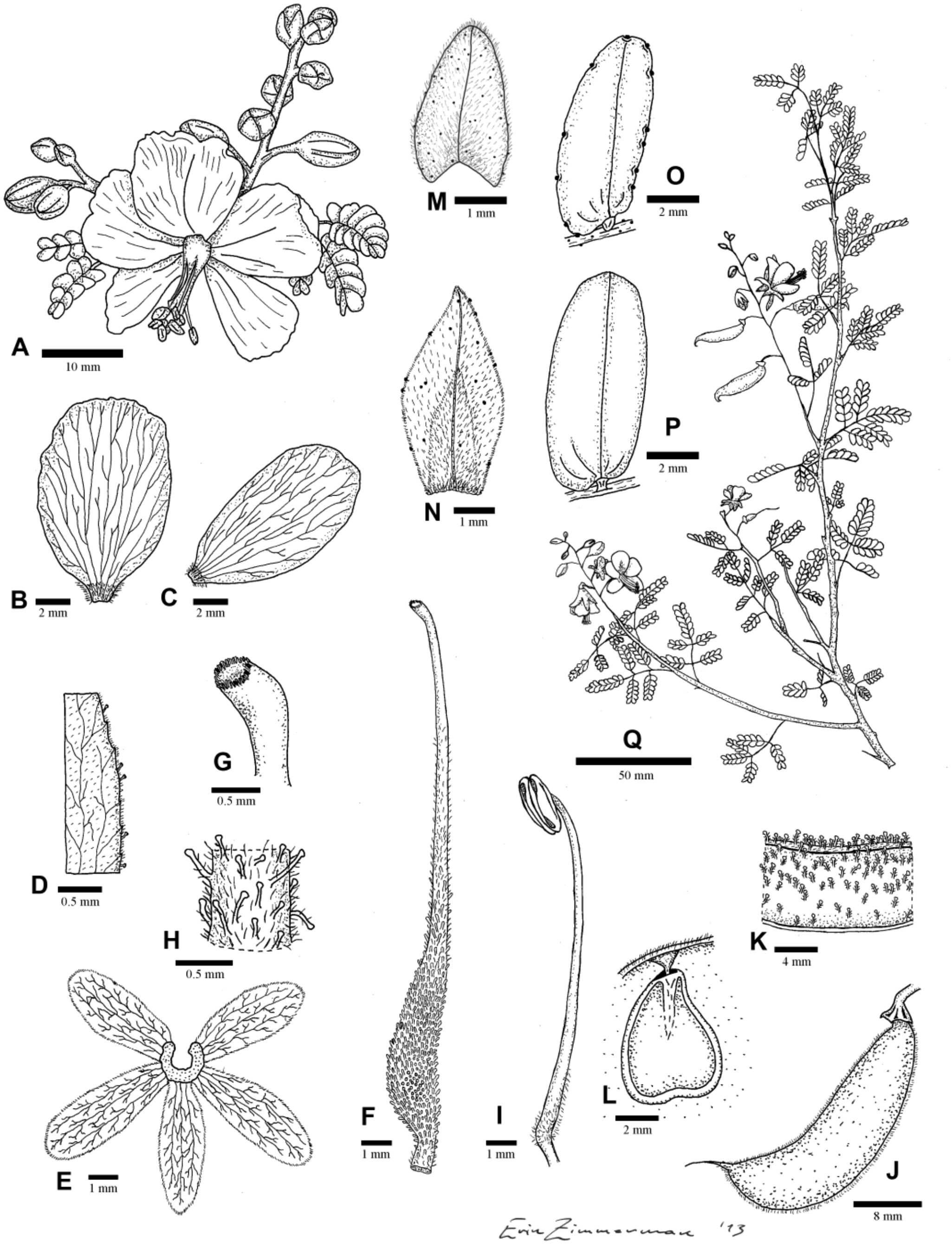
Figure 4.7 ***Arquita grandiflora*****: Illustration by Erin Zimmerman.** A- Inflorescence with a flower at anthesis; B- Standard petal; C- Upper lateral petal; D- Detail of the margin of the calyx lobe; E- Calyx opened up, flattened on the outer side; F- Gynoecium; G- Detail of the stigma; H- Detail of the ovary trichomes; I- Stamen; J- Fruit; K- Detail of fruit trichomes; L- Seed; M- Stipule; N- Bract; O- Undersurface of median leaflet with crenulated glands; P- Undersurface of median leaflet, eglandular; Q- Flowering and fruiting branchlet.



Conclusions

La délimitation des genres

La délimitation des genres est un sujet qui est moins souvent abordé dans la littérature systématique que celui de la délimitation des espèces, malgré les nombreuses études moléculaires des dernières décennies qui ont amené de nombreux changements quant à la classification des genres chez les gymnospermes et angiospermes. Small (1989) décrivait les genres comme étant le produit du processus de la « génériation », soit une sorte d'extension de la spéciation qui menant à « l'établissement de différences et d'écarts morphologiques entre des groupes d'espèces inclus dans un genre, et d'autres espèces ». Mais combien de différences doit-on soulever avant de pouvoir considérer un groupe d'espèce comme un genre distinct, et quel est le processus qui mène les espèces à évoluer en groupes distincts? C'est probablement l'absence de réponses à ces questions qui font en sorte que les botanistes ont des points de vue partagés quand on leur pose la question, à savoir si ce rang représente ou non une catégorie biologique 'réelle'. Certains considèrent que le genre désigne des groupes arbitraires pour permettre d'organiser et de nommer la biodiversité, plutôt que des unités 'naturelles', alors que d'autres sont d'avis que les genres représentent des groupes qui ont une histoire évolutive partagée et sont formés par des processus évolutifs (Barraclough & Humphreys, 2015).

Malgré l'absence de consensus quant à la réalité des genres, l'objectif principal lorsqu'on se prête à l'exercice de délimiter des genres au sein d'un groupe d'organisme est d'arriver à une classification stable, et qui reflète les relations phylogénétiques entre espèces et différents rangs à travers la classification (Humphreys & Linder, 2009). Par ailleurs une considération fondamentale lorsqu'on crée une nouvelle classification est d'établir un système de nomenclature stable acceptable non seulement par les spécialistes du groupe taxonomique en question, mais qui sera aussi adapté pour une communauté plus large d'utilisateurs, tels que les écologistes, les gestionnaires de territoires, les politiciens, les chimistes, etc. (Diggs & Liscomp, 2002). L'étude des critères et méthodes utilisés par différents auteurs pour délimiter les genres révèle qu'ils ne sont pas utilisés de manière constante auprès de différents groupes de plantes (Humphreys & Linder, 2009). Souvent, on cherche à définir des genres en se basant sur des similarités morphologiques entre espèces, ce qui correspond à un concept phénétique de la classification des organismes. Toutefois, le principal critère utilisé dans l'ère de la systématique moléculaire est le monophylétisme des genres, qui est déterminée en se basant sur des analyses cladistiques moléculaires et morphologiques. D'autres méthodes ont aussi été proposées, comme un test des limites des fertilités entre orchidées permettant d'utiliser le critère d'isolation reproductive pour déterminer les limites entre les genres (Scopece & al., 2010). On a aussi proposé une extension de la méthode « Generalized Mixed Yuled Coalescent Model » pour la délimitation des espèces, mais à l'échelle des genres (Humphreys & Barraclough, 2014). Toutefois, aucun de ces modèles n'a été utilisé à l'extérieur des études dans lesquelles elles ont été présentées.

En fin de compte, la délimitation des genres est une décision que les auteurs prennent en tenant compte des patrons phylogénétiques, de la variation morphologique entre espèces, de l'historique nomenclatural du groupe, et de la possibilité que les groupes délimités seront acceptés et facile à identifier ou non par un plus large groupe d'utilisateurs. Par exemple, à travers cette thèse, les résultats de nos analyses phylogénétiques étaient suffisamment robustes pour permettre une interprétation de l'homoplasie et de l'homologie des caractères. Ceci nous a permis d'établir une nouvelle classification au niveau des genres, qui ne comprend que des groupes monophylétiques et qui maximise la possibilité de reconnaitre des genres grâce à une combinaison de caractères provenant des feuilles, des fleurs et des fruits. Nous avons même délimité dans certains cas des genres monospécifiques, tel que *Paubrasilia, Hererolandia* et *Hultholia*, car il était clair que ces espèces n'étaient reliées à aucun autre clade, et présentaient chacune des apomorphies ou des combinaisons à caractère unique.

Toutefois, dans quelques cas nous n'avons pas pu délimiter des groupes qui étaient identifiables par des synapomorphies. Par exemple, dans le cas de *Denisophytum* et *Caesalpinia* s.s., bien qu'il ait été impossible d'identifier des synapomorphies permettant de distinguer ces deux genres, le patron phylogénétique démontrait clairement le polyphylétisme de ces espèces et forçait donc à reconnaître deux genres distincts. La décision taxonomique la plus difficile, et qui demeurera sans doute controversée, a été celle d'élever au rang générique le clade andin *Arquita*. Selon Lewis (1998), les cinq espèces faisant partie de ce genre appartenaient au groupe Poincianella-Erytrostemon, en raison d'une très grande ressemblance morphologique.

Cependant, nos analyses phylogénétiques ont démontré qu'il était dans un clade de position intermédiaire, c'est-à-dire que le clade *Arquita* était sœur avec le genre *Pomaria* Cav., et que le genre *Erythrostemon* était la lignée sœur de ces deux clades. Conséquemment, si *Arquita* était inclus avec le genre *Erythrostemon*, cela mènerait à l'établissement d'un genre paraphylétique d'*Erythrostemon,* un choix peu judicieux dans le contexte des pratiques modernes de systématique qui s'entendent pour dire que l'on ne devrait reconnaître que des groupes monophylétiques dans un système de classification moderne (Humphreys & Linder, 2009). Pour éviter la délimitation d'un genre paraphylétique, une autre option aurait été d'abolir le genre *Pomaria* Cav. et de l'inclure dans le genre *Erythrostemon.* Néanmoins, cette option paraissait inacceptable, car elle abolissait l'un des genres les plus distincts morphologiquement dans le groupe Caesalpinia, dont le statut taxonomique est déjà accepté de longue date et reconnu par la communauté. Conséquemment, même si les cinq espèces du clade *Arquita* ne peuvent être distinguées du genre *Erythrostemon*, dû à leur grande ressemblance avec une espèce de Baja California (*Erythrostemon placida)*, le choix qui a été fait au niveau taxonomique favorise d'une certaine manière la compréhension que le groupe *Arquita* a une histoire évolutive distincte du groupe *Erythrostemon*, malgré la proximité de ces groups au plan de leur relation phylogénétique et de leur apparence morphologique.

Le nombre total de genres dans le groupe *Caesalpinia* passe donc de 21 à 26, mais il est fort probable que des changements mineurs auront lieu à l'avenir. Au niveau de la délimitation générique, tel que souligné au chapitre 2, il reste trois zones problématiques: l'inclusion ou non du genre *Lophocarpinia* dans *Haematoxylum,* l'inclusion ou non du genre *Stenodrepanum* dans *Hoffmannseggia,* ainsi la question quant à la reconnaissance ou non du clade *Ticanto* en tant que genre distinct au sein du groupe Caesalpinia. Le défi principal sera de trouver des échantillons permettant d'extraire de l'ADN pour ces taxons. Au cours de mon doctorat, je n'ai pas pu extraire de l'ADN pour les genres monospécifiques *Stenodrepanum* et *Lophocarpinia.* J'ai donc eu recours à des séquences d'une autre étude pour représenter ces taxons cruciaux dans ma phylogénie. Malheureusement, ceux-ci n'étaient pas suffisamment informatifs pour résoudre et valider la position de ces taxons dans l'arbre phylogénétique du groupe Caesalpinia. Similairement, j'ai aussi éprouvé des difficultés à obtenir des extractions ADN d'espèces appartenant au genre *Ticanto*, qui se retrouvent principalement en Asie du Sud-Ouest. Souvent, les spécimens avec lesquels j'ai dû travailler étaient très vieux, ou avaient été préservés dans des conditions qui ne favorisaient pas la conservation de l'ADN chez les spécimens d'herbier (p. ex. l'alcool). Il a été impossible d'inclure des espèces du clade *Ticanto* qui ont des fruits avec de minces ailes, et dont la morphologie semble intermédiaire avec les espèces des genres *Mezoneuron* et *Pterolobium.* L'inclusion de séquences moléculaires de ces espèces, ainsi que de ceux de *Lophocarpinia* et *Stenodrepanum*, permettra de résoudre les derniers éléments du casse-tête de la taxonomie et la classification du groupe Caesalpinia.

L'histoire biogéographique et l'écologie du groupe Caesalpinia

Cette thèse s'est aussi penchée sur l'histoire biogéographique du groupe Caesalpinia, en s'intéressant tout particulièrement à son évolution écologique. L'histoire biogéographique du groupe Caesalpinia offre un exemple intéressant de l'évolution d'un groupe relativement ancien (autour de 60 Ma) avec une forte affinité pour les milieux arides et semi-arides à travers le monde. L'étude du chapitre 3 a démontré qu'à l'échelle des biomes, il y avait une tendance de conservation de niche à travers la phylogénie du groupe Caesalpinia, et qu'il était plus fréquent d'observer à travers la phylogénie des disjonctions intercontinentales entre le même biome, que des changements de biomes. L'absence de changement dans le taux de diversification des espèces, même lorsque les plantes évoluent vers d'autres biomes ou manifestent de nouveaux types de port de plantes (herbacées ou lianes), nous a permis aussi d'émettre l'hypothèse que même lorsque les espèces du groupe Caesalpinia semblent pousser dans des biomes différents, elles n'évoluent pas des caractéristiques biologiques qui leur permettant de s'établir avec succès (ou autant de succès que d'autres lignées) dans les conditions écologiques qui caractérisent les différents biomes, incluant les savanes, les forêts tropicales sèches, et les milieux arides tempérés; à la place, ils ont tendance à occuper des habitats écologiques marginaux (particulièrement dans les savanes et les forêts tropicales humides), qui ont souvent des caractéristiques écologiques qui rappellent ceux du biome succulent (tel que des conditions édaphiques sèches, des sols plus riches, etc.).

Bien qu'intéressante, cette étude ne peut être considérée comme une preuve convaincante de conservation de niche, en raison de la méthode simpliste que nous avons utilisée pour caractériser les niches des espèces. Néanmoins, les analyses biogéographiques effectuées dans cette thèse offrent à présent des opportunités de mener des études plus précises et détaillées pour comprendre l'évolution des niches au sein de différents groupes et genres de Caesalpinia, afin de comprendre à quel point les niches sont réellement conservées entre espèces sœurs qui occupent des habitats similaires mais disjoints, sur différents continents. Par exemple, bien que l'idée d'un biome succulent sensu Schrire & al. (2005) caractérisé par une végétation connaissant une forte conservation de niche au niveau phylogénétique soit attirante, elle découle d'une comparaison qualitative de la végétation plutôt que de tests rigoureux comparant des paramètres quantitatifs écologiques, tels que les facteurs climatiques, les caractéristiques du sol, et la fréquence des feux. On peut relever des exemples de ce type d'études chez d'autres familles de plantes (les Caprifoliaceae, Smith & Donoghue, 2010; les Restionaceae, Wüest & al., 2015), mais celles-ci ne visent pas spécifiquement des plantes évoluant dans le biome succulent, et n'offrent pas de comparaison entre des espèces sœurs se retrouvant dans le biome succulent des Néotropiques et de l'Afrique. Une telle étude pourrait être réalisée en accumulant de l'information sur la distribution géographique des espèces sœurs sur différents continents, dans le but de réaliser des études sur la modélisation de niches (p. ex. Maxent (Phillips & al., 2006), ou des analyses de multivariées, afin de tester l'hypothèse que ces niches sont conservées et de contribuer à une meilleure définition de ce que constitue ce biome succulent global. D'autres projets pourraient aussi être réalisés pour tenter de déterminer s'il existe des corrélations entre le changement des facteurs climatiques et le changement des ports des plantes, tel qu'observé dans les clades *Hoffmannseggia, Pomaria,* et *Erythrostemon*, où il semble y avoir une tendance répétée à développer un port de plante herbacée lorsque les espèces au sein de ce groupe évoluent vers un biome « chaud » tempéré (p. ex. Evans & al. 2014).

La délimitation des espèces

Finalement, nous avons tenté d'évaluer si les populations isolées d'*Arquita trichocarpa* au Pérou, séparées de plus de 1350 km des populations localisées en Bolivie et Argentine, représentaient une espèce distincte. Pour ce faire, nous avons présenté une étude minutieuse et approfondie de la variation génétique et morphologique de ces taxons, en incluant un échantillonnage taxonomique couvrant l'entièreté de la distribution géographique de ce groupe. Alors que l'on pourrait s'attendre à ce que seules les populations péruviennes soient génétiquement et morphologiquement distinctes, nos résultats indiquent plutôt que les populations boliviennes formaient un clade distinct au niveau génétique.

Par ailleurs, les analyses phylogénétiques basées sur trois gènes chloroplastiques et le gène ribosomal nucléaire n'arrivaient pas a priori à résoudre les relations entre ces trois clades et l'espèce *A. mimosifolia*. Mais des analyses subséquentes incluant le gène chloroplastique *matK* gene et son intron *3'-trnK* (chapitre 2) ont démontré que les espèces du Pérou étaient sœurs avec les espèces d'*A. mimosifolia*, et non avec les clades d'*A. trichocarpa* en Bolivie et en Argentine. La distinction génétique de ces trois populations était aussi apparente dans des résultats préliminaires de séquençage de marqueurs génétiques nucléaires à copie unique (dont *At103, CTP, Eif3E, SHMT* et *tRals*,des marqueurs initialement testés dans Babineau & al., 2013).

Il serait intéressant de poursuivre ce travail en incluant ces loci nucléaires au sein d'un arbre d'espèces, basé sur des méthodes de coalescence, avec le logiciel *Beast (Heled & al., 2010). Ceci serait une méthode plus robuste pour tester les relations phylogénétiques entre les trois clades *d'A.trichocarpa* et *A. mimosifolia*. Ceci aurait aussi permis de vérifier une des hypothèses concernant l'évolution des espèces dans les forêts tropicales sèches et le biome succulent, qui suggère que ces taxons forment des clades réciproquement monophylétiques qui réflètent la fragmentation de ces habitats arides ou semi-arides, qui a été comparé à des îles continentales (Lavin & al., 2004). Ceci aété démontré avec les gènes chloroplastiques et ITS chez les Légumineuses (Lavin, 2006; Pennington & al., 2010; Särkinen & al., 2012), mais jamais avec des gènes nucléaires.

Malgré l'absence d'un arbre d'espèces basé sur l'analyse de plusieurs loci nucléaires, je demeure néanmoins persuadée que les populations du Pérou représentent une lignée évolutionnaire distincte génétiquement et morphologiquement. De surcroît, elle est probablement isolée des autres lignées en Argentine et en Bolivie depuis plusieurs millions d'années, comme l'ont démontré les résultats des analyses de datation au chapitre 3.

La décision d'accorder le rang taxonomique d'espèce à ces populations a aussi été motivée par le fait que c'étaient principalement les caractères reproductifs (la taille de fleurs) qui permettaient de diagnostiquer les populations péruviennes. En comparaison, seule la longueur du pédicelle, un caractère végétatif, permettait de réellement discriminer les populations boliviennes. Le nom choisi pour cette nouvelle espèce correspondant aux populations péruviennes, *A. grandiflora,* reflète cette décision. Enfin, pour mettre en valeur la distinction entre les populations boliviennes et leurs populations sœurs argentines, ces dernières ont été élevées au rang de variété (*A. trichocarpa* var. *boliviana*).

Par ailleurs, la délimitation de l'espèce d'*Arquita grandiflora* illustre bien les problèmes de délimitations d'espèces qui demeurent dans le groupe Caesalpinia. Tel que mentionné au chapitre 1 et 2, il y a, pour certains groupes, une prolifération de noms d'espèces pour des taxons très similaires. Le phénomène est prépondérant chez les taxons caribéens, ainsi que chez le genre pantropicale *Guilandina*. Ces problèmes pourraient être résolus par des études recensant la nomenclature des espèces de ces groupes, en testant leurs limites grâce à des phylogénies densément échantillonnées, ou encore par des analyses morphométriques tentant de déterminer s'il y a des différences marquées entre ces espèces.

De plus, plusieurs autres genres auraient besoin d'études phylogénétiques et morphologiques approfondies pour mieux discerner la délimitation de leurs espèces. Par exemple, nos analyses phylogénétiques ont indiqué que plusieurs espèces chez *Coulteria, Gelrebia, Libidibia* et *Cenostigma* n'étaient pas monophylétiques. Le polyphylétisme révélé pour ces espèces pourrait être expliqué par un manque de résolution phylogénétique avec les marqueurs génétiques choisis, mais pourrait aussi être dû à l'hybridation, fortement soupçonnée comme étant un phénomène important entre espèces du genre *Cenostigma* (Lewis, 1998). Des phylogénies plus complètes des genres asiatiques *Pterolobium, Mezoneuron, Biancaea* et *Hultholia* seraient aussi nécessaires pour évaluer les limites des espèces, car leur distribution géographique est souvent très étendue, avec une variation morphologique prononcée entre populations. Par ailleurs, la diversité spécifique de ces groupes est probablement sous-estimée; on peut donc envisager que plusieurs nouvelles espèces, sous-espèces ou variétés seront reconnues et décrites dans le futur.

Finalement, il pourrait y avoir dans certains groupes des évènements de polyploïdies insoupçonnées, un phénomène qui a été démontré dans le groupe Caesalpinia chez *Libidibia ferrea* var. *parviflora* (Borges & al., 2012). Ceci serait particulièrement intéressant à vérifier pour *Paubrasilia echinata,* une espèce qui présente trois morphotypes avec des feuilles de tailles très différentes, et dont la distribution géographique à travers la forêt atlantique au Brésil est fortement structurée. Toutes ces études de délimitations d'espèces pourraient aussi être combinées à des analyses phylogéographiques, ce qui pourrait permettre de comprendre à l'échelle locale l'histoire biogéographique de ces espèces.

Bibliographie

Albach, D.C. 2008. Further arguments for the rejection of paraphyletic taxa: *Veronica* subgen. *Pseudolysimachium* (Plantaginaceae). Taxon 57: 1–6.

Allorge, V., Allorge, P. 1930. Marcel Denis (1897–1929). Bulletin de la Société Botanique de France, 77(4) : 693-696.

Altschul, S.F., Gish, W., Miller, W., Myers, E.W., Lipman, D.J. 1990. Basic local alignment search tool. Journal of Molecular Biology 215: 403–410.

Anderson, E. 1940. The Concept of the genus: II. A survey of modern opinion. Bulletin of the Torrey Botanical Club 67(5): 363-369.

Ansari, A.A. 1990. Extended distribution of an endemic monotypic genus Wagatea Dalz. Journal of Economic and Taxonomic Botany 14(3): 746-747.

Arakaki, M., Christin, P.-A., Nyffeler, R., Lendel, A., Eggli, U., Ogburn, R M., Spriggs, E., Moore, M.J., Edwards, E.J. 2011. Contemporaneous and recent radiations of the world's major succulent plant lineages. Proceedings of the National Academy of Sciences 108(20): 8379-8384.

Axelrod, D.I. 1992. Climatic pulses, a major factor in Legume evolution. In: Herendeen, P.S., Dilchner, D.L. (Eds.) *Advances in legume systematics, part 4: the fossil record*. Royal Botanical Gardens, Kew, United Kingdom. pp. 259-279.

Babineau, M. 2013. Systématique moléculaire et biogéographie de trois genres malgaches menacés d'extinction Delonix, Colvillea et Lemuropisum (Caesalpinioideae: Leguminosae). Master's dissertation, University of Montreal, Canada. http://hdl.handle.net/1866/9958

Babineau, M., Gagnon, E., Bruneau, A., 2013. Phylogenetic utility of 19 low copy nuclear genes in closely related genera and species of caesalpinioid legumes. Journal of South African Botany 89: 94–105.

Bachman, S., Moat, J., Hill, A., Torre, J. de la, Scott, B. 2011. Supporting Red List threat assessments with GeoCAT: Geospatial conservation assessment tool. ZooKeys 150: 117–126.

Bacon, C.D., Silvestro, D., Jaramillo, C., Smith, B. T., Chakrabarty, P., Antonelli, A. 2015. Biological evidence supports an early and complex emergence of the Isthmus of Panama. Proceedings of the National Academy of Sciences 112(19): 6110-6115.

Ball, O.M. 1931. A contribution to the paleobotany of the Eocene of Texas. Bulletin of Agriculture and Mechanical College of Texas, 4th ser. vol. 2, no. 5.

Baranzelli, M., Johnson, C., Leigh, A., Cosacov, A., Sérsic, A.N. 2014. Historical and ecological divergence among populations of *Monttea chilensis* (Plantaginaceae), an endemic endangered shrub bordering the Atacama Desert, Chile. Evolutionary Ecology 28: 751–774.

Barraclough, T.G. 2010. Evolving entities: towards a unified framework for understanding diversity at the species and higher levels. Philosophical Transactions of the Royal Society B-Biological Sciences 365(1547): 1801-1813.

Barraclough, T.G., Humphreys, A.M. 2015. The evolutionary reality of species and higher taxa in plants: a survey of post-modern opinion and evidence. New Phytologist, doi: 10.1111/nph.13232.

Barreto Valdés, A. 2013. *Flora de la Republica de Cuba. Serie A, Plantas vasculares. Fasciculo 18. Caesalpiniaceae*. Koeltz Scientific Books, Königstein, Germany. 210 pages.

Baum, D.A., Smith, S.D. 2013. *Tree-thinking: An Introduction to Phylogenetic Biology*. Roberts & Company, Colorado, U.S.A. 476 pages.

Beerling, D.J., Osborne, C.P. 2006. The origin of the savanna biome. Global Change Biology, 12(11): 2023-2031.

Bell, E.A., 1981. Non-protein amino acids in the Leguminosae. In: Pohill, R.M., Raven, P.H. (Eds.), *Advances in legume systematics, part 2*. Royal Botanic Gardens, Kew, Richmond, United Kingdom, pp. 489–500.

Bell, C.D., & Donoghue, M.J. 2005. Phylogeny and biogeography of Valerianaceae (Dipsacales) with special reference to the South American valerians. Organisms Diversity & Evolution 5(2): 147-159.

Benson, D.A., Cavanaugh, M., Clark, K., Karsch-Mizrachi, I., Lipman, D.J., Ostell, J., Sayers, E.W. 2013. GenBank. Nucleic Acids Research. 41(D1): D36–D42.

Bentham, G., 1865. Leguminosae-Eucaesalpinieae. In: Bentham, G., Hooker, J.D. (Eds.), *Genera Plantarum, 1*. Reeve, London, United Kingdom. pp. 458–459 (565–570).

Berry, E.W. 1916. The lower Eocene floras of southeastern North America. U.S. Geological Survey Prof. Paper 91. Washington, U.S.A. 481 pages.

Berry, E.W. 1930. Revision of the lower Eocene Wilcox flora of the southeastern states. U.S. Geological Survey Prof. Paper 156.

Beyra-Matos, A., Lavin, M. 1999. Monograph of *Pictetia* (Leguminosae-Papilionoideae) and review of the Aeschynomeneae. Systematic Botany Monographs 56: 93 pages.

Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K.L., Meier, R., Winker, K., Ingram, K.K., Das, I. 2007. Cryptic species as a window on diversity and conservation. Trends in Ecology and Evolution 22: 148–155.

Bolus, L. 1920. *Caesalpinia pearsonii*. Annals of the Bolus Herbarium 3: 4.

Borges, L., Souza, L., Guerra, M., Machado, I., Lewis, G., Lopes, A. 2012. Reproductive isolation between diploid and tetraploid cytotypes of *Libidibia ferrea* (= *Caesalpinia ferrea*) (Leguminosae): ecological and taxonomic implications. Plant Systematics and Evolution 298(7): 1371-1381.

Bouchenak-Khelladi, Y., Maurin, O., Hurter, J., van der Bank, M. 2010. The evolutionary history and biogeography of Mimosoideae (Leguminosae): an emphasis on African acacias. Molecular Phylogenetics and Evolution 57(2): 495-508.

Bowman, D.M.J.S. 2000. Australian rainforests: islands of green in a land of fire. Cambridge University Press, Cambridge, U.K. 360 pages.

Bray, W.L. 1898. On the relation of the flora of the lower Sonoran zone in North America to the flora of the arid zones of Chili and Argentine. Botanical Gazette 26(2): 121-147.

Brenan, J.P.M. 1963. Notes on African Caesalpinioideae. Kew Bulletin 17: 197–218.

Brenan, J.P.M. 1967. Leguminosae, part 2: Caesalpinioideae. In: Milne-Redhead, E., Polhill, R.M. (Eds.), *Flora of Tropical East Africa*. Crown Agents, London, United Kingdom, p. 173.

Bridgewater S., Pennington R.T., Reynel C., Daza A., Pennington T.D. 2003. A preliminary floristic and phytogeographic analysis of the woody flora of seasonally dry forests in northern Peru. Candollea 58: 129-148.

Brink, M. 2006. *Cordeauxia edulis* Hemsl. [Internet] Record from PROTA4U. Brink, M., Belay, G. (Eds). PROTA (Plant Resources of Tropical Africa / Ressources végétales de l’Afrique tropicale), Wageningen, Netherlands. <http://www.prota4u.org/search.asp>. Accessed 15 May 2015.

Britton, M.N., Hedderson, T.A., Verboom, G.A. 2014. Topography as a driver of cryptic speciation in the high-elevation cape sedge *Tetraria triangularis* (Boeck.) C. B. Clarke (Cyperaceae: Schoeneae). Molecular Phylogenetics and Evolution. 77: 96–109.

Britton, N.L. 1927. *Stahlia monosperma*, Cobana negra, native of Puerto Rico, Family Caesalpiniaceae. Adansonia 12: 33.

Britton, N.L., Rose, J.N. 1930. Caesalpiniaceae, Krameriaceae, (Rosales). North American Flora 23: 301–342.

Brooks, T.M., Mittermeier, R.A., Fonseca, G.A.B. da, Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D., Rodrigues, A.S.L. 2006. Global biodiversity conservation priorities. Science 313: 58–61.

Brown, C.M., Arbour, J.H., Jackson, D.A. 2012. Testing of the effect of missing data estimation and distribution in morphometric multivariate data analyses. Systematic Biology 61: 941–954.

Brummitt, R.K., Ross, J. 1974. The African species of *Hoffmannseggia* (Leguminosae-Caesalpinioideae). Kew Bulletin 29(2): 415-424.

Brummitt, R.K., Chikuni, A.C., Lock, J.M., Polhill, R.M. 2007. Leguminosae. In: Timberlake, J.R., Pope, G.V., Polhill, R.M., Martins, E.S. (Eds.), *Flora Zambesiaca, vol. 3(2)*. Royal Botanic Gardens, Kew, Richmond, United Kingdom, pp. 1–218.

Bruneau, A., Herendeen, P.S., Klitgaard, B.B., Lewis, G.P. 2001. Phylogenetic relationships in the Caesalpinioideae (Leguminosae) as inferred from chloroplast trnL intron sequences. Systematic Botany 26: 487–514.

Bruneau, A., Mercure, M., Lewis, G.P., Herendeen, P.S., 2008. Phylogenetic patterns and diversification in the Caesalpinioid legumes. Botany 86: 697–718.

Burkart, A. 1936. Las especias argentinas y uruguayas del género *Caesalpinia*. Revista Argentina de Agronomía 3(3): 67–112.

Burkart, A. 1940. Nota sobre algunas Leguminosas indigenas o introducidas en Chile. Revista Chilena Historia Natural 43: 156-164.

Burkart, A. 1944. Tres nuevas Leguminosas del Paraguay: coleccionadas por el Señor Teodoro Rojas. Darwiniana 6(3): 477-493.

Burkart, A. 1952. *Las Leguminosas argentinas silvestres y cultivadas*. Acme Agency, Buenos Aires, Argentina. 569 pages.

Burkart, A. 1957. Leguminosas nuevas o críticas, V. Darwiniana 11(2): 256-271.

Burnham, R.J. 1995. A new species of winged fruit from the Miocene of Ecuador: *Tipuana ecuatoriana* (Leguminosae). American Journal of Botany 82: 1599–1607.

Burnham, R.J., Carranco, N.L. 2004. Miocene winged fruits of *Loxopterygium* (Anacardiaceae) from the Ecuadorian Andes. American Journal of Botany 91: 1767–1773.

Calvillo-Canadell, L., Cevallos-Ferriz, S.R.S. 2005. Diverse assemblage of Eocene and Oligocene leguminosae from Mexico. International Journal of Plant Sciences 166(4): 671-692.

Candolle, A.P.de, 1825. Prodromus Systematis Naturalis, 2. Treuttel & Würtz, Paris, pp. 480–485.

Caponio, I., Anton, A.M., Fortunato, R.H., Norrmann, G.A. 2012. Ploidy dimorphism and reproductive biology in *Stenodrepanum bergii* (Leguminosae), a rare South American endemism. Genome 55(1):1-7.

Capuron, R. 1967. Deux *Caesalpinia* nouveaux pour Madagascar. Adansonia, sér. 2, 7(2): 199-205.

Cardoso, M.A., Provan, J., Powell, W., Ferreira, P.C.G., de Oliveira, D.E., 1998. High genetic differentiation among remnant populations of the endangered *Caesalpinia echinata* Lam. (Leguminosae-Caesalpinioideae). Molecular Ecology 7: 601–608.

Cardoso, S.R.S., Provan, J., Lira, C.D.F., Pereira, L.D.O.R., Ferreira, P.C.G., Cardoso, M.A., 2005. High levels of genetic structuring as a result of population fragmentation in the tropical tree species *Caesalpinia echinata* Lam. Biodiversity and Conservation 14(5): 1047–1057.

Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V. Ehleringer, J.R. 1997. Global vegetation change through the Miocene/Pliocene boundary. Nature 389(6647): 153-158.

Chen, D., Zhang, D., Hou, D. 2010a. *Caesalpinia*. In: Wu, C.Y., Raven, P. eEds.), Flora of China, vol. 10. : Missouri Botanical Garden Press, St. Louis, U.S.A. pp. 41-47.

Chen, D., Zhang, D., Hou, D. 2010b. *Pterolobium*. InL Wu, C.Y., Raven, P. (eds.), Flora of China, Vol. 10. Missouri Botanical Garden Press, St. Louis, U.S.A. pp. 47-48

Christin, P.A., Besnard, G., Samaritani, E., Duvall, M.R., Hodkinson, T.R., Savolainen, V., Salamin, N. 2008. Oligocene CO2 decline promoted C-4 photosynthesis in grasses. Current Biology 18(1): 37-43.

Clark, R., Gagnon, E. 2015. A revision of *Mezoneuron* (Leguminosae: Caesalpinioideae) in New Caledonia, with perspectives on vegetation, geology, and conservation. Phytotaxa 207(1): 68-92.

Coccuci, A.A., Galetto, L., Sersic, A, 1992. El sindrome floral de *Caesalpinia gilliesii* (Fabaceae-Caesalpinioideae). Darwiniana 31: 111–135.

Cody, S., Richardson, J.E., Rull, V., Ellis, C., Pennington, R.T. 2010. The great american biotic interchange revisited. Ecography 33(2): 326-332.

Couvreur, T.L.P., Kissling, W.D., Condamine, F.L., Svenning, J.-C., Rowe, N.P., Baker, W.J. 2015. Global diversification of a tropical plant growth form: environmental correlates and historical contingencies in climbing palms. Frontiers in Genetics, 5. doi: 10.3389/fgene.2014.00452

Cowling, R., Proches, S., Vlok, J.H.J. 2005. On the origin of southern African subtropical thicket vegetation. South African Journal of Botany 71(1): 1-23.

Coyne J.A., Orr H.A. 2004. *Speciation*. Sinauer Associates, Sunderland, Massachusetts, U.S.A. 545 pages.

Crisp, M.D., Arroyo, M.T.K., Cook, L.G., Gandolfo, M.A., Jordan, G.J., McGlone, M.S., Weston, P.H., Westoby, M., Wilf, P., Linder, H.P. 2009. Phylogenetic biome conservatism on a global scale. Nature 458(7239): 754-756.

Cruden, R.W., Hermann-Parker, S.M., 1979. Butterfly pollination of *Caesalpinia pulcherrima*, with observations ona psychophilous syndrome. Journal of Ecology 67: 155–168.

Curtis, B., Mannheimer, C. 2005. *Tree Atlas of Namibia*. National Botanical Research Institute, Windhoek, Namibia.

Darriba, D., Taboada, G.L., Doallo, R., Posada, D. 2012. jModelTest 2: More models, new heuristics and parallel computing. Nature Methods 9(8): 772.

Davis, J.I., Stevenson, D.W., Petersen, G., Seberg, O., Campbell, L.M., Freudenstein, J.V., Goldman, D.H., Hardy, C.R., Michelangeli, F.A., Simmons, M.P., Specht, C.D., Vergara- Silva, F., Gandolfo, M., 2004. A phylogeny of the monocots, as inferred from rbcL and atpA sequence variation, and a comparison of methods for calculating jackknife and bootstrap values. Systematic Botany 29: 467–510.

Delgado-Salinas, A., Thulin, M., Pasquet, R., Weeden, N., Lavin, M. 2011. *Vigna* (Leguminosae) sensu lato: the names and identities of the American segregate genera. American Journal of Botany 98(10): 1694-1715.

De-Nova, J.A., Medina, R., Montero, J.C., Weeks, A., Rosell, J.A., Olson, M.E., Magallón, S. 2012. Insights into the historical construction of species-rich Mesoamerican seasonally dry tropical forests: the diversification of *Bursera* (Burseraceae, Sapindales). New Phytologist 193: 276–287.

Dercourt, J., Zonenshain, L.P., Ricou, L.E., Kazmin, V.G., Lepichon, X., Knipper, A.L., Grandjacquet, C., Sbortshikov, I.M., Geyssant, J., Lepvrier, C., Pechersky, D.H., Boulin, J., Sibuet, J.C., Savostin, L.A., Sorokhtin, O., Westphal, M., Bazhenov, M.L., Lauer, J.P., Bijuduval, B. 1986. Geological evolution of the Tethys belt from the Atlantic to the Pamirs since the Lias. Tectonophysics 123(1-4): 241-315.

Dexter, K.G., Smart, B., Baldauf, C., Baker, T.R., Balinga, M.P.B., Brienen, R.J.W., Fauset, S., Feldpausch, T.R., Ferreira-Da Silva, L., Ilunga Muledi, J., Lewis, S.L., Lopez-Gonzalez, G., Parthasarathy, N., Phillips, O.L., Sunderland, T.C.H., Theilade, I., Weintritt, J., Affum-Baffoe, K., Araujo, A., Arroyo, L., Begne, S.K., Carvalho-Das Neves, E., Collins, M., Cuni-Sanchez, A., Djuikouo, M.N.K., Elias, F., Foli, E.G., Jeffery, K.J., Killeen, T.J., Malhi, Y., Maracahipes, L., Mendoza, C., Monteagudo-Mendoza, A., Morandi, P., Oliveira-Dos Santos, C., Parada, A.G., Pardo, G., Peh, K.S.-H., Salomão, R.P., Silveira, M., Sinatora-Miranda, H., Slik, J.W.F., Sonke, B., Taedoumg, H.E., Toledo, M., Umetsu, R.K., Villaroel, R.G., Vos, V.A., White, L.J.T., Pennington, R.T. 2015. Floristics and biogeography of vegetation in seasonally dry tropical regions. International Forestry Review 17(2): 10-32.

Dickinson T.A. 1999. Species concepts in agamic complexes. In: Raamsdonk, L.W.D. van, Nijs J.C.M. den (Eds.), *Evolution in man-made habitats*. Institute for Systematics & Ecology, Amsterdam, pp. 319–339.

Diggs, G.M. Jr., Lipscomb, B.L. 2002. What is the writer of a flora to do? Evolutionary taxonomy of phylogenetic systematics? SIDA, Contributions to Botany 20(2): 647-674.

Dilcher, D.L. 1973. A revision of the Eocene flora of southeastern North America. The Palaeobotanist 20: 7-18.

Dillenberger, M.S., Kadereit, J.W. 2014. Maximum polyphyly: multiple origins and delimitation with plesiomorphic characters require a new circumscription of *Minuartia* (Caryophyllaceae). Taxon 63: 64–88.

Dillon, M.O., Rundel, P.W. 1990. The botanical response of the Atacama and Peruvian desert floras to the 1982-83 El Niño event. In: Glynn, P.W. (Ed.), *Elsevier Oceanography Series, volume 52.* Elsevier, pp. 487-504.

Dludlu, M.N., Stirton, C.H., Chimphango, S.B.M., Bello, A., Muasya, A.M. 2013. Phylogenetic position of the southern African members of the tribe Psoraleeae based on molecular and morphological data. South African Journal of Botany 89: 150-155.

Donoghue, M.J. 2008. A phylogenetic perspective on the distribution of plant diversity. Proceedings of the National Academy of Sciences 105(Supp. 1): 11549-11555.

Donoghue, M.J., Edwards, E.J. 2014. Biome shifts and niche evolution in plants. Annual Review of Ecology, Evolution, and Systematics 45(1): 547-572.

Donoghue, M.J., Sanderson, M.J. 2015. Confluence, synnovation, and depauperons in plant diversification. New Phytologist, 207(2): 260-274.

Douzery, E.J.P., Pridgeon, A.M., Kores, P., Linder, H.P., Kurzweil, H., Chase, M.W. 1999. Molecular phylogenetics of Diseae (Orchidaceae): a contribution from nuclear ribosomal ITS sequences. American Journal of Botany 86: 887–899.

Doyle, J.J. 2012. Polyploidy in Legumes. In: Soltis, P.S., Soltis, D.E. (Eds.), *Polyploidy and Genome Evolution*. Springer-Verlag Berlin Heidelberg, Germany. pp. 147-180.

Drummond, A.J., Suchard, M.A., Xie, D., Rambaut, A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Molecular Biology and Evolution 29(8): 1969-1973.

Du Puy, D.J., Rabevohitra, R. 2002. Tribe Caesalpinieae. In: Du Puy, D.K., Labat, J.N., Rabevohitra, R., Villiers, J., Bosser, J., Moat, J. (eds.), *The Leguminosae of Madagascar*. Royal Botanic Gardens, Kew, United Kingdom. 737 pages.

Durán, R.C., Ramírez, J.J. 2008. *Haematoxylum sousanum* (Leguminosae, Caesalpinioideae), una especie nueva del Sur de México. Novon: A Journal for Botanical Nomenclature 18(1): 25-28.

Durán, R.C., Sousa S.M. 2014. *Haematoxylum calakmulense* (Leguminosae, Caesalpinoideae), una nueva especie mesoamericana. Novon: A Journal for Botanical Nomenclature 23(1): 31-36.

Edwards, E.J., Donoghue, M.J. 2013. Is it easy to move and easy to evolve? Evolutionary accessibility and adaptation. Journal of Experimental Botany. doi: 10.1093/jxb/ert220

Egan, A.N., Crandall, K.A. 2008. Incorporating gaps as phylogenetic characters across eight DNA regions: ramifications for North American Psoraleeae (Leguminosae). Molecular Phylogenetics and Evolution 46(2): 532-546.

Ehleringer, J.R., Cerling, T.E., Helliker, B.R. 1997. C4 photosynthesis, atmospheric CO2, and climate. Oecologia 112(3): 285-299.

Evans, M., Aubriot, X., Hearn, D., Lanciaux, M., Lavergne, S., Cruaud, C., Lowry, P.P., Haevermans, T. 2014. Insights on the evolution of plant succulence from a remarkable radiation in Madagascar (*Euphorbia*). Systematic Biology 63(5): 697-711.

Fazekas, A.J., Steeves, R., Newmaster, S.G. 2010. Improving sequencing quality from PCR products containing long mononucleotide repeats. BioTechniques 48: 277–285.

Ford, C. 1995. A preliminary revision of the Libidibia group of the genus *Caesalpinia* (Caesalpinioideae, Leguminosae). Unpublished first year dissertation, University of Bradford, United Kingdom.

Freire, F.T. 1994. *Cenostigma tocantinum* Ducke (Leg. Caes.): uma redescricao da especie. Bradea, 6(36): 297-303.

Gagnon, E., Hughes, C.E., Lewis, G.P., Bruneau, A. 2015. A new cryptic species in a new cryptic genus in the Caesalpinia Group (Leguminosae) from the seasonally dry inter-Andean valleys of South America. Taxon 64(3), p. 468-490.

Gagnon, E., Lewis, G.P., Sotuyo, J.S., Hughes, C.E., Bruneau, A. 2013. A molecular phylogeny of Caesalpinia sensu lato: increased sampling reveals new insights and more genera than expected. South African Journal of Botany 89: 111–127.

Garnock-Jones, P.J. 2014) Evidence-based review of the taxonomic status of New Zealand's endemic seed plant genera. New Zealand Journal of Botany, 52(2) : 163-212.

Gasson, P., Warner, K., Lewis, G.P. 2009. Wood anatomy of *Caesalpinia* s.s., *Coulteria*, *Erythrostemon*, *Guilandina*, *Libidibia*, *Mezoneuron*, *Poincianella*, *Pomaria* and *Tara* (Leguminosae, Caesalpinioideae, Caesalpinieae). IAWA Journal 30: 247–276.

George, A.S. 1998. *Caesalpinia*. In: *Flora of Australia, vol. 12*. Australian Biological Resources Study/CSIRO, Melbourne, Australia. pp. 59-67.

Germishuizen, G. 1991. *Caesalpinia bracteata*, a new species from the Onseepkans area of the Northern Cape Province. Bothalia 21(2): 152-154.

Gillis, W.T., Proctor, G.R. 1974. *Caesalpinia* subg. *Guilandina* in the Bahamas. Journal of the Arnold Arboretum 55(3): 425–430.

Good-Avila, S.V., Souza, V., Gaut, B.S., Eguiarte, L.E. 2006. Timing and rate of speciation in *Agave* (Agavaceae). Proceedings of the National Academy of Sciences 103(24): 9124-9129.

Govindarajulu, R., Hughes, C.E., Bailey, C.D. 2011. Phylogenetic and population genetic analyses of diploid *Leucaena* (Leguminosae; Mimosoideae) reveal cryptic species diversity and patterns of divergent allopatric speciation. American Journal of Botany 98(12): 2049–2063.

Guerrero, P.C., Rosas, M., Arroyo, M.T.K., Wiens, J.J. 2013. Evolutionary lag times and recent origin of the biota of an ancient desert (Atacama–Sechura). Proceedings of the National Academy of Sciences 110(28): 11469-11474.

Gunn, C.R., Dennis, J.V. 1976. World guide to tropical drift seeds and fruits. Quadrangle/the New York Times Book Co., New York, U.S.A. 256 pages.

Hall, R. 2009. Southeast Asia's changing palaeogeography. Blumea - Biodiversity, Evolution and Biogeography of Plants 54(1-1): 148-161.

Haston, E.M., Lewis, G.P., Hawkins, J.A. 2005. A phylogenetic reappraisal of the Peltophorum group (Caesalpinieae: Leguminosae) based on the chloroplast trnL-F, rbcL and rps16 sequence data. American Journal of Botany 92(8): 1359–1371.

Hattink, T.T. 1974. A revision of Malesian *Caesalpinia*, including *Mezoneuron* (Leguminosae–Caesalpiniaceae). Reinwardtia 9(1): 1–69.

Hawkins, J.A., Boutaoui, N., Cheung K.Y., van Klinken, R.D., Hughes, C.E. 2007. Intercontinental dispersal prior to human translocation revealed in a cryptogenic invasive tree. New Phytologist 175(3): 575–587.

Heald, J. 1994. An overview of the genus *Guilandina*. Unpublished final year undergraduate project. University of Bradford, United Kingdom.

Heled, J., Drummond, A.J. 2010. Bayesian inference of species trees from multilocus data. Molecular Biology and Evolution 27(3): 570-580.

Hemsley, W.B. 1907. *Cordeauxia edulis* Hemsl. Hooker's Icon Pl. 20 ser. 4, 9, tab.s 2838 and 2839.

Herendeen, P.S. 1992. The fossil history of the Leguminosae from the Eocene of southeastern North America. In: Herendeen, P.S., Dilcher, D.L. (Eds.), *Advances in legume systematics, part 4: the fossil record*. Royal Botanic Gardens, Kew, United Kingdom, pp. 85-160.

Herendeen, P.S., Dilcher, D.L. 1991. *Caesalpinia* subgenus *Mezoneuron* (Leguminosae, Caesalpinioideae) from the Tertiary of North America. American Journal of Botany 78: 1–12.

Herendeen, P.S., Zarucchi, J.L. 1990. Validation of *Caesalpinia* subgenus *Mezoneuron* (Desf.) Vidal and new combinations in *Caesalpinia* for two species of *Mezoneuron* from Africa. Annals of the Missouri Botanical Garden 77(4): 854–855.

Herendeen, P.S., Bruneau, A., Lewis, G.P. 2003. Phylogenetic relationships in caesalpinioid legumes: a preliminary analysis based on morphological and molecular data. In: Klitgaard, B.B., Bruneau, A. (Eds.), *Advances in legume systematics, part 10: higher level systematics*. Royal Botanic Gardens, Kew, Richmond, United Kingdom. pp. 37–62.

Hernández-Hernández, T., Brown, J.W., Schlumpberger, B.O., Eguiarte, L.E., & Magallón, S. 2014. Beyond aridification: multiple explanations for the elevated diversification of cacti in the New World Succulent biome. New Phytologist 202(4): 1382-1397.

Hey, J. 2006. On the failure of modern species concepts. Trends in Ecology and Evolution 21: 447-450.

Higgins, S.I., Nathan, R., Cain, M.L. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? Ecology 84(8): 1945-1956.

Hinchliff, C.E., Roalson, E.H. 2013. Using supermatrices for phylogenetic inquiry: an example using the sedges. Systematic Biology, 62(2): 205-219.

Hou, D., Larsen, K., Larsen, S.S. 1996. Caesalpiniaceae. In: Hou, D., Larsen, K., Larsen, S.S., Laferrier, J.F., Duyfjes, B.E.E. (Eds.), *Flora Malesiana, vol. 12(2).* Rijksherbarium/Hortus Botanicus, Leiden University, Leiden, Netherlands. pp. 409-784.

Hu, J.-M., Lavin, M., Wojciechowski, M.F., Sanderson, M.J. 2000. Phylogenetic systematics of the tribe Millettieae (Leguminosae) based on chloroplast trnK/matK sequences and its implications for evolutionary patterns in Papilionoideae. American Journal of Botany 87(3): 418-430.

Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey, U.S.A. 375 pages.

Hughes, C.E., Pennington, R.T., Antonelli, A. 2013. Neotropical plant evolution: assembling the Big Picture. Botanical Journal of the Linnean Society 171: 1–18.

Hughes, C.E., Atchison, G.W. 2015. The ubiquity of alpine plant radiations: from the Andes to the Hengduan Mountains. New Phytologist 207(2) : 275-282.

Hul Thol, S. 1976. Contribution à la révision de quelques genres de Caesalpiniaceae, représentés en Asie. (Doctoral thesis), Université Pierre et Marie Curie (Paris VI), 209 pages.

Hul Thol, S., Hideux, M. 1977. Taxonomie du genre *Pterolobium* (Caesalpiniaceae) avec traitement numérique des caractères macromorphologiques et palynologiques. Bulletin du Museum National d'Histoire Naturelle (Paris), 3e série (502): 1-165.

Humphreys, A M., Barraclough, T.G. 2014. The evolutionary reality of higher taxa in mammals. Proceedings of the Royal Society of London B: Biological Sciences 281(1783): 20132750.

Humphreys, A.M., Linder, H.P. 2009. Concept versus data in delimitation of plant genera. Taxon 58(4): 1054–1074.

Huson, D.H., Bryant, D. 2006. Application of phylogenetic networks in evolutionary studies. Molecular Biology and Evolution 23: 254–267.

Iturralde-Vinent, M.A., MacPhee, R.D.E. 1999 Paleogeography of the Caribbean region: implications for Cenozoic biogeography. Bulletin of the American Museum Natural History 238: 1-95.

Jansen, P.C.M. 2005. *Caesalpinia sappan* L. [Internet] Record from PROTA4U. Jansen, P.C.M., Cardon, D. (Eds.). PROTA (Plant Resources of Tropical Africa / Ressources végétales de l'Afrique tropicale), Wageningen, Netherlands. <http://www.prota4u.org/search.asp>. Accessed 15 May 2015.

Janzen, D.H. 1988. Tropical dry forests: the most endangered major tropical ecosystem. In: Wilson E.O. (Ed), *Biodiversity*. National Academy Press, Washington, U.S.A. pp. 130–137.

Johnson, K.A., Holland, B.R., Heslewood, M.M., Crayn, D.M. 2012. Supermatrices, supertrees and serendipitous scaffolding: inferring a well-resolved, genus-level phylogeny of Styphelioideae (Ericaceae) despite missing data. Molecular Phylogenetics and Evolution 62(1): 146-158.

Johnston, I.M. 1940. The floristic significance of shrubs common to North and South American deserts. Journal of the Arnold Arboretum 21: 356-363.

Joly, S., Bruneau, A. 2006. Incorporating allelic variation for reconstructing the evolutionary history of organisms from multiple genes: an example from *Rosa* in North America. Systematic Biology 55: 623–636.

Kajita, T., Vataranpast, M., Takayama, K., Wakita, N., Nagashima, R., Tateishi, Y. 2013. Sea dispersal and the distribution of pantropical legumes. Oral Presentation, 6th International Legume Conference. University of Johannesburg, Johannesburg, South Africa.

Kantz, K.E. 1996. Floral development in the Caesalpinioid tribe, Caesalpinieae (Fabaceae). (Doctoral Dissertation) Louisiana State University, Baton Rouge, U.S.A.

Kantz, K.E., Tucker, S.C. 1994. Developmental basis of floral characters in the Caesalpinieae. In: Ferguson, I.K., Tucker, S.C. (Eds.), *Advances in legume systematics, part 6: structural botany*. Royal Botanic Gardens, Kew, Richmond, United Kingdom, pp. 33–40.

Kass, R.E., Raftery, A.E. 1995. Bayes factors. Journal of the American Statistical Association 90(430): 773-795.

Kiesling, R., Mulgura, M.E., Ulibarri, E.A. 1994. *Flora de San Juan, Republica Argentina, vol. 1.* Vazquez Mazzini Editores, Buenos Aires, Argentina.

Kite, G., Lewis, G.P. 1994. Chemotaxonomy of seed non-protein amino acids in *Caesalpinia* s.l. In: Sprent, J.I., McKey, D. (Eds.), *Advances in legume systematics, part 5: the nitrogen factor.* Royal Botanic Gardens, Kew, Richmond, United Kingdom, pp. 101–105.

Knapp, S. 2002. Assessing patterns of plant endemism in neotropical uplands. Botanical Review 68: 22–37.

Koch, C.U., Guitiérrez, J.E., Rodriguez, A., von Helversen, O., 2004. Bat pollination in a Cuban ultramafic endemic *Caesalpinia bahamensis* Lam. subps. *orientensis* Borhidi. In: Boyd, R.S., Barker, A.J.M., Protor, J. (Eds.), *Ultramafic rocks: their soils, vegetation and fauna*. Science Reviews 2000 Ltd, St-Albans, United Kingdom. pp. 243–253.

Koenen, E.J.M., Vos, J.M. de, Atchison, G.W., Simon, M.F., Schrire, B.D., de Souza, E.R., de Queiroz, L.P., Hughes, C.E. 2013. Exploring the tempo of species diversification in legumes. South African Journal of Botany 89: 19-30.

Kozak, K.H., Weisrock, D.W., Larson, A. 2006. Rapid lineage accumulation in a nonadaptive radiation: phylogenetic analysis of diversification rates in eastern North American woodland salamanders (Plethodontinae: Plethodon). Proceedings of the Royal Society B: Biological sciences 27: 539–546.

Kreft, H., Jetz, W. 2007. Global patterns and determinants of vascular plant diversity. Proceedings of the National Academy of Sciences, 104(14) : 5925-5930.

Kunth, C.S. 1824. *Coulteria*. In : *Voyage de Humbold et Bonplad, sixième partie*. Botanique. Nova Genera et Species Plantarum 6 : 328-332.

Ky, C.L., Barre, P., Lorieux, M., Trouslot, P., Akaffou, S., Louarn, J., Charrier, A., Hamon, S., Noirot, M., 2000. Interspecific genetic linkagemap, segregation distortion and genetic conversion in coffee (*Coffea* sp.). Theoretical and Applied Genetics 101: 669–676.

Lavin, M. 2006. Floristic and geographical stability of discontinuous seasonally dry tropical forests explains patterns of plant phylogeny and endemism. In: Pennington, R.T., Ratter, J.A., Lewis, G.P. (Eds.), *Neotropical savannas and seasonally dry forests: Plant biodiversity, biogeographic patterns and conservation*. CRC Press, Boca Raton, Florida, U.S.A. pp. 433–447.

Lavin, M., Beyra-Matos, A. 2008. The impact of ecology and biogeography on Legume diversity, endemism, and phylogeny in the Caribbean region: a new direction in historical biogeography. The Botanical Review 74(1): 178-196.

Lavin, M., Herendeen, P.S., Wojciechowski, M.F. 2005. Evolutionary rates analysis of Leguminosae implicates a rapid diversification of lineages during the Tertiary. Systematic Biology 54(4): 575-594.

Lavin, M., Thulin, M., Labat, J.-N., Pennington, R.T. 2000. Africa, the odd man out: molecular biogeography of Dalbergioid Legumes (Fabaceae) suggests otherwise. Systematic Botany 25(3): 449-467.

Lavin, M., Wojciechowski, M.F., Richman, A., Rotella, J., Sanderson, M.J., & Beyra-Matos, A. 2001. Identifying Tertiary radiations of Fabaceae in the Greater Antilles: alternatives to cladistic vicariance analysis. International Journal of Plant Sciences 162(S6): S53-S76.

Lavin, M., Wojciechowski, M.F., Gasson, P., Hughes, C.E., Wheeler, E. 2003. Phylogeny of Robinioid Legumes (Fabaceae) revisited: *Coursetia* and *Gliricidia* recircumscribed, and a biogeographical appraisal of the Caribbean endemics. Systematic Botany 28: 387–409.

Lavin, M., Schrire, B.D., Lewis, G.P., Pennington, R.T., Delgado-Salinas, A., Thulin, M., Hughes, C.E., Matos, A.B., Wojciechowski, M.F. 2004. Metacommunity process rather than continental tectonic history better explains geographically structured phylogenies in legumes. Philosophical Tarnsactions of the Royal Society B: Biological Sciences 359: 1509–1522.

Legendre, P., Legendre, L. 2012. *Numerical ecology, 3rd edition*. Elsevier Science, Amsterdam. 1006 pages.

Legume Phylogeny Working Group (LPWG). 2013. Legume phylogeny and classification in the 21st century: orogress, prospects and lessons for other species-rich clades. Taxon 62(2): 217-248.

Lemmens, R.H.M.J., 2010. *Stuhlmannia moavi* Taub. [Internet] Record from PROTA4U. Lemmens, R.H.M.J., Louppe, D. & Oteng-Amoako, A.A. (Editors). PROTA (Plant Resources of Tropical Africa / Ressources végétales de l'Afrique tropicale), Wageningen, Netherlands. <http://www.prota4u.org/search.asp>. Accessed 15 May 2015.

Lersten, N.R., Curtis, J.D., 1994. Leaf anatomy in *Caesalpinia* and *Hoffmannseggia* (Leguminosae, Caesalpinioidae) with emphasis on secretory structures. Plant Systematics and Evolution 192: 231–255

Lersten, N.R., Curtis, J.D., 1996. Survey of leaf anatomy, especially secretory structures, of tribe Caesalpinieae (Leguminosae, Caesalpinioideae). Plant Systematics and Evolution 200: 21–39.

Lewis, G.P. 1987. Legumes of Bahia. Royal Botanic Gardens, Kew, United Kingdom. 369 pages.

Lewis, G.P. 1996. Notes on *Stuhlmannia* Taub. and the correct placement of *Caesalpinia insolita* (Harms) Brenan & J.B. Gillett (Leguminosae: Caesalpinioideae: Caesalpinieae). Kew Bulletin 51(2): 377-379.

Lewis, G.P. 1998. Caesalpinia*: a revision of the Poincianella-Erythrostemon group*. Royal Botanic Gardens, Kew, United Kindgom. 233 pages.

Lewis, G.P., 2005. Tribe Caesalpinieae. In: Lewis, G., Schrire, B., Mackinder, B., Lock, M. (Eds.), *Legumes of the World.* Royal Botanic Gardens, Kew, Richmond, United Kingdom. pp. 127–159.

Lewis, G.P., Schrire, B., Mackinder, B., Lock, M. 2005. *Legumes of the World.* Royal Botanic Gardens, Kew, U.K. 577 pages.

Lewis, G.P., Hughes, C.E., Daza Yomona, A., Solange Sotuyo, J., Simon, M.F. 2010. Three new legumes endemic to the Marañón Valley, Perú. Kew Bulletin 65(2): 209–220.

Lewis, G.P., Schrire, B.D. 1995. A reappraisal of the Caesalpinia Group (Caesalpinioideae: Caesalpinieae) using phylogenetic analysis. In: Crisp, M.D., Doyle, J.J. (Eds.), *Advances in legume systematics, part 7: phylogeny*. Royal Botanic Gardens, Kew, United Kingdom. pp. 41-52.

Lewis, G.P., Sotuyo, J.S. 2010. *Hoffmannseggia aphylla* (Leguminosae: Caesalpinieae), a new name for a Chilean endemic. Kew Bulletin 65(2): 221-224.

Lima, H.C.de, Lewis, G.P., Bueno, E. 2002. Pau-brasil: uma biografia. In: Bueno, E. (Ed.), *Pau-brasil*. Axis Mundi, São Paulo, Brazil. pp. 39-76.

Linares-Palomino, R. 2006. Phytogeography and floristics of seasonally dry tropical forests of Peru. In: Pennington, R.T., Lewis, G.P., Ratter, J.A. (Eds.), *Neotropical savannas and seasonally dry forests: plant diversity, biogeography and conservation*. CRC Press, Boca Raton, Florida, U.S.A. pp. 257–280.

Linares-Palomino, R., Kvist, L., Aguirre-Mendoza, Z., Gonzales- Inca, C. 2010. Diversity and endemism of woody plant species in the Equatorial Pacific seasonally dry forests. Biodiversity & Conservation 19: 169–185.

Linares-Palomino, R., Oliveira-Filho, A., Pennington, R.T. 2011. Neotropical seasonally dry forests: diversity, endemism, and biogeography of woody plants. In: Dirzo, R., Young, H., Mooney, H., Ceballos, G. (Eds.), *Seasonally dry tropical forests: ecology and conservation.* Island Press, Washington, D.C., U.S.A. pp. 3-21.

Linder, H.P., Baeza, M., Barker, N.P., Galley, C., Humphreys, A.M., Lloyd, K.M., Orlovich, D.A., Pirie, M.D., Simon, B.K., Walsh, N., Verboom, G.A. 2010. A generic classification of the Danthonioideae (Poaceae). Annals of the Missouri Botanical Garden 97(3): 306–364.

Lira, C.F., Cardoso, S.R.S., Ferreira, P.C.G., Cardoso, M.A., Provan, J. 2003. Long-term population isolation in the endangered tropical tree species *Caesalpinia echinata* Lam. revealed by chloroplast microsatellites. Molecular Ecology 12(12): 3219–3225.

Little, E.L., Wadsworth, F.H. 1964. Common trees of Puerto Rico and the Virgin islands. U.S. Department of Agriculture, Forest Service, Washington D.C., U.S.A.

Liu, H., Edwards, E., Freckleton, R., Osborne, C. 2012. Phylogenetic niche conservatism in C4 grasses. Oecologia, 170(3), 835-845.

Lock, J.M. 1989. *Legumes of Africa: a check-list*. Royal Botanical Gardens, Kew, United Kingdom. 626 pages.

Lock, J.M. 2006. The seasonally dry vegetation of Africa: parallels and comparisons with the Neotropics. In: Pennington, R.T., Lewis, G.P., and Ratter, J.A. (Eds.), *Neotropical savannas and seasonally dry forests: plant diversity, biogeography, and conservation.* CRC Press, Boca Raton, U.S.A. pp. 450-467.

Luckow, M. 1995. Species Concepts: Assumptions, Methods, and Applications. Systematic Botany 20:589-605.

Luebert, F., Weigend, M. 2014. Phylogenetic insights into Andean plant diversification. Frontiers in Ecology and Evolution 2: 1-17.

Macbride, J.F. 1943. *Flora of Peru, vol. 8, part 3, no. 1 : Leguminosae.* Field Museum of Natural History, Chicago, U.S.A. 507 pages.

Mace, G.M. 2004. The role of taxonomy in species conservation. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 359(1444): 711-719.

Mackinder, B.A., Saslis-Lagoudakis, H., Wieringa, J.J., Devey, D., Forest, F., Bruneau, A. 2013. The tropical African legume *Scorodophloeus* clade includes two undescribed *Hymenostegia* segregate genera and *Micklethwaitia*, a rare, monospecific genus from Mozambique. South African Journal of Botany 89: 156-163.

Mackinder, B.A., Wieringa, J.J. 2013. *Annea* gen. nov. (Detarieae, Caesalpinioideae, Leguminosae): a home for two species long misplaced in *Hymenostegia* sensu lato. Phytotaxa 142(1): 1-14.

Maddison, W.P., Maddison, D.R. 2011. Mesquite: a modular system for evolutionary analysis. Version 2.75. http://mesquiteproject.org

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K. 2014. cluster: cluster analysis basics and extensions. R package, version 1.15.2. http://cran.r-project.org/web/packages/cluster/

Manzanilla, V., Bruneau, A., 2012. Phylogeny reconstruction in the Caesalpinieae grade (Leguminosae) based on duplicated copies of the sucrose synthase gene and plastid markers. Molecular Phylogenetics and Evolution 65: 149–162.

Marazzi, B., Ané, C., Simon, M. F., Delgado-Salinas, A., Luckow, M., Sanderson, M.J. 2012. Locating evolutionary precursors on a phylogenetic tree. Evolution 66(12): 3918-3930.

Marazzi, B., Endress, P.K., Queiroz, L.P.de, Conti, E., 2006. Phylogenetic relationships within Senna (Leguminosae, Cassiinae) based on three chloroplast DNA regions: patterns in the evolution of floral symmetry and extrafloral nectaries. American Journal of Botany 93: 288–303.

Marazzi, B., Sanderson, M.J. 2010. Large-scale patterns of diversification in the widespread legume genus *Senna* and the evolutionary role of extrafloral nectaries. Evolution 64: 3570–3592.

Matzke, N.J. 2012. Founder-event speciation in BioGeoBEARS package dramatically improves likelihoods and alters parameter inference in Dispersal-Extinction-Cladogenesis (DEC) analyses. Frontiers of Biogeography 4(suppl. 1): 210.

Mayden, R.L. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. In: Claridge, M.F., Dawah, H.A., Wilson, M.R. (Eds.), *Species: the units of biodiversity*. Chapman & Hall Ltd., London, United Kingdom. pp. 381-424.

Mayle, F.E. 2006. The late Quartenary biogeographical history of South American seasonally dry tropical forests: insight from palaeo-ecological data. In: Pennington, R.T., Lewis, G.P., Ratter, J.A. (Eds.), *Neotropical savannas and seasonally dry forests: plant diversity, biogeography and conservation*. CRC Press, Boca Raton, Florida, U.S.A. pp. 395-416.

Mayle, F.E., Beerling, D.J., Gosling, W.D., Bush, M.B. 2004. Responses of amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. Philosophical Transactions: Biological Sciences 359: 499-514.

Mayr, E. 1995. Species, classification, and evolution. In: Arai R., Kata M., Doi Y. (Eds.), *Biodiversity and Evolution*. National Science Museum Foundation, Tokyo, Japan. pp. 3-12.

McDaniel, S.F., Shaw, A.J. 2003. Phylogeographic structure and cryptic speciation in the trans-Antarctic moss *Pyrrhobryum mnioides*. Evolution 57: 205–215.

McKey, D. 1994. Legumes and nitrogen: the evolutionary ecology of a nitrogen-demanding lifestyle. In: Sprent J.I., McKey D. (Eds.), *Advances in legume systematics, part 5: the nitrogen factor*. Royal Botanic Gardens, Kew, United Kingdom. pp. 211–228.

Meseguer, A.S., Lobo, J.M., Ree, R., Beerling, D.J., Sanmartín, I. 2015. Integrating fossils, phylogenies, and niche models into biogeography to reveal ancient evolutionary history: the case of *Hypericum* (Hypericaceae). Systematic Biology 64(2): 215-232.

Miles, L., Newton, A. C., DeFries, R. S., Ravilious, C., May, I., Blyth, S., Kapos, V., Gordon, J.E. 2006. A global overview of the conservation status of tropical dry forests. Journal of Biogeography 33(3): 491-505.

Miller, J.T., Seigler, D. 2012. Evolutionary and taxonomic relationships of *Acacia* s.l. (Leguminosae: Mimosoideae). Australian Systematic Botany 25(3): 217-224.

Miller, M.A., Pfeiffer, W., Schwartz, T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, Louisiana, 14 Nov 2010. pp. 45–52.

Montes, C., Cardona, A., Jaramillo, C., Pardo, A., Silva, J. C., Valencia, V., Ayala, C., Pérez-Angel, L.C., Rodriguez-Parra, L.A., Ramirez, V., Niño, H. 2015. Middle Miocene closure of the Central American Seaway. Science 348(6231): 226-229.

Morrone, J.J., Crisci, J.V. 1995. Historical biogeography: introduction to methods. Annual Review of Ecology and Systematics 26: 373-401.

Moore, M.J., Jansen, R.K. 2006. Molecular evidence for the age, origin, and evolutionary history of the American desert plant genus *Tiquilia* (Boraginaceae). Molecular Phylogenetics and Evolution 39(3): 668-687.

Moore, M.J., Tye, A., Jansen, R.K. 2006. Patterns of long-distance dispersal in *Tiquilia* subg. *tiquilia* (Boraginaceae): Implications for the origins of amphitropical disjuncts and Galápagos Islands endemics. American Journal of Botany 93: 1163–1177.

Moritz, C. 2002. Strategies to protect biological diversity and the evolutionary processes that sustain it. Systematic Biology 51: 238–254.

Müller, K., 2005. SeqState — primer design and sequence statistics for phylogenetic DNA data sets. Applied Bioinformatics 4: 65–69.

Murphy, D. 2008. A review of the classification of *Acacia* (Leguminosae, Mimosoideae). Muelleria 26(1):10-26.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B. da, Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A. 2008. Mechanisms of long-distance seed dispersal. Trends in Ecology & Evolution 23(11): 638-647.

Nicolson, D.H. 1980. *Moullava* Adanson, recently *Wagatea* Dalzell (Fabaceae-Caesalpinioideae). In: Manilal, K.S. (Ed.), *Botany and History of Hortus Malabaricus.* Oxford & IBH Publi. Co., New Delhi, India. pp. 181-185.

Nogales, M., Heleno, R., Traveset, A., Vargas, P. 2012. Evidence for overlooked mechanisms of long-distance seed dispersal to and between oceanic islands. New Phytologist, 194(2): 313-317.

Nores, M.J., Simpson, B.B., Hick, P., Anton, A.M., Fortunato, R.H. 2012. The phylogenetic relationships of four monospecific caesalpinioids (Leguminosae) endemic to southern South America. Taxon 61(4): 790–802.

Oliveira-Filho, A.T., Jarenkow, J.A., Rodal, M.J.N. 2006. Floristic relationships of seasonally dry forests of eastern South America based on tree species distribution patterns**.** In: Pennington, R.T., Lewis, G.P., Ratter, J.A. (Eds.), *Neotropical savannas and seasonally dry forests: plant diversity, biogeography and conservation*. CRC Press, Boca Raton, Florida, U.S.A. pp.159-192.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R. 2001. Terrestrial ecoregions of the world: a new map of life on Earth: a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. BioScience 51(11): 933-938.

Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.-S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J, Owens, I.P.F. 2005. Global hotspots of species richness are not congruent with endemism or threat. Nature 436: 1016–1019.

Orthia, L.A., Cook, L.G., Crisp, M.D. 2005. Generic delimitation and phylogenetic uncertainty: an example from a group that has undergone an explosive radiation. Australian Systematic Botany 18(1): 41-47.

Orwa, C., Mutua, A., Kindt, R. Jamnadass, R., Anthony, S. 2009 Agroforestree Database: a tree reference and selection guide version 4.0 [consulté le 13 juin 2015] (http://www.worldagroforestry.org/sites/treedbs/treedatabases.asp /).

Oxelman, B., Lidén, M., Berglund, D. 1997. Chloroplast rps16 intron phylogeny of the tribe Sileneae (Caryophyllaceae). Plant Systematics and Evolution 206: 393–410.

Paradis, E., Claude, J., Strimmer, K. 2004. APE: Analyses of phylogenetics and evolution in R language. Bioinformatics 20: 289–290.

Parrish, J.T. 1993. The palaeogeography of the opening South Atlantic. In: George, W., Lavocat, R. (Eds.), *The Africa-South America connection*. Clarendon, Oxford, United Kingdom. pp. 8-27.

Pedley, L. 1997. Notes on *Caesalpinia* subg. *Mezoneuron* (Leguminosae: Caesalpinioideae) in Australia. Austrobaileya 5(1): 97-102.

Pennington, R.T., Lavin, M., Oliveira-Filho, A., 2009. Woody plant diversity, evolution, and ecology in the tropics: perspectives from seasonally dry tropical forests. Annual Review of Ecology, Evolution, and Systematics 40: 437–457.

Pennington, R.T., Prado, D.E., Pendry, C.A. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. Journal of Biogeography 27: 261–273.

Pennington, R.T., Richardson, J.E., Lavin, M. 2006. Insights into the historical construction of species-rich biomes from dated plant phylogenies, neutral ecological theory and phylogenetic community structure. New Phytologist 172(4): 605-616.

Pennington, R.T., Daza, A., Reynel, C., Lavin, M. 2011. *Poissonia eriantha* (Leguminosae) from Cuzco, Peru: an overlooked species underscores a pattern of narrow endemism common to seasonally dry neotropical vegetation. Systematic Botany 36: 59–68.

Pennington, R.T., Lavin, M., Prado, D.E., Pendry, C.A., Pell, S.K., Butterworth, C.A. 2004. Historical climate change and speciation: neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. Philosophical Transactions series B: Biological sciences 359: 515–537.

Pennington, R.T., Lavin, M., Särkinen, T., Lewis, G.P., Klitgaard, B.B., Hughes, C.E. 2010. Contrasting plant diversification histories within the Andean biodiversity hotspot. Proceedings of the National Academy of Sciences 107: 13783–13787.

Philippe, H., Snell, E.A., Bapteste, E., Lopez, P., Holland, P.W.H., Casane, D. 2004. Phylogenomics of Eukaryotes: impact of missing data on large alignments. Molecular Biology and Evolution 21(9): 1740-1752.

Pitman, N.C.A., Terborgh, J.W., Silman, M.R., Núñez V.P., Neill, D.A., Cerón, C.E., Palacios, W.A., Aulestia, M. 2001. Dominance and distribution of tree species in upper Amazonian Terra Firme forests. Ecology 82(8): 2101-2117.

Pitman, N.C.A., Terborgh, J., Silman, M.R., Nuñez V.P. 1999. Tree species distributions in upper Amazonian forest. Ecology 80(8): 2651-2661.

Polhill, R., Vidal, J. 1981. Caesalpinieae. In: Polhill, R., Raven, P.H. (Eds.), *Advances in legume systematics, part 1.* Royal Botanic Gardens, Kew, Richmond, United Kingdom. pp. 81–95.

Pons J., Barraclough T.G., Gomez-Zurita J., Cardoso A., Duran D.P., Hazell S., Kamoun S., Sumlin W.D. & Vogler A.P. 2006. Sequence-based species delimitation for the DNA taxonomy of undescribed insects. Systematic Biology 55: 595-609.

Prado, D.E., Gibbs, P.E. 1993. Patterns of species distributions in the dry seasonal forests of South America. Annals of the Missouri Botanical Garden 80(4): 902-927.

Price, J.P., Clague, D.A. 2002. How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. Proceedings of the Royal Society B: Biological Science 269(1508): 2429-2435.

Pyron, R.A., Burbrink, F.T., Colli, G.R., de Oca, A.N.M., Vitt, L.J., Kuczynski, C.A., & Wiens, J.J. 2011. The phylogeny of advanced snakes (Colubroidea), with discovery of a new subfamily and comparison of support methods for likelihood trees. Molecular Phylogenetics and Evolution, 58(2): 329-342.

Queiroz K.de, Donoghue M.J. 1988. Phylogenetic systematic and the species problem. Cladistics 4: 317-338.

Queiroz K.de. 2005 A unified concept of species and its consequences for the future of taxonomy. Proceedings of the California Academy of Sciences 56(18): 196-215.

Queiroz, K.de. 2007. Species concepts and species Delimitation. Systematic Biology 56(6): 879-886.

Queiroz L.P.de. 2006. The Brazilian Caatinga: phytogeographical patterns inferred from distribution data of the Leguminosae. In: Pennington, R.T., Lewis, G.P., Ratter, J.A. (Eds.), *Neotropical savannas and seasonally dry forests: plant diversity, biogeography and conservation*. CRC Press, Boca Raton, Florida, U.S.A. pp. 121–58.

Queiroz, L.P.de, 2009. *Leguminosas da Caatinga*. Universidade Estadual de Feira de Santana, Associacao Plantas do Nordeste and Royal Botanic Gardens, Kew, Richmond, United Kingdom. 443 pages.

Queiroz, L.P.de, Lavin, M. 2011. *Coursetia* (Leguminosae) from eastern Brazil: nuclear ribosomal and chloroplast DNA sequence analysis reveal the monophyly of three Caatinga-inhabiting species. Systematic Botany 36: 69–79.

R Core Team 2012. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Rabosky, D.L. 2014. Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. PLoS ONE: 9(2) e89543. doi: 10.1371/journal.pone.0089543

Rabosky, D.L., Donnellan, S.C., Grundler, M., Lovette, I.J. 2014. Analysis and visualization of complex macroevolutionary dynamics: an example from Australian Scincid lizards. Systematic Biology 63(4): 610-627.

Rabosky, D.L., Grundler, M., Anderson, C., Title, P., Shi, J.J., Brown, J.W., Huang, H. Larson, J.G. 2014. BAMMtools: an R package for the analysis of evolutionary dynamics on phylogenetic trees. Methods in Ecology and Evolution 5(7): 701-707.

Rambaut A., Suchard, M.A., Xie, D., Drummond, A.J. 2014. Tracer v1.6, retrieved September 2014, http://beast.bio.ed.ac.uk/Tracer

Rambaut, A., Suchard, M.A., Drummond, A.J. 2009. Tracer v.1.5., retrieved 8 June, 2015, from http://beast.bio.ed.ac.uk/software/tracer/

Raven, P.H., Pohill, R.M. 1981. Biogeography of the Leguminosae. In: Polhill, R.M., Raven, P.H. (Eds.), *Advances in legume systematics part 1*. Royal Botanic Gardens, Kew, United Kingdom. pp. 27-34.

Ree, R.H., Moore, B.R., Webb, C.O., Donoghue, M.J. 2005. A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. Evolution, 59(11): 2299-2311.

Richardson, J.E., Pennington, R.T., Pennington, T.D., Hollingsworth, P.M. 2001. Rapid diversification of a species-rich genus of neotropical rain forest trees. Science 293(5538): 2242-2245.

Ricklefs, R. E. (2006). Evolutionary diversification and the origin of the diversity-environment relationships. Ecology*,* 87: S3-S13.

Ricklefs, R.E., Jenkins, D.G. 2011. Biogeography and ecology: towards the integration of two disciplines. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 366(1576): 2438-2448.

Rieseberg L.H., Wood T.E., Baack E.J. (2006) The nature of plant species. Nature 440: 524-527.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A., Huelsenbeck, J.P. 2012. MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542.

Ross, J.H. 1977. *Caesalpinioideae, Fabaceae, Flora of Southern Africa, vol. 16, no. 2*. Botanical Research Institute, Pretoria, South Africa. 142 pages.

Roti-Michelozzi, G. 1957. Adumbratio Florae Aethiopicae: 6. Caesalpiniaceae (excl. gen. Cassia). Webbia 13(1): 133-228.

Roux, J.P. 2003. *Caesalpinia*. In: Germishuizen, G., Meyer, L. (Eds.), *Plants of Southern Africa: An Annotated Checklist, Strelitzia 14*. National Botanical Institute, Pretoria, South Africa. 1231 pages.

Rudall, P.J., Myers, G., Lewis, G.P. 1994. Floral secretory structures in *Caesalpinia* sensu lato and related genera. In: Ferguson, I.K., Tucker, S. (Eds.), *Advances in legume* *systematics, part 6: structural botany*. Royal Botanic Gardens, Kew, United Kingdom, pp. 41–52.

Rundel, P.W., Dillon, M.O., Palma, B., Mooney, H., Gulmon, S., Ehleringer, J. 1991. The phytogeography and ecology of the coastal Atacama and Peruvian deserts. Aliso 13(1): 1-49.

Sanderson, M. J., Boss, D., Chen, D., Cranston, K.A., Wehe, A. 2008. The PhyLoTA browser: processing GenBank for molecular phylogenetics research. Systematic Biology 57(3): 335-346.

Sanjappa, M. 1992. *Legumes of India.* Bishen Singh Mahendra Pal Singh, Dehra Dun, India. 338 pages.

Särkinen, T.E., Iganci, J., Linares-Palomino, R., Simon, M., Prado, D. 2011a. Forgotten forests - issues and prospects in biome mapping using Seasonally Dry Tropical Forests as a case study. BMC Ecology 11(1): 27.

Särkinen, T.E., Marcelo-Peña, J.L., Yomona, A.D., Simon, M.F., Pennington, R.T., Hughes, C.E. 2011b. Underestimated endemic species diversity in the dry inter-Andean valley of the Río Marañón, northern Peru: an example from Mimosa (Leguminosae, Mimosoideae). Taxon 60: 139–150.

Särkinen, T.E., Pennington, R.T., Lavin, M., Simon, M.F. & Hughes, C.E. 2012. Evolutionary islands in the Andes: persistence and isolation explain high endemism in Andean dry tropical forests. Journal of Biogeography 39: 884–900.

Schrire, B.D., Lewis, G.P., Lavin, M., 2005. Biogeography of the Leguminosae. In: Lewis, G., Schrire, B., Mackinder, B., Lock, M. (Eds.), *Legumes of the World*. Royal Botanic Gardens, Kew, Richmond, United Kingdom. pp. 21–54.

Schrire, B.D., Lavin, M., Barker, N.P. Forest, F. 2009. Phylogeny of the tribe Indigofereae (Leguminosae–Papilionoideae): geographically structured more in succulent-rich and temperate settings than in grass-rich environments. American Journal of Botany 96: 816–852.

Scopece G., Cozzolino, S., Bateman, R.M. 2010. Just what is a genus? Comparing levels of postzygotic isolation to test alternative taxonomic hypotheses in Orchidaceae subtribe Orchidinae. Taxon 59: 1754-1764.

Scotese, C.R. 2001. *Atlas of earth history, vol. 1.* PALEOMAP Project, Arlington, Texas, U.S.A. 52 pages.

Senut, B., Pickford, M., Ségalen, L. 2009. Neogene desertification of Africa. Comptes Rendus Geoscience 341(8–9): 591-602.

Shaw, J., Lickey, E.B., Beck, J.T., Farmer, S.B., Liu, W., Miller, J., Siripun, K.C., Winder, C.T., Schilling, E.E., Small, R.L., 2005. The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. American Journal of Botany 92: 142–166.

Shaw, J., Lickey, E.B., Schilling, E.E., Small, R.L., 2007. Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: the tortoise and the hare III. American Journal of Botany 94: 275–288.

Shi, J.J., Rabosky, D.L. 2015. Speciation dynamics during the global radiation of extant bats. Evolution 69(6): 1528-1545.

Shorthouse, D.P. 2010. SimpleMappr, an online tool to produce publication-quality point maps. http://www.simplemappr.net (accessed 29 Aug 2014)

Silva, M.J.d., Queiroz, L.P.d., Tozzi, A.M.G.d.A., Lewis, G.P., Sousa, A.P. d. 2012. Phylogeny and biogeography of *Lonchocarpus* sensu lato and its allies in the tribe Millettieae (Leguminosae, Papilionoideae). Taxon 61(1): 93-108.

Simmons, M.P., Ochoterena, H. 2000. Gaps as characters in sequence-based phylogenetic analyses. Systematic Biology 49: 369–381.

Simon, M.F., Grether, R., de Queiroz, L.P., Skema, C., Pennington, R.T., Hughes, C.E. 2009. Recent assembly of the Cerrado, a Neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. Proceedings of the National Academy of Sciences 106: 20359–20364.

Simpson, B., Ulibarri, E. 2006. A synopsis of the genus *Hoffmannseggia* (Leguminosae). Lundellia (9): 7-33.

Simpson, B.B. 1998. A revision of *Pomaria* (Fabaceae) in North America. Lundellia 1: 46-71.

Simpson, B.B. 1999. A revision of *Hoffmannseggia* (Fabaceae) in North America. Lundellia 2: 14-54.

Simpson, B.B., Larkin, L., Weeks, A. 2003. Progress towards resolving the relationships of the Caesalpinia Group (Caesalpinieae: Caesalpinioideae: Leguminosae). In: Klitgaard, B.B., Bruneau, A. (Eds.), *Advances in Legume Systematics, part 10: Higher Level Systematics*. Royal Botanic Gardens, Kew, United Kindgdom. pp. 124–148.

Simpson, B.B., Larkin, L., Weeks, A., McDill, J. 2006. Phylogeny and biogeography of *Pomaria* (Caesalpinioideae: Leguminosae). Systematic Botany 31(4): 792–804.

Simpson, B.B., Lewis, G.P. 2003. New combinations in *Pomaria* (Caesalpinioideae: Leguminosae). Kew Bulletin 58 (1): 175–184.

Simpson, B.B., Miao, B.M. 1997. The circumscription of *Hoffmannseggia* (Fabaceae, Caesalpinioideae, Caesalpinieae) and its allies using morphological and cpDNA restriction site data. Plant Systematics and Evolution 205:157–178.

Simpson, B.B., Tate, J.A., Weeks, A. 2004. Phylogeny and character evolution of *Hoffmannseggia* (Caesalpinieae: Caesalpinioideae: Legminosae). Systematic Botany 29(4): 933–946.

Simpson, B.B., Tate, J.A., Weeks, A. 2005. The biogeography of *Hoffmannseggia* (Leguminosae, Caesalpinioideae, Caesalpinieae): a tale of many travels. Journal of Biogeography 32(1): 15–27.

Sirichamorn, Y., Adema, F.A.C.B., Roos, M.C., van Welzen, P.C. 2014. Molecular and morphological phylogenetic reconstruction reveals a new generic delimitation of Asian *Derris* (Fabaceae): Reinstatement of *Solori* and synonymisation of *Paraderris* with *Derris*. Taxon 63(3): 522-538.

Small, E. 1989. The evolution of genera in the Leguminosae. In: Stirton, C.H., Zarucchii, J.L. (Eds.), *Advances in legume biology*. Proceedings of the 2nd International Legume Conference, St.Louis, Missouri. pp. 467-486.

Smith, K.L., Harmon, L.J., Shoo, L.P., Melville, J. 2011. Evidence of constrained phenotypic evolution in a cryptic species complex of agamid lizards. Evolution 65: 976–992.

Smith, S.A., Donoghue, M.J. 2010. Combining historical biogeography with niche modeling in the Caprifolium clade of *Lonicera* (Caprifoliaceae, Dipsacales). Systematic Biology 59(3): 322-341.

Solbrig, O.T. 1972. Floristic disjunctions between monte in Argentina and Sonoran desert in Mexico and United States. Annals of the Missouri Botanical Garden 59(2): 218-223.

Souza-Neto, A.C., Cianciaruso, M.V., Collevatti, R.G. 2015. Habitat shifts shaping the diversity of a biodiversity hotspot through time: insights from the phylogenetic structure of

Caesalpinioideae in the Brazilian Cerrado. Journal of Biogeography. doi: 10.1111/jbi.12634

Sotuyo, J.S., Delgado-Salinas, A., Chase, M., Lewis, G.P., Oyama, K. 2007. Cryptic speciation in the *Caesalpinia hintonii* complex (Leguminosae: Caesalpinioideae) in a seasonally dry Mexican forest. Annals of Botany 100: 1307–1314.

Sotuyo, S., Lewis, G.P. 2007. A new species of *Caesalpinia* from the Río Balsas Depression, Mexico and an updated taxonomic circumscription of the *Caesalpinia hintonii* complex (Leguminosae: Caesalpinioideae: Caesalpinieae: Poincianella Group). Brittonia 59: 33–36.

Sprague, T. 1931. The botanical name of "Tara". Bulletin of Miscellaneous Information, Royal Botanic Gardens, Kew (2): 91-96.

Sprent, J.I. 2009. *Legume nodulation : a global perspective*. Wiley-Blackwell, Chicester, United Kingdom. 200 pages.

Stamatakis, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30(9): 1312-1313.

Standley, P.C., Steyermark, J.A. 1946. *Haematoxylon* L., Flora of Guatemala. Fieldiana: Botanical series 24(5): 137-141.

Stefano, R.D. de, Fernández-Concha, G.C., Can-Itza, L.L., Lavin, M. 2010. The morphological and phylogenetic distinctions of *Coursetia greenmanii* (Leguminosae): taxonomic and ecological implications. Systematic Botany 35: 289–295.

Stevens, P.F. 2002. Why do we name organisms? Some reminders from the past. Taxon 51(1): 11-26.

Strömberg, C.A.E. 2005. Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. Proceedings of the National Academy of Sciences of the United States of America 102(34): 11980-11984.

Strömberg, C.A.E. 2011. Evolution of grasses and grassland ecosystems. Annual Review of Earth and Planetary Sciences 39: 517-544.

Swenson, J., Young, B., Beck, S., Comer, P., Cordova, J., Dyson, J., Embert, D., Encarnacion, F., Ferreira, W., Franke, I., Grossman, D., Hernandez, P., Herzog, S., Josse, C., Navarro, G., Pacheco, V., Stein, B., Timana, M., Tovar, A., Tovar, C., Vargas, J., Zambrana-

Torrelio, C. 2012. Plant and animal endemism in the eastern Andean slope: challenges to conservation. BMC Ecology 12: 1.

Swofford, D.L. 2003. PAUP*, Phylogenetic analysis using parsimony (*and other methods).Version 4. Sinauer Associates, Sunderland, Massachusetts.

Taberlet, P., Gielly, L., Pautou, G., Bouvet, J. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. Plant Molecular Biology 17(5): 1105-1109.

Takayama, K., Kajita, T., Murata, J., Tateishi, Y. 2006. Phylogeography and genetic structure of *Hibiscus tiliaceus* — speciation of a pantropical plant with sea-drifted seeds. Molecular Ecology 15: 2871–2881.

Templeton, A.R. 1989. The meaning of species and speciation: A genetic perspective. In: Otte, D., Endler, J.A., (Eds.), *Speciation and its consequences*. Sinauer Associates, Sunderland, Massachusetts, U.S.A. pp.3-27.

Therneau, T., Atkinson, B., Ripley, B. 2012. rpart: Recursive partitioning. R package, version 3.1-55. http://cran.r-project.org/web/packages/rpart/index.html

Thorne, R.F. 1973. Floristic relationships between tropical Africa and tropical America. In: Meggers, B.J., Ayensu, E.S., Duckworth, W.D. (Eds.), *Tropical forest ecosystems in Africa and South America.* Smithsonian Institution Press, Washington, D.C., U.S.A. pp. 27–47.

Thulin, M. 1980. A new *Caesalpinia* (Leguminosae) from northeast Kenya. Kew Bulletin 34(4): 819-820.

Thulin, M. 1983. Leguminosae of Ethiopia. Opera Botanica 68: 1-223.

Thulin, M. 1993. Fabaceae (Leguminosae). In: Thulin, M. (Ed.), *Flora of Somalia, vol. 1.* Royal Botanical Gardens, Kew, United Kingdom. pp. 341-465.

Thulin, M., Lavin, M., Pasquet, R., Delgado-Salinas, A. 2004. Phylogeny and biogeography of *Wajira* (Leguminosae): a monophyletic segregate of *Vigna* centered in the Horn of Africa region. Systematic Botany 29(4): 903-920.

Tiffney, B.H. 1985. The Eocene North-Atlantic land-bridge – its importance in Tertiary and modern phytogeography of the northern hemisphere. Journal of the Arnold Arboretum 66(2): 243-273.

Trejo, I., Dirzo, R. 2002. Floristic diversity of Mexican seasonally dry tropical forests. Biodiversity Conservation, 11: 2063–84.

Tye, A. 2000. Las plantas vasculares endemicas de Galapagos. In: Valencia, R., Pitman, N., Leon-Yanez, S., Jorgensen, P.M. (eds.), *Libro rojo de las plantas endemicas del Ecuador 2000*. Herbario QCA, Pontificia Universidad Catolica del Ecuador, Quito, Ecuador. pp. 24-28.

U.S. Fish and Wildlife Service. 1995. *Stahlia monosperma* (cobana negra) Recovery Plan. U.S. Fish and Wildlife Service, Atlanta, Georgia. 15 pages. http://www.fws.gov/caribbean/ES/PDF/Recovery%20Plans/Stahlia%20monosperma.pdf, (consulté juin 2015).

Ulibarri, E.A. 1979. Las especies argentinas del genero *Hoffmannseggia* Cav. (Legum.-Caesalp.). Darwiniana 22(1-3): 135-158.

Ulibarri, E.A. 1996. Sinopsis de *Caesalpinia* y *Hoffmannseggia* (Leguminosae-Caesalpinioideae) de Sud América. Darwiniana 34(1-4): 299–348.

Ulibarri, E.A. 2005. *Zuccagnia punctata* (Leguminosae): ¿nuevo o viejo endemismo argentino? Darwiniana 43: 212-215.

Ulibarri, E.A. 2008. The genera of Caesalpinioideae (Leguminosae) from South America. Darwiniana 46(1): 69-163.

Uribe-Convers, S., Tank, D.C. 2015. Shifts in diversification rates linked to biogeographic movement into new areas, an example of disparate continental distributions and a recent radiation in the Andes. American Journal of Botany 102(11): 1854-1869.

Valencia, R., Balslev, H., Paz Y Miño C, G. 1994. High tree alpha-diversity in Amazonian Ecuador. Biodiversity & Conservation 3(1): 21-28.

Vataranpast, M., Takayama, K., Sousa, M.S., Tateishi, Y., Kajita, T. 2011. Origin of Hawaiian endemic species of *Canavalia* (Fabaceae) from sea-dispersed species revealed by chloroplast and nuclear DNA sequences. Journal of Japanese Botany 86: 15–25.

Vences, M., Guayasamin, J.M., Miralles, A., Riva, I.D.L. 2013. To name or not to name: criteria to promote economy of change in Linnaean classification schemes. Zootaxa 3636(2): 201-244.

Verdcourt, B. 1979. *A manual of New Guinea Legumes*. Office of Forests, Division of Botany, Lae, Papua New Guinea. Botany Bulletin, vol. 11. 646 pages.

Vidal, J.E., Hul Thol, S. 1974. Révision du genre *Pterolobium* (Caesalpiniaceae). Bulletin du Muséum National d'histoire naturelle, 3e série 227(15): 1–29.

Vidal, J.E., Hul Thol, S., 1976. Révision des *Caesalpinia* asiatiques. Bulletin du Muséum National d'histoire naturelle, 3e série 395: 27–81.

Viguier, R. 1949. Leguminosae madagascarienses novae. Notulae Systematicae, Herbier du Muséum de Paris 13 : 333–369.

Vlok, J.H.J., Euston-Brown, D.I.W., Cowling, R.M. 2003. Acocks' Valley Bushveld 50 years on: new perspectives on the delimitation, characterisation and origin of subtropical thicket vegetation. South African Journal of Botany 69(1): 27-51.

Vrba, E.S. 1985. African bovidae – evolutionary events since the Miocene. South African Journal of Science 81(5): 263-266.

Wagner, W.L., Herbst, D.R., Sohmer, S.H. 1999. Manual of the Flowering Plants of Hawai'i, Vols. 1 and 2: University of Hawai'i and Bishop Museum Press, Hawaii, U.S.A.

Ward, J., Seely, M.K., Lancaster, N. 1983. On the antiquity of the Namib. South African Journal of Botany 79:175-183.

Warwick, M.C., Lewis, G.P. 2009. A revision of *Cenostigma* (Leguminosae – Caesalpinioideae – Caesalpinieae), a genus endemic to Brazil. Kew Bulletin 64(1): 135-146.

Webb, C.O., Ackerly, D.D., McPeek, M., Donoghue, M.J. 2002. Phylogenies and community ecology. Annual Reviews in Ecology Evolution and Systematics 33: 475–505.

Weigend, M. 2002. Observations on the biogeography of the Amotape-Huancabamba zone in northern Peru. Botanical Review 68: 38–54.

Weigend, M., Gottschling, M., Hilger, H.H., Nürk, N.M. 2010. Five new species of *Lithospermum* L. (Boraginaceae, tribe Lithospermeae) in Andean South America: another radiation in the Amotape-Huancabamba zone. Taxon 59: 1161–1179.

Wen, J., Ree, R.H., Ickert-Bond, S.M., Nie, Z., Funk, V. 2013. Biogeography: where do we go from here? Taxon 62(5): 912-927.

White, T., Bruns, T., Lee, S., Taylor, J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis, M., Gelfand, D., Shinsky, J. White, T. (eds.), *PCR protocols: A guide to methods and applications*. Academic Press, New York, U.S.A. pp. 315–322

Wiens, J.J., Donoghue, M.J. 2004. Historical biogeography, ecology and species richness. Trends in Ecology & Evolution 19(12): 639-644.

Wiens, J.J. 2003. Missing data, incomplete taxa, and phylogenetic accuracy. Systematic Biology 52(4): 528-538.

Wiens, J.J. 2006. Missing data and the design of phylogenetic analyses. Journal of Biomedical Informatics 39(1): 34-42.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Davies, J.T., Grytnes, J.-A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M., Stephens, P.R. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13(10): 1310-1324.

Wieringa, J.J. 1999. Monopetalanthus exit. A systematic study of Aphanocalyx, Bikinia, Icuria, Michelsonia and Tetraberlinia (Leguminosae, Caesalpinioideae). (Doctoral Dissertation) Wageningen Agricultral University, Wageningen, Netherlands. 320 pages.

Wieringa, J.J., Mackinder, B.A., van Proosdij, A.S.J. 2013. *Gabonius* gen. nov. (Leguminosae, Caesalpinioideae, Detarieae), a distant cousin of *Hymenostegia* endemic to Gabon. Phytotaxa 142(1): 15-24.

Wilczek, R. 1951. Deux nouvelles espèces de *Caesalpinia* du Congo Belge. Bulletin du Jardin botanique de l'État à Bruxelles 21 : 83-86.

Wiley, E.O. 1978 The evolutionary species concept reconsidered. Systematic Zoology 27: 17-26.

Wojciechowski, M.F., Lavin, M., Sanderson, M.J. 2004. A phylogeny of legumes (Leguminosae) based on analysis of the plastid matK gene resolves many well-supported subclades within the family. American Journal of Botany 91(11): 1846-1862.

Wood, J.R.I. 2006. Inter-Andean dry valleys of Bolivia: Floristic affinities and patterns of endemism; insights from Acanthaceae, Asclepiadaceae and Labiatae. In: Pennington, R.T., Lewis, G.P., Ratter, J.A. (Eds.), *Neotropical savannas and seasonally dry forests: plant diversity, biogeography and conservation*. CRC Press, Boca Raton, Florida, U.S.A. pp. 257–280.

Wüest, R.O., Antonelli, A., Zimmermann, N.E., Linder, H.P. 2015. Available climate regimes drive niche diversification during range expansion. The American Naturalist 185(5): 640-652.

Young, K.R., Ulloa, C., Luteyn, J.L., Knapp, S. 2002. Plant evolution and endemism in Andean South America: an introduction. Botanical Review 68: 4–21.

Zamora Villalobos, N. 2010. Fabaceae. In: Hammel, B.E., Grayum, M.H., Herrera Mora, C., Zamora Villalobos N. (Eds.), *Manual de plantas de Costa Rica*. Missouri Botanical Garden, St. Louis, St. Louis, Missouri, U.S.A.

Zinderen Bakker, E.M. van, 1975. The origin and palaeoenvironment of the Namib desert biome. Journal of Biogeography 2(2): 65-73.

Annex 1.

Accessions included in the study for chapter 2. Species of the Caesalpinia Group are classified sensu Lewis (2005), and the number of species sampled over the total number of species recognized in the genus is given in parentheses. Type species for genera in the Caesalpinia Group are preceded by an asterisk (*). Collector names and numbers (and herbarium acronym) of voucher specimens are listed for all material that was taken from herbarium specimens and for the voucher specimens of seed collections and silica-dried leaf samples, if known. Accession numbers are provided for published sequences downloaded directly from Genbank; with the exception of 22 sequences for the species *Caesalpinia crista, C. decapetala, C. sappan, Cenostigma gardnerianum, Coulteria platyloba, Guilandina bonduc, Libidibia coriaria, P.exostemma, P. bracteosa, P. pyramidalis* and *Pterolobium stellatum*, the majority of the sequences downloaded from Genbank come from the following published studies: Bruneau & al. (2001), Simpson & al. (2003), Haston & al. (2005), Simpson & al. (2005), Marazzi & al. (2006), Simpson & al. (2006), Marazzi & Sanderson (2010), Babineau & al. (2013), Gagnon & al. (2013, chapter 1), and Gagnon & al. (2015, chapter 4). In bold are accessions that were combined togheter in the analysis. GenBank accession numbers will be provided upon acceptance of the manuscript.

Genus (no. of species sampled/total no. species) ***Species***	**Voucher specimen (Herbarium)**	**Collection Locality**	***rps16***	***trnD-trnT***	***ycf6-psbM***	***ITS***	***trnL-trnF***	***matK***

OUTGROUP								
Cassia javanica L.	Fougère-Danezan 6 (MT)	Singapore, cultivated	KF522255	X	X	X	EU361782	EU361910
***Colvillea racemosa* Bojer ex Hook.**	**Haston V200303 (RNG)**	**Madagascar**	**AY899794**	**–**	**–**	**–**	**AY899739**	**–**
***Colvillea racemosa* Bojer ex Hook.**	**Bruneau 1397 (MT)**	**Madagascar**	**–**	**KF379366**	**–**	**KF379221**	**–**	**KF379241**
***Conzattia multiflora* (B.L. Rob.) Standl.**	**Du 600 (K),Haston V200303 (RNG)**	**Mexico**	**AY899785**	**–**	**–**	**–**	**–**	**–**
***Conzattia multiflora* (B.L. Rob.) Standl.**	**Hughes 1815 (NY)**	**Mexico**	**–**	**KF379378**	**–**	**KF379219**	**–**	**–**
***Conzattia multiflora* (B.L. Rob.) Standl.**	**Simpson 17-XI-97 (TEX)**	**Mexico**	**–**	**–**	**–**	**–**	**AF430770**	**–**
***Conzattia multiflora* (B.L. Rob.) Standl.**	**Werling 399 (ASU)**	**Mexico**	**–**	**–**	**–**	**–**	**–**	**AY386918**
***Gymnocladus chinensis* Baill.**	**Herendeen II-V-02-1 (US)**	**USA, cultivated**	**KF522308**	**X**	**X**	**X**	**X**	**–**
***Gymnocladus chinensis* Baill.**	**Herendeen 8-V-2003-1 (US)**	**USA, cultivated**	**–**	**–**	**–**	**–**	**–**	**AY386928**
***Pterogyne nitens* Tul.**	**Pennington 244 (FHO)**	**Brazil**	**AY899747**	**–**	**–**	**–**	**AY899689**	**–**
***Pterogyne nitens* Tul.**	**Herendeen 13-XII-97-1 (US)**	**Tanzania**	**–**	**X**	**X–**	**X**	**–**	**EU362031**
***Senna covesii* (A. Gray) H.S. Irwin & Barneby**	**Marazzi BM297 (ARIZ)**	**USA, cultivated**	**HM236885**	**–**	**–**	**–**	**–**	**–**

***Senna covesii* (A. Gray) H.S. Irwin & Barneby**	**Wojciechowski 876 (ASU)**	**USA**	**–**	**–**	**–**	**X**	**EU361835**	**AY386850**
***Senna spectabilis* (DC.) H.S. Irwin & Barneby**	**Marazzi et al. BM029 (PY, CTES, Z)**	**Paraguay**	**AM086983**	**–**	**–**	**–**	**–**	**AM086900**
***Senna spectabilis* (DC.) H.S. Irwin & Barneby**	**Herendeen & Pooma 24–IV–99–6 (US)**	**Thailand**	**–**	**X**	**X**	**X**	**–**	**–**
Senna alata (L.) Roxb.	Bruneau 1076 (MT)	Cameroun, cultivated	–	X	X	X	AF365091	EU362042
***Tetrapterocarpon geayi* Humbert**	**Noyes 1049 (K)**	**Madagascar**	**AY899742**	**–**	**–**	**–**	**AY899684**	**–**
***Tetrapterocarpon geayi* Humbert**	**Bruneau & Ranaivojaona 1395 (WAG)**	**Madagascar**	**–**	**X**	**X**	**X**	**–**	**GU321972**
CAESALPINIA GROUP								
Arquita E.Gagnon & al. (5/5 species)								
* *Arquita mimosifolia* (Griseb.) E.Gagnon & al.	Gagnon & al. EG203 (MT)	Argentina	KF522160	KP003760	KP003707	KP003654	–	X
* *Arquita mimosifolia* (Griseb.) Gagnon & al.	Gagnon & Atchison EG211 (MT)	Argentina	KF522159	KP003759	KP003706	KP003653	–	X
* *Arquita mimosifolia* (Griseb.) E.Gagnon & al.	Särkinen et al. 2006 (FHO)	Argentina	KF522161	KP003761	KP003708	KP003655	–	KF379244
* *Arquita mimosifolia* (Griseb.) E.Gagnon & al.	Chumley 7387 (TEX)	Argentina	–	–	–	AY549893	AY535818-AY535805	–

Arquita ancashiana (Ulibarri) E.Gagnon & al.	Hughes & al. 3021 (MT, Z)	Peru	KF522164	KP003747	KP003696	KP003643	–	X
Arquita ancashiana (Ulibarri) E.Gagnon & al.	Hughes & al. 3070 (MT, Z)	Peru	KF522167	KP003749	KP003698	KP003644	–	–
Arquita ancashiana (Ulibarri) E.Gagnon & al.	Lewis & Klitgaard 2266 (K)	Ecuador	KF522170	KP003753	KP003792	KP003647	X	–
Arquita celendiniana (G.P. Lewis & C.E. Hughes) E.Gagnon & al.	Hughes & al. 2210 (FHO)	Peru	KF522148	KP003756	KP003703	KP003650	X	X
Arquita celendiniana (G. P. Lewis & C.E. Hughes) E.Gagnon & al.	Hughes & al. 3097 (MT, Z)	Peru	KF522149	KP003757	KP003704	KP003651	–	X
Arquita celendiniana (G.P. Lewis & C.E. Hughes) E.Gagnon & al.	Hughes & al. 3102 (MT, Z)	Peru	KF522147	KO003758	KP003705	KP003652	–	X
Arquita celendiniana (G.P. Lewis & C.E. Hughes) E.Gagnon & al.	Pennington 17567 (E)	Peru	–	–	–	X	–	–
Arquita trichocarpa var. *trichocarpa* (Griseb.) E.Gagnon & al.	Lewis & Klitgaard 2166 (K)	Argentina	KF522163	KP003762	KP003709	KP003659	AF430740	X
Arquita trichocarpa var. *boliviana* E.Gagnon & al.	Hughes & al. 2442 (FHO)	Bolivia	KF522162	KP003764	KP003711	KP003657	–	X
Arquita grandiflora E.Gagnon & al.	Särkinen & al. 2225 (FHO)	Peru	KF522151	KP003763	KP003710	KP003656	–	X
Balsamocarpon Clos (1/1 species)								
**Balsamocarpon* *brevifolium* Clos.	Baxter DCI 1869 (E)	Chile	KF522135	KP003801	KP003743	KP003689	EU361739	EU361864

**Balsamocarpon brevifolium* Clos.	Taylor 745 (K)	Chile	KF522136	X	X	X	–	–
**Balsamocarpon brevifolium* Clos.	Coccuci & Sérsic 365 (CORD)	Chile	–	–	–	AY308548	JX219457	AF430761
Caesalpinia L. sensu stricto (21/~25 species)								
**Caesalpinia brasiliensis* L.	Leonard & Leonard 13904 (US, K)	Haiti	KF522092	X	X	X	–	–
Caesalpinia anacantha Urb.	Liogier 16639 (P)	Dominican Republic	X	X	–	X	–	–
Caesalpinia bahamensis Lam.	Baker B27 (K)	Bahamas	KF522091	X	–	X	–	–
Caesalpinia bahamensis Lam.	Michael 8975 (MEXU)	Bahamas	KF522093		–		–	–
Caesalpinia barahonensis Urb.	Ekman 5965 (K)	Haiti	KF522094	X	–	X	–	–
Caesalpinia bracteata Germish.	Van Hoepen 2018 (K)	South Africa	KF522258	X	X	X	–	–
Caesalpinia buchii Urb.	Acevedo-Rodriguez et al. 8522 (US, K)	Dominican Republic	KF522115	X	X	X	–	–
Caesalpinia buchii Urb.	Ekman 8491 (K)	Haiti	–	X	–	–	–	–
Caesalpinia cassioides Willd.	Hughes & al. 2023 (FHO)	Peru	KF522097	X	X	X	–	–
Caesalpinia cassioides Willd.	Hughes & al. 2228 (FHO)	Peru	KF522098	X	X	X	–	–
Caesalpinia cassioides Willd.	Hughes & al. 2641 (FHO)	Peru	KF522095	X	X	X	–	–

Caesalpinia cassioides Willd.	Pennington & al. 789 (E)	Peru	KF522096	X	X	X	X	
Caesalpinia cassioides Willd.	Lewis & al. 3281 (K)	Ecuador	–	–	–	–	AF430711	–
Caesalpinia dauensis Thulin	Gilbert & al. 7695 (K)	Ethiopia	KF522266	X	X	X	–	–
Caesalpinia erianthera Chiov.	Friis & al. 4698 (K)	Somalia	KF522123	X	X	X	–	–
Caesalpinia erianthera Chiov.	Radcliffe-Smith 5518 (K)	Oman	KF522122	X	X	X	–	–
Caesalpinia erianthera Chiov.	Thulin & Mohamed 6941 (K)	Somalia	KF522125	X	X	X	–	–
Caesalpinia erianthera Chiov. var. *erianthera* Chiov.	Thulin 5557 (K)	Somalia	KF522118	–	–	–	–	–
Caesalpinia erianthera var. *pubescens* Brenan	Boulos & al. 17000 (K)	Yemen	KF522117	X	X	X	–	–
Caesalpinia glandulosopedicellata R.Wilczek	Bamps & Malaisse 8647 (K)	Zaire	KF522261	X	X	X	X	X
***Caesalpinia madagascariensis* (R.Vig) Senesse**	**Bruneau 1348 (MT)**	**Madagascar**	**KF522119**	**X**	**X**	**X**	–	**KF379246**
***Caesalpinia madagascariensis* (R.Vig) Senesse**	**Lewis & al. 2158 (K)**	**Madagascar**	**KF522120**	**X**	**X**	**X**	**AF430726**	**–**
Caesalpinia nipensis Urb.	Marie-Victorin & al. 21500 (MT)	Cuba	–	X	–	–	–	–

Caesalpinia nipensis Urb.	Marie-Victorin & al. 21509 (MT)	Cuba	X	X	–	X	–	–
Caesalpinia nipensis Urb.	Lewis 1838 (K)	Cuba	X	X	X	X	–	X
Caesalpinia oligophylla Harms.	Hassan 70 (FHO, K)	Somalia	KF522262	X	–	X	–	–
Caesalpinia pauciflora (Griseb.) C.Wright	Ekman 9703 (K)	Cuba	KF522124	X	X	X	–	–
Caesalpinia pauciflora (Griseb.) C.Wright	Liogier & Liogier 20521 (NY)	Hispaniola	KF522116	X	X	–	X	–
Caesalpinia pauciflora (Griseb.) C.Wright	Lewis 1854 (K)	Cuba, cultivated	–	X	–	X	–	–
Caesalpinia pulcherrima (L.) Sw.	Cox 1, RBG Liv.Coll. 1975-3028 (K)	cultivated	KF522174	–	–	–	–	–
Caesalpinia pulcherrima (L.) Sw.	Fougère-Danezan 19 (MT)	Singapore, cultivated	KF522172	X	X	X	X	KF379245
Caesalpinia pulcherrima (L.) Sw.	Lewis & Hughes 1715 (K)	Guatemala	KF522171	X	–	X	AF430733	–
Caesalpinia pulcherrima (L.) Sw.	Montreal Botanical Garden 7089-92 (MT)	Canada, cultivated	KF522173	X	X	X	–	–
Caesalpinia reticulata Britton	Pollard & al. 1295 (K)	Tuks & Caicos Islands	X	X	–	X	–	–
Caesalpinia rosei Urb.	Ekman H13620 (K, TEX)	Dominican Republic	X	X		X	AF430735	

Caesalpinia rostrata N.E.Br.	ILC6-5 (PRE)	South Africa, cultivated	X	X	X	X	X	–	
Caesalpinia rubra (Engl.) Brenan	de Winter 3164 (K)	South Africa	KF522260	–	–	–	–	–	
Caesalpinia rubra (Engl.) Brenan	Oshikoto 1917BD (K)	Namibia	KF522259	–	–	–	–	–	
***Caesalpinia sessilifolia* S.Watson**	**Palmer 533 (K, MO)**	**Mexico**	**X**	**X**	**X**	**X**	**–**	**–**	
***Caesalpinia sessilifolia* S.Watson**	**Neff 8–24–91–4 (TEX)**	**Mexico**	**–**	**–**	**–**	**–**	**AF430737**	**–**	
Caesalpinia sessilifolia S.Watson	Hinton 24737 (MEXU)	Mexico	KF522121	–	–	–	–	–	
Caesalpinia stuckertii Hassl.	Beck 9443 (NY)	Bolivia	KF522126	X	X	X	X	–	
Caesalpinia stuckertii Hassl.	Kaprovickas 4626 (K)	Argentina	KF522127	–	–	–	–	–	
Caesalpinia trothae subsp. *erlangeri* (Harms) Brenan	Beckett & White 1711 (K)	Somalia	KF522263	X	X	X	–	X	
Caesalpinia trothae subsp. *erlangeri* (Harms) Brenan	Thulin & Warfa 5816 (K)	Somalia	KF522267	X	–	–	–	–	
Caesalpinia trothae subsp. *erlangeri* (Harms) Brenan	Vollesen & Hassan 4873 (K)	Somalia	KF522264	–	–	–	–	–	
Caesalpinia trothae subsp. *trothae* Harms	Bidgood et al. 559 (K)	Tanzania	KF522265	X	X	–	X	X	
Caesalpinia trothae subsp. *trothae* Harms	Gilletttt 21088 (K)	Kenya	–	X	–	X	–	–	
Cenostigma Tul. (2/2 species)									
**Cenostigma macrophyllum* Tul.	Coradin & al. 6306 (K)	Brazil, Bahia	KF522053	X	X	–	–	–	

**Cenostigma macrophyllum* Tul.	Thomas 9615 (K)	Brazil, Piaui	KF522069	–	X	–	–	–
**Cenostigma macrophyllum* Tul.	de Queiroz 9147 (HUEFS)	Brazil, Bahia	KF522037	X	X	–	–	–
Cenostigma tocantinum Ducke	Klitgaard & de Lima 88 (K)	Brazil, cultivated	KF522071	KP003803	KP003740	KP003694	–	X
Cenostigma tocantinum Ducke	Klitgaard s.n. (INPA)	Brazil	KF522070	X	X	X	–	–
Cenostigma gardnerianum Tul.	(retrieved from Genbank)	Brazil	–	–	–	DQ787400	–	–
Cordeauxia Hemsl. (1/1 species)								
**Cordeauxia edulis* Hemsl.	Gillett & Beckett 23305 (K)	Somalia	KF522083	–	–	–	–	–
**Cordeauxia edulis* Hemsl.	Hassan 232 (FHO, K)	Somalia	AY899748	–	–	–	AY899690	–
**Cordeauxia edulis* Hemsl.	Kuchar 17803 (K)	Somalia	KF522084	X	X	X	X	X
* *Cordeauxia edulis Hemsl.*	Annable & Collins 3541 (NY)	Hawaii, cultivated	–	–	–	–	AF430771	–
Coulteria Kunth (7/9–10 species)								
**Coulteria mollis* Kunth	Way NMLW 28 (K)	Venezuela	KF522187	X	X	X	–	–
Coulteria platyloba (S. Watson) N. Zamora	Gagnon & Marazzi, EG2010.007 (MT)	USA, cultivated	KF522175	X	X	X	–	–

Coulteria platyloba (S. Watson) N. Zamora	Espinoza, BioBot01994 BOLD rec.: MHPAF1646-11	Costa Rica	–	–	–	–	–	JQ587526
Coulteria platyloba (S. Watson) N. Zamora	Lorea Lozada 685 (MEXU)	Mexico	KF522183	–	–	–	–	–
Coulteria platyloba (S. Watson) N. Zamora	MacQueen 178 (K)	Mexico	KF522178	X	X	X	–	–
Coulteria platyloba (S. Watson) N. Zamora	Steinmann 3199 (INIREB, K)	Mexico	KF522184	–	–	–	–	–
Coulteria platyloba (S. Watson) N. Zamora	Espinoza, BioBot01995 BOLD rec.: MHPAF1647–11	Costa Rica	–	–	–	–	–	JQ587527
Coulteria platyloba (S. Watson) N. Zamora	Espinoza, BioBot01996 BOLD rec.: MHPAF1648–11	Costa Rica	–	–	–	–	–	JQ587528
***Caesalpinia colimensis* F.J.Herm.**	**Sousa 6163 (K)**	**Mexico**	**KF522176**	**X**	**X**	**X**	**–**	**–**
***Caesalpinia colimensis* F.J.Herm.**	**Sousa 7659 (TEX)**	**Mexico**	**–**	**–**	**–**	**–**	**AF430713**	**–**
***Caesalpinia pringlei* (Britton & Rose) Standl.**	**Cruz Duran 926 (MEXU)**	**Mexico**	**KF522180**	**–**	**–**	**–**	**–**	**–**
***Caesalpinia pringlei* (Britton & Rose) Standl.**	**Panero 4037 (TEX)**	**Mexico**	**–**	**–**	**–**	**–**	**AF430732**	**–**
Caesalpinia pumila (Britton & Rose) F.J.Herm.	Gagnon & Marazzi EG 2010.014 (MT)	USA, cultivated	KF522182	X	X	X	–	–

Caesalpinia pumila (Britton & Rose) F.J.Herm.	Lewis & al. 2067 (K)	Mexico	KF522177	X	X	X	KF379385	KF379247	
Caesalpinia pumila (Britton & Rose) F.J.Herm.	Nabhan & al. 1988 (MEXU)	Mexico	KF522185	–	–	–	–	–	
Caesalpinia pumila (Britton & Rose) F.J.Herm.	Cavan 5535 (TEX)	Mexico	–	–	–	–	AF430720	–	
Caesalpinia velutina (Britton & Rose) Standl.	Hughes & al. 2087 (FHO)	Mexico	KF522189	X	X	X	–	–	
Caesalpinia velutina (Britton & Rose) Standl.	Lewis 1797 (NY)	Mexico	KF522179	X	X	X	–	–	
Caesalpinia velutina (Britton & Rose) Standl.	Tenorio 296 (MEXU)	Mexico	KF522191	–	–	–	–	–	
Caesalpinia velutina (Britton & Rose) Standl.	Torres 1590 (MEXU)	Mexico	KF522186	–	–	–	–	–	
Caesalpinia velutina (Britton & Rose) Standl.	Way & al. JIC 22176 (K)	Mexico	KF522190	X	X	X	–	–	
Caesalpinia velutina (Britton & Rose) Standl.	Hughes 255 (FHO)	Guatemala	AY899752	–	–	–	AY899694	–	
Caesalpinia velutina (Britton & Rose) Standl.	Torres 10741 (K)	Mexico	–	–	–	–	AF430741	–	
Caesalpinia violacea (Mill.) Standl.	Lewis & al. 1763 (NY)	Mexico	KF522188	X	X	–	X	JX099334	
Caesalpinia violacea (Mill.) Standl.	Tenorio 4442 (MEXU)	Mexico	KF522181	–	–	–	–	–	
Erythrostemon (Hook.) Klotzsch (9/9 species)									
**Erythrostemon gilliesii* Klotzsch	Marazzi & al. BM131 (CTES, Z)	Argentina	AM086914	–	–	–	–	AM086829	
**Erythrostemon gilliesii* Klotzsch	Spellenberg 12701 (MT)	USA, cultivated	KF522296	KP003786	KP003729	KP003681	JX073265	JX099328	

**Erythrostemon gilliesii* Klotzsch	Jodrell 688-86 (K)	Chile	–	–	–	AY549891	AF430721	–
**Erythrostemon gilliesii* Klotzsch	Wojciechowski 882 (ASU)	USA	–	–	–	–	–	AY386845
**Erythrostemon gilliesii* Klotzsch	Hick & Bertone 34 (CORD)	Argentina	–	–	–	–	JX219458	–
Erythrostemon calycina (Benth) L.P.Queiroz	Giuletti 2045 (HUEFS)	Brazil	KF522304	X	X	–	–	–
Erythrostemon calycina (Benth) L.P.Queiroz	Lewis & Andrade 2003 (K)	Brazil	AY899749	–	–	–	X	–
Erythrostemon calycina (Benth) L.P.Queiroz	Lewis & Andrade 1885 (K)	Brazil	KF522303	–	X	X	X	X
Caesalpinia angulata (Hook & Arn.) Baill.	Brownless & al. 591 (E)	Chile	KF522288	X	X	X	–	–
Caesalpinia angulata (Hook & Arn.) Baill.	Nee 37585 (K)	Chile	KF522287	–	–	–	–	–
Caesalpinia argentina Burkart	Hughes & al. 2460 (FHO)	Bolivia	KF522289	X	X	X	–	–
Caesalpinia argentina Burkart	Pennington & al. 13323 (K)	Bolivia	KF522290	X	X	X	–	–
***Caesalpinia caudata* (A. Gray) Fisher**	**Simpson I-IV-01-3 (TEX)**	**USA**	**KF522298**	**X**	**X**	**–**	**–**	**–**
***Caesalpinia caudata* (A. Gray) Fisher**	**Neff 99-3-16-1 (TEX)**	**USA**	**–**	**–**	**–**	**–**	**AF430712**	**–**
Caesalpinia coluteifolia Griseb.	Gagnon et al. EG207 (MT)	Argentina	KF522291	X	X	X	–	–
Caesalpinia coluteifolia Griseb.	Gagnon &Atchison EG223 (MT)	Argentina	KF522292	X	X	X	–	–

Caesalpinia coulterioides Griseb. Emend. Burkart	Gagnon &Atchison EG209 (MT)	Argentina	KF522285	X	X	X	–	–
Caesalpinia exilifolia Griseb.	Gagnon et al. EG201 (MT)	Argentina	KF522295	X	X	X	–	–
Caesalpinia exilifolia Griseb.	Gagnon &Atchison EG219 (MT)	Argentina	KF522293	X	X	X	–	–
***Caesalpinia exilifolia* Griseb.**	**Gagnon &Atchison EG222 (MT)**	**Argentina**	**X**	**X**	**X**	**X**	**–**	**–**
***Caesalpinia exilifolia* Griseb.**	**Galleto 167 (CORD)**	**Argentina**	**–**	**–**	**–**	**–**	**AF430716**	**–**
Caesalpinia fimbriata Tul.	Hughes et al. 2441 (FHO)	Bolivia	KF522284	KP003785	KP003728	KP003680	–	–
Caesalpinia fimbriata Tul.	Hughes et al. 2466 (FHO)	Bolivia	KF522286	X	X	X	–	–
Caesalpinia fimbriata Tul.	Wood 10627 (K)	Bolivia	KF522211	–	–	–	–	–
Caesalpinia fimbriata Tul.	Solomon & Nee 16062 (NY)	Bolivia	KF522297	X	X	X	X	–
Guilandina L. (6/7–18 species)								
**Guilandina bonduc* L.	Bruneau 1342 (MT)	Madagascar	KF522062	X	X	X	–	KF379242
**Guilandina bonduc* L.	van Balooy s.n., Krukoff coll. (K)	Malaysia	KF522063	–	–	–	AF430708	–
**Guilandina bonduc* L.	Herendeen 9-XII-97-3 (US)	Tanzania	–	–	–	KF379229	X	–

**Guilandina bonduc* L.	Espinoza, BioBot02010 BOLD rec.: MHPAF1662-11	Costa Rica	–	–	–	–	–	JQ587518
**Guilandina bonduc* L.	Espinoza, BioBot02011 BOLD rec.: MHPAF1663-11	Costa Rica	–	–	–	–	–	JQ587519
**Guilandina bonduc* L.	Espinoza, BioBot02012 BOLD rec.: MHPAF1664-11	Costa Rica	–	–	–	–	–	JQ587520
Guilandina ciliata Wikstr.	Ekman 5413 (K)	Haiti	X	–	–	–	–	–
Guilandina ciliata Wikstr.	Walker 51 (K)	British Virgin Islands	X	X	–	X	–	–
Guilandina major L.	Herendeen & Pooma 30-IV-1999-1 (US)	USA, cultivated	KF522253	X	X	–	X	–
Caesalpinia minax Hance	Li Shi Jin 802 (CAS, IBSC)	China	KF522131	X	–	X	–	–
Caesalpinia minax Hance	Living collection National Botanic Garden of Belgium 19645275 (BR)	China, cultivated	KF522132	–	–	–	–	–
Caesalpinia minax Hance	PS1368MT01, Genbank	N.A.	–	–	–	GU217664	–	HM049550
Caesalpinia murifructa Gillis & Proctor	Gillis 13096 (K)	Bahamas	KF522064	X	X	X	–	–

Caesalpinia volkensii Harms	Archbold 2861 (K)	Tanzania	KF522065	–	–	–	–	–
Caesalpinia volkensii Harms	Friis & al. 3516 (K)	Ethiopia	KF522066	X	X	X	–	–
Caesalpinia volkensii Harms	Somers s.n., RBG Liv.Coll. 1978-891 (K)	Kenya	KF522067	X	X	X	–	–
Haematoxylum L. (3/5 species)								
**Haematoxylum campechianum* L.	Bruneau 1313 (MT)	Mexico	KF522200	X	X	–	–	–
**Haematoxylum campechianum* L.	du Puy & al. M356 (K)	Madagascar	KF522208	–	–	–	–	–
**Haematoxylum campechianum* L.	Hughes 1273 (FHO)	Guatemala	AY899754	–	–	–	AY889697	–
**Haematoxylum campechianum* L.	Miller & Morello 8849 (MO)	Dominica	KF522201	X	X	X	–	–
Haematoxylum brasiletto H.Karst.	Bernandes et al. 891 (MO)	Colombia	KF522209	X	X	X	–	–
Haematoxylum brasiletto H.Karst.	Gagnon & Marazzi EG2010.011 (MT)	USA, cultivated	KF522207	X	X	X	–	–
***Haematoxylum brasiletto* H.Karst.**	**Gagnon & Marazzi EG2010.013 (MT)**	**USA, cultivated**	**KF522206**	**X**	**X**	**X**	**–**	**–**

***Haematoxylum brasiletto* H.Karst.**	**Haston V200307 (RNG), OFI 14/83 (OFI)**	**Mexico**	**–**	**–**	**–**	**–**	**AY899696**	**–**
***Haematoxylum brasiletto* H.Karst.**	**Wojciechowski 953 (ASU)**	**USA**	**–**	**–**	**–**	**–**	**–**	**AY386905**
Haematoxylum brasiletto H.Karst.	Lewis et al. 2057 (FHO)	Mexico	AY899753	–	–	–	AY899695	–
Haematoxylum brasiletto H.Karst.	Simpson 17–XI–97 (TEX)	USA	–	–	–	–	AF430777	–
***Haematoxylum dinteri* Harms**	**Sucheach s.n. (OFI), Haston V200308 (RNG)**	**Namibia**	**AY899755**	**–**	**–**	**–**	**AY899698**	**–**
***Haematoxylum dinteri* Harms**	**Millenium seed bank project, HK2728 (K)**	**Namibia**	**X**	**X**	**X**	**X**	**–**	**–**
Hoffmannseggia Cav.(24/24 species)								
*_Hoffmannseggia glauca_ (Ortega) Eifert	Gagnon & Marazzi EG2010.05 (MT)	USA	KF522214	X	X	X	–	–
*_Hoffmannseggia glauca_ (Ortega) Eifert	Gagnon & Marazzi EG2010.19 (MT)	USA	KF522212	X	X	X	–	–
*_Hoffmannseggia glauca_ (Ortega) Eifert	Wojciechowski 1501 (ASU)	USA	–	–	–	–	–	JQ619977
*_Hoffmannseggia glauca_ (Ortega) Eifert	Spellenberg 12699 (MT)	USA	KF522213	KP003796	KP003744	KP003690	AF365069	EU361969

**Hoffmannseggia glauca* (Ortega) Eifert	Hick & Bertone 5 (CORD)	Argentina	–	–	–	–	JX219459	JX219465
**Hoffmannseggia glauca* (Ortega) Eifert	Cocucci 15-VI-1991 (CORD)	Argentina	–	–	–	X	AF430747	–
**Hoffmannseggia glauca* (Ortega) Eifert	Simpson 91-VII-22-1 (TEX)	Mexico	–	–	–	X	AY308488	–
Hoffmannseggia aphylla (Phil.) G.P.Lewis & Sotuyo	Gardner & Knees 6503 (E)	Chile	KF522146	X	X	X	–	–
Hoffmannseggia aphylla (Phil.) G.P.Lewis & Sotuyo	Gardner & Knees 6557 (E)	Chile	KF522144	–	–	–	–	–
Hoffmannseggia arequipensis Ulibarri	Simpson 20-II-00-1 (TEX)	Peru	–	–	–	AY308550	AY308483	–
Hoffmannseggia arequipensis Ulibarri	Simpson 20-II-00-2 (TEX)	Peru	–	–	–	AY308551	AY308484	–
Hoffmannseggia doelli Philippi	Simpson 11-II-00-2 (TEX)	Chile	–	–	–	AY308552	AY308485	–
Hoffmannseggia doelli subsp. *argentina* Ulibarri	Gagnon & Atchison EG220 (MT, K)	Argentina	X	X	X	X	–	–
Hoffmannseggia drepanocarpa A.Gray	Simpson 29-V-89 (TEX)	Mexico	–	–	–	AY308553	AF430745	–
Hoffmannseggia drummondii Torr. & A.Gray	Simpson 05-15-92-2 (TEX)	Mexico	–	–	–	AY308554	AF430747	–
Hoffmannseggia erecta Philippi	Chumley 7379 (TEX)	Argentina	–	–	–	AY308555	AY308486	–
Hoffmannseggia eremophila (Phil.) Ulibarri	Aranoi & Sequeo 10334 (CORD)	Chile	–	–	–	AY308556	AY308487	–

Hoffmannseggia humilis (M. Martens & Galeotti) Hemsl.	Mayfield et al. 898 (TEX)	Mexico	–	–	–	AY308559	AF430748	–
Hoffmannseggia intricata Brandegee	Irwin 2371 (TEX)	Mexico	–	–	–	AY308560	AY308489	–
Hoffmannseggia microphylla Torr.	Holmgrenn 6505 (NY)	USA	KF522145	X	X	X		–
Hoffmannseggia microphylla Torr.	Simpson 03-15-03-1 (TEX)	Mexico	–	–	–	AY308561	AF430749	–
Hoffmannseggia minor (Phil.) Ulibarri	Simpson 1-II-00-9 (TEX)	Argentina	–	–	–	AY308562	AY308534	–
Hoffmannseggia miranda Sandwith	FLSP 945 (NY)	Peru	KF522239	X	X	X	–	–
Hoffmannseggia miranda Sandwith	Hughes & Daza 2358 (FHO)	Peru	KF522240	X	X	X	–	–
Hoffmannseggia miranda Sandwith	Simpson 22-II-00-2 (TEX)	Peru	–	–	–	AY308565	AY308492	–
Hoffmannseggia miranda Sandwith	Simpson 21-II-00-1 (TEX)	Peru	–	–	–	AY308564	AY308491	–
Hoffmannseggia miranda Sandwith	Dillon & Dillon 3958 (F)	Peru	–	–	–	AY308563	AF430750	–
Hoffmannseggia oxycarpa subsp. *arida* (Rose) B.B.Simpson	Simpson 91-VII-21-2 (TEX)	Mexico	–	–	–	AY308566	AF430751	–
Hoffmannseggia peninsularis (Britton) Wiggins	Simpson 03-15-93-5 (TEX)	Mexico	–	–	–	AY308567	AF430752	–
Hoffmannseggia prostrata DC.	Hughes & Daza 2359 (FHO)	Peru	KF522241	X	X	X	–	–
Hoffmannseggia prostrata DC.	Dillon & Dillon 5926 (F)	Chile	–	–	–	AY308568	AF430753	–

***Hoffmannseggia pumilio* (Griseb.) B.B.Simpson**	**Gagnon & Atchison EG221 (MT, K)**	**Argentina**	**X**	**X**	**–**	**X**	**–**	**–**	
***Hoffmannseggia pumilio* (Griseb.) B.B.Simpson**	**Simpson 1-II-00-1 (TEX)**	**Argentina**	**–**	**–**	**–**	**AY308549**	**AF430791**	**–**	
Hoffmannseggia repens (Eastw.) Cockerell	Simpson 27-V-89-7 (TEX)	USA	–	–	–	AY308569	AF430755	–	
Hoffmannseggia tenella Tharp & L.O.Williams	Neff 4-XI-88 (TEX)	USA	–	–	–	AY308570	AF430755	–	
Hoffmannseggia ternata DC.	Dillon & Dillon 3746 (F)	Peru	–	–	–	AY308571	AF430756	–	
Hoffmannseggia ternata DC.	Simpson 22-II-00-1 (TEX)	Peru	–	–	–	AY308574	AY308495	–	
Hoffmannseggia ternata DC.	Simpson 15-II-00-1 (TEX)	Chile	–	–	–	AY308572	AY308493	–	
Hoffmannseggia ternata DC.	Simpson 21-II-00-2 (TEX)	Peru	–	–	–	AY308573	AY308494	–	
Hoffmannseggia ternata DC.	Simpson 22-II-00-3 (TEX)	Peru	KF522139	–	–	AY308575	AY308496	–	
Hoffmannseggia trifoliata Cav.	Simpson 21-I-00-3A (TEX)	Argentina	–	–	–	AY308576	AY308497	–	
Hoffmannseggia viscosa Hook. & Arn.	Eastwood & al. RJE35 (FHO)	Peru	KF522138	X	X	X	–	–	
Hoffmannseggia viscosa Hook. & Arn.	Hughes & al. 2221 (FHO)	Peru	KF522137	X	X	X	–	–	
Hoffmannseggia viscosa Hook. & Arn	Sagastegui 11465 (MO)	Peru	–	–	–	AY308577	AY308498	–	
Hoffmannseggia viscosa Hook. & Arn	Richardson 2039	Peru	–	–	–	AY308578	AY308499	–	
Hoffmannseggia watsonii (Fisher) Rose	Hunter 25354 (TEX)	Mexico	–	–	–	AY308579	AY308500	–	

Hoffmannseggia yaviensis Ulibarri	Simpson 30-I-00-1 (TEX)	Argentina	–	–	–	AY308580	AY308501	–
Libidibia (DC.) Schltdl. (6/6–8 species)								
**Libidibia coriaria* (Jacq.) Schltdl.	Fougère–Danezan 20 (MT)	Singapore, cultivated	KF522109	X	X	–	–	–
***_Libidibia coriaria_ (Jacq.) Schltdl.**	**Hughes 1495 (K)**	**Mexico**	**AY899750**	–	–	–	**AY899692**	–
***_Libidibia coriaria_ (Jacq.) Schltdl.**	**Hughes & al. 2163 (FHO)**	**Mexico**	**KF522107**	**KP003797**	**KP003745**	**KP003691**	–	–
***_Libidibia coriaria_ (Jacq.) Schltdl.**	**Espinoza, BioBot00788 BOLD rec.: MHPAD924-09**	**Costa Rica**	–	–	–	–	–	**JQ587521**
**Libidibia coriaria* (Jacq.) Schltdl.	Espinoza, BioBot00789 BOLD rec.: MHPAD925-09	Costa Rica	–	–	–	–	–	JQ587522
**Libidibia coriaria* (Jacq.) Schltdl.	Espinoza, BioBot00790 BOLD rec.: MHPAD926-09	Costa Rica	–	–	–	–	–	JQ587523
Libidibia ferrea (Mart. ex Tul.) L.P.Queiroz	Fougère-Danezan 21 (MT)	Singapore, cultivated	KF522105	X	X	–	JX073260	EU361901
Libidibia ferrea (Mart. ex Tul.) L.P.Queiroz	Lewis & al. 1623 (K)	Brazil	KF522114	–	–	–	–	–
Libidibia ferrea (Mart. ex Tul.) L.P.Queiroz	Kew Living coll. 1973-21715 (K)	Brazil	–	–	–	–	AF430718	–

Libidibia glabrata (Kunth) Castellanos & G.P. Lewis	Delgado 2097 (MEXU)	Peru	KF522103	–	–	–	–	–
Libidibia glabrata (Kunth) Castellanos & G.P. Lewis	Eastwood & al. RJE84 (FHO)	Peru	KF522102	X	X	X	–	–
Libidibia glabrata (Kunth) Castellanos & G.P. Lewis	Lewis & Lozano 3043 (K)	Ecuador	KF522101	X	X	–	X	–
Libidibia glabrata (Kunth) Castellanos & G.P. Lewis	Särkinen & al. 2151 (FHO)	Peru	KF522104	X	X	–	–	–
Libidibia glabrata (Kunth) Castellanos & G.P. Lewis	Lewis & Klitgaard 3337 (K)	Ecuador	–	–	–	–	AF430722	–
Libidibia paraguariensis (Parodi) G.P.Lewis	Hughes & al. 2307 (FHO)	Bolivia	KF522110	X	X	–	–	–
Libidibia paraguariensis (Parodi) G.P.Lewis	Hughes & al. 2475 (FHO)	Bolivia	KF522111	X	X	–	–	–
Libidibia paraguariensis (Parodi) G.P.Lewis	Lewis & Klitgaard 2170 (K)	Argentina	KF522112	X	X	KF379233	AF365062	EU361905
Libidibia paraguariensis (Parodi) G.P.Lewis	Zardini & Velazquez 19907 (K)	Paraguay	KF522113	–	–	–	–	–
Libidibia punctata (Willd.) Britton	Cardenas 4071 (K)	Venezuela	KF522106	X	X	–	–	–
***Libidibia sclerocarpa* (Standl.) Britton & Rose**	**Lewis & Hughes 1778 (K)**	**Mexico**	**KF522108**	**X**	**X**	–	–	–
***Libidibia sclerocarpa* (Standl.) Britton & Rose**	**Kew seed collection s.n.**	**Mexico**	–	–	–	–	**AF430736**	–
Lophocarpinia Burkart ***(1/1 species)***								

**Lophocarpinia aculeatifolia* (Burkart) Burkart	Fortunato 8639 (BAB)	Argentina	–	–	–	–	JX219460	JX219466
Mezoneuron Desf. (11/26 species)									
Mezoneuron andamanicum Prain	Herendeen 29-IV-1999-1 (US)	Thailand	KF522305	–	X	X	–	AY386931
Mezoneuron angolense Welw. ex Oliv.	Herendeen 12-XII-97-1 (US)	Tanzania	–	–	–	–	AF365068	EU361897
Mezoneuron benthamianum Baill.	Ern 2602 (K)	Togo	KF522196	X	X	X	–	–
Mezoneuron benthamianum Baill.	Morton & Jarr SL3295 (K)	Sierra Leone	KF522195	X	X	X	–	–
Mezoneuron benthamianum Baill.	Vigne 3487 (FHO)	Ghana	KF522197	–	–	–	–	–
Mezoneuron cucullatum (Roxb.) Wight & Arn.	Grierson & Long 3623 (K)	Bhutan	KF522194	X	–	X	–	–
Mezoneuron deverdiana Guillaumin	McPherson 6211 (K)	New Caledonia	KF522078	–	–	–	–	–
Mezoneuron hildebrandtii Vatke	Lewis & al. 2137 (K)	Madagascar	KF522198	X	X	X	X	X
Mezoneuron hildebrandtii Vatke	Simpson 17-XI-97 (TEX)	Madagascar	–	–	–	–	AF430780	–
Mezoneuron hymenocarpum Prain	Larsen &Larsen 34232 (K)	Thailand	–	X	X	X	–	–
Mezoneuron kauaiensis (H. Mann) Hillbr.	Lorence & Wagner 8904 (NTBG)	Hawaii, USA	KF522192	X	X	X	EU361770	EU361903
Mezoneuron kauaiensis (H. Mann) Hillbr.	Melville 71/1033 (K)	Hawaii, USA				X		

Mezoneuron scortechinii F. Muell.	Wieringa et al. 4195 (WAG)	Australia	KF522077	X	X	KF379231	X	KF379249
Mezoneuron sumatranum (Roxb.) Wight & Arn.	Beaman 9642 (NY, MO)	Malaysia	KF522199	–	–	X	–	–
Mezoneuron sp.	Pullen 7619 (K)	New Guinea	KF522193	–	–	–	–	–
Caesalpinia erythrocarpa Pedley	Schodde 2246 (K)	Papua New Guinea	KF522257	X	X	X	–	–
Caesalpinia nitens (F.Muell ex Benth.) Pedley	Bean 18033 (MO)	Australia	KF522076	X	X	X	–	–
Moullava Adans. (1/1 species)								
**Moullava spicata* (Dalzell) Nicolson	Critchett 11/79 (K)	Zambia, cultivated	KF522252	X	–	X	JX073267	JX099331
**Moullava spicata* (Dalzell) Nicolson	Hutchison 2784 (TEX)	Sri Lanka	–	–	–	–	AF430782	–
Poincianella Britton &Rose (32/~35 species)								
**Poincianella mexicana* (A.Gray) Britton & Rose	Hughes & al. 1606 (NY, FHO)	Mexico	KF522218	X	X	–	EU361772	EU361904
**Poincianella mexicana* (A.Gray) Britton & Rose	Delgado 01-2114 (MEXU)	Mexico	KF522219	–	–	–	EF177387	–
**Poincianella mexicana* (A.Gray) Britton & Rose	Lewis s.n., Kew Living Coll. 1973-21714 (K)	Mexico	KF522215	KP03788	KP003730	KP00383	–	–
**Poincianella mexicana* (A.Gray) Britton & Rose	Gagnon & Marazzi EG2010.015 (MT)	USA, cultivated	KF522217	X	X	–	–	–

**Poincianella mexicana* (A.Gray) Britton & Rose	Mason s.n. (K)	USA	–	–	–	AY549892	AF430727	–
Poincianella aff. mexicana	Contreras s.n. (MEXU)	Mexico	KF522227	–	–	–	–	–
Poincianella acapulcensis (Standl.) Britton & Rose	Lott 3205 (K)	Mexico	KF522233	–	–	–	–	–
Poincianella acapulcensis (Standl.) Britton & Rose	MacQueen & al. 406 (K)	Mexico	KF522235	X	X	–	–	–
Poincianella bracteosa (Tul.) L.P.Queiroz	Carvalho–Sobrinho 218 (HUEFS)	Brazil	KF522035	X	X	–	–	–
Poincianella bracteosa (Tul.) L.P.Queiroz	de Queiroz 10085 (HUEFS)	Brazil	KF522079	X	–	–	–	–
Poincianella bracteosa (Tul.) L.P.Queiroz	de Queiroz 7845 (HUEFS)	Brazil	KF522036	X	X	–	–	–
Poincianella bracteosa (Tul.) L.P.Queiroz	(retrieved from Genbank)	Brazil	–	–	–	DQ787395	–	–
Poincianella caladenia (Standl.) Britton & Rose	Contreras 2868 (MEXU)	Mexico	KF522234	–	–	–	–	–
***Poincianella caladenia* (Standl.) Britton & Rose**	**Contreras 2818 (MEXU)**	**Mexico**	–	–	–	–	**EF177383**	–
***Poincianella caladenia* (Standl.) Britton & Rose**	**Lewis & al. 2072 (K)**	**Mexico**	**KF522228**	**X**	**X**	**–**	**–**	**–**
Poincianella eriostachys (Benth.) Britton & Rose	Hughes 1832 (K)	Mexico	AY899751	–	–	–	AY899693	–
Poincianella eriostachys (Benth.) Britton & Rose	Lewis & al. 1799 (K)	Mexico	KF522029	X	X	X	AF430715	–
Poincianella eriostachys (Benth.) Britton & Rose	MacQueen 449 (MEXU)	Mexico	–	–	–	–	EF177389	–
Poincianella exostemma (DC.) Britton & Rose	Contreras s.n. febrero 2000 (MEXU)	Mexico	KF522237	–	–	–	–	–

Poincianella exostemma (DC.) Britton & Rose subsp. *exostemma*	Bruneau 1317 (MT)	Mexico	KF522221	X	X	–	–	–
Poincianella exostemma (DC.) Britton & Rose subsp. *exostemma*	Lewis & Hughes 1712, RBG Liv.Coll. 1989–3073 (K)	Guatemala	KF522224	X	–	–	AF430717	–
Poincianella exostemma (DC.) Britton & Rose *subsp. exostemma*	Lewis & Hughes 1753 (K)	Guatemala	KF522222	X	X	–	–	–
Poincianella exostemma (DC.) Britton & Rose	Espinoza, BioBot00766 BOLD rec.: MHPAD902–09	Costa Rica	–	–	–	–	–	JQ587524
Poincianella exostemma (DC.) Britton & Rose	Espinoza, BioBot00767 BOLD rec.: MHPAD903–09	Costa Rica	–	–	–	–	–	JQ587525
Poincianella gaumeri (Greenm.) Britton & Rose	Calzada 19333 (K, MEXU)	Mexico	KF522030	–	–	–	–	–
Poincianella gaumeri (Greenm.) Britton & Rose	Hughes 492 (K)	Mexico	KF522034	X	–	–	–	–
Poincianella gaumeri (Greenm.) Britton & Rose	Lewis & Hughes 1762 (K)	Mexico	KF522044	KP003799	KP003739	KP003692	–	–
Poincianella glandulosa (DC.) Britton & Rose	Ekman 9838 (K)	Haiti	X	X	–	–	–	–
Poincianella laxa (Benth.) Britton & Rose	Delgado 2337 (MEXU)	Mexico	KF522274	–	–	–	–	–
Poincianella laxiflora (Tul.) L.P. Queiroz	de Queiroz 7063 (HUEFS)	Brazil	KF522051	X	–	X	–	–

Poincianella laxiflora (Tul.) L.P. Queiroz	Lewis & Andrade 2012 (MO)	Brazil	–	–	–	X	–	–
Poincianella melanadenia (Rose) Britton & Rose	Hughes & al. 2091 (FHO)	Mexico, Oaxaca	KF522275	X	X	–	–	–
Poincianella melanadenia (Rose) Britton & Rose	Contreras 7369 (MEXU)	Mexico	KF522277	–	–	–	–	–
***Poincianella melanadenia* (Rose) Britton & Rose**	**Hughes & al. 2074 (FHO)**	**Mexico, Puebla**	**KF522276**	**X**	–	**X**	–	–
***Poincianella melanadenia* (Rose) Britton & Rose**	**Sotuyo & Gonzalez s.n. (MEXU)**	**Mexico, Puebla**	–	–	–	–	**DQ208904**	–
Poincianella microphylla (Mart. ex. G.Don) L.P.Queiroz	Coradin & al. 5941 (K)	Brazil	KF522040	–	–	–	–	–
Poincianella microphylla (Mart. ex. G.Don) L.P.Queiroz	de Queiroz 9060 (HUEFS)	Brazil	KF522039	X	X	X	–	–
Poincianella nelsonii Britton & Rose	Contreras & Sotuyo s.n. (MEXU)	Mexico	KF522300	X	X	–	–	–
Poincianella nelsonii Britton & Rose	Lewis & al. 1794 (K)	Mexico	–	–	–	–	AF430728	–
Poincianella nelsonii Britton & Rose	Sotuyo, s.n., RBG Liv.Coll. 2002–3577 (K)	Mexico	KF522301	KP003789	KP003731	KP003684	EF177385	–
Poincianella palmeri (S.Watson) Britton & Rose	Gagnon & al. EG2010.010 (MT)	USA, cultivated	KF522230	X	X	–	–	–

Poincianella palmeri (S.Watson) Britton & Rose	Gagnon & al. EG2010.023 (MT)	USA, cultivated	KF522229	X	X	–	–	–
Poincianella palmeri (S.Watson) Britton & Rose	Lewis 2064 (K)	Mexico	KF522232	–	–	–	–	–
Poincianella palmeri (S.Watson) Britton & Rose	Lewis & al. 2065 (K)	Mexico	KF522231	KP003790	KP003732	KP003685	X	KF379243
Poincianella pannosa (Standl.) Britton & Rose	Gentry 4365 (MEXU)	Mexico	KF522283	–	–	–	–	–
Poincianella pannosa (Standl.) Britton & Rose	Lewis 2051 (K)	Mexico	KF522282	KP003791	KP003734	KP003686	X	–
Poincianella pannosa (Standl.) Britton & Rose	Turner s.n. (TEX)	Mexico	–	–	–	AY549890	AY535804-AY535817	–
Poincianella pellucida (Vogel) Britton & Rose	Ekman 4999 (K)	Haiti	–	X	–	–	–	–
Poincianella phyllanthoides (Standl.) Britton & Rose	Nee 32666 (K)	Mexico	KF522220	X	X	–	–	–
Poincianella phyllanthoides (Standl.) Britton & Rose	Steinmann 3718 (INIREB, MEXU)	México	KF522216	–	–	–	–	–
*Poincianella placida (*Brandegee) Britton & Rose	Lewis & al. 2032 (K)	Mexico	KF522273	KP003792	KP003735	KP003687	–	–
*Poincianella placida (*Brandegee) Britton & Rose	Lewis 2046 (K)	Mexico	KF522272	X	X	X	X	–
Poincianella pluviosa (DC.) L.P.Queiroz	de Queiroz 12795 (HUEFS)	Brazil	KF522049	KP003800	KP003735	KP003687	–	–

Poincianella pluviosa (DC.) L.P.Queiroz	Wood & al. 26552 (K)	Bolivia	KF522047	X	X	X	–	–
Poincianella pluviosa (DC.) L.P.Queiroz var. *pluviosa*	Wood 8838 (K)	Bolivia	KF522052	X	–	X	–	–
Poincianella pluviosa (DC.) L.P.Queiroz var. *pluviosa*	Nee 40000 (K)	Bolivia	KF522054	–	–	X	–	–
Poincianella pluviosa (DC.) L.P.Queiroz	Nee 38223 (TEX)	Bolivia	–	–	–	–	AF430731	–
Poincianella pluviosa var. peltophoroides (DC.) L.P.Queiroz	Lewis & al. 1632 (K, NY)	Brazil	–	–	–	X	–	–
Poincianella pluviosa var. *sanfranciscana* (G.P.Lewis) L.P.Queiroz	Lewis & Andrade 1896 (K)	Brazil	KF522050	X	X	X	–	–
Poincianella pyramidalis (Tul.) L.P.Queiroz	Dorea 117 (HUEFS)	Brazil	KF522041	X	X	X	–	–
Poincianella pyramidalis (Tul.) L.P.Queiroz	de Queiroz 9020 (HUEFS)	Brazil	KF522042	X	X	X	–	–
Poincianella pyramidalis (Tul.) L.P.Queiroz	Taylor et al. 1361 (MO, NY)	Brazil	–	–	–	X	–	–
Poincianella pyramidalis (Tul.) L.P.Queiroz	Mori & Boom 14207 (K)	Brazil	KF522038	–	–	–	–	–
Poincianella pyramidalis (Tul.) L.P.Queiroz	Sampaio s.n. (retrieved from Genbank)	Brazil	–	–	–	–	–	JX850053
Poincianella standleyii Britton & Rose	Contreras 2745 (K)	Mexico	KF522236	X	X	–	–	–
Poincianella yucatanensis (Greenm.) Britton & Rose subsp. *yucatanensis*	Lewis 1765 (K)	Mexico	KF522280	X	X	–	AF430743	–

Poincianella yucatanensis (Greenm.) Britton & Rose subsp. *yucatanensis*	Lewis & Hughes 1766 (K, NY)	Mexico	KF522281	X	–	–	–	–
Caesalpinia coccinea G.P.Lewis & J.L.Contr.	Lewis 1802 (K)	Mexico	KF522225	X	–	X	–	–
Caesalpinia coccinea G.P.Lewis & J.L.Contr.	Lewis 1803 (K)	Mexico	KF522226	–	–	–	EF177386	–
Caesalpinia echinata Lam.	Filgueiras 3391 (NY)	Brazil, cultivated	KF522099	KP003802	KP003746	KP003695	X	
Caesalpinia echinata Lam.	Lewis et al. 1624 (K)	Brazil	KF522072	X	X	X		X
Caesalpinia echinata Lam.	Miranda 76 (HUEFS)	Brazil	KF522100	X	X	X	X	X
***Caesalpinia epifanioi* J.L.Contr.**	**Contreras 2039 (K)**	**Mexico**	**KF522278**	**KP003787**	**KP003733**	**KP003682**	–	–
Caesalpinia epifanioi J.L.Contr.	Sotuyo & Sotuyo 20 (MEXU)	Mexico	KF522279	–	–	–	–	–
***Caesalpinia epifanioi* J.L.Contr.**	**Sotuyo & al. 63 (MEXU)**	**Mexico**	–	–	–	–	**DQ208901**	–
Caesalpinia hintonii Sandwith.	Sotuyo 46 (MEXU)	Mexico	KF522270	X	X	X	DQ208882	–
Caesalpinia hughesii G.P.Lewis	Lewis & al. 1795 (K)	Mexico	KF522223	X	X	–	AF430725	–
Caesalpinia macvaughii J.L.Contr. & G.P.Lewis	Sotuyo & al. 8 (MEXU)	Mexico	KF522299	X	X	X	DQ208918	–
Caesalpinia macvaughii J.L.Contr. & G.P.Lewis	Sotuyo & al. 54 (MEXU)	Mexico	KF522269	–	–	–	–	–
Caesalpinia macvaughii J.L.Contr. & G.P.Lewis	Steinmann 3175 (INIREB, K, MEXU)	Mexico	KF522268	X	–	–	DQ208916	–

Caesalpinia marginata Tul.	Dubs 1746 (K)	Brazil	KF522045	–	–	X	–	–
Caesalpinia marginata Tul.	Wood & al. 26514 (K)	Bolivia	KF522048	X	X	X	–	–
Caesalpinia marginata Tul.	Wood & al. 26561 (K)	Bolivia	KF522046	X	X	X	–	X
Caesalpinia nicaraguensis G.P.Lewis	Hawkins & Hughes 4 (K)	Nicaragua	KF522302	–	–	X	–	–
Caesalpinia oyamae Sotuyo & G.P.Lewis	Hawkins & Hughes 23 (FHO, MEXU, TEX)	Mexico	KF522210	X	X	–	AF430724	–
Caesalpinia pluviosa var. *maraniona* G.P.Lewis & C.E.Hughes	Hughes & al. 2215 (FHO)	Peru	KF522033	X	X	X	X	–
Caesalpinia pluviosa var. *maraniona* G.P.Lewis & C.E.Hughes	Hughes & al. 3105 (MT)	Peru	KF522032	X	X	X	–	X
Caesalpinia pluviosa var. *maraniona* G.P.Lewis & C.E.Hughes	Pennington & al. 793 (E, K)	Peru	KF522031	X	X	X	–	–
Caesalpinia pluviosa var. *maraniona* G.P.Lewis & C.E.Hughes	Särkinen & al. 2191 (FHO)	Peru	KF522043	X	X	X	–	–
Caesalpinia yucatanensis subsp. *chiapensis* G.P.Lewis	Hughes 1353 (FHO)	Mexico	KF522271	X	X	X	–	–
Pomaria Cav. (15/16 species)								

**Pomaria glandulosa* Cav.	Ventura & López 9294 (TEX)	Mexico	KF522088	–	–	AY549901	AY535823-AY535810	–
Pomaria austrotexana B.B.Simpson	Simpson 1-IV-01-2 (TEX)	USA	–	–	–	AY549895	AF430757	–
Pomaria brachycarpa (A. Gray) B.B.Simpson	Simpson 92-06-22-3 (TEX)	USA	–	–	–	AY549896	AF430758	–
Pomaria burchellii (DC.) B.B.Simpson & G.P.Lewis	Mott 766 (MO)	South Africa	–	–	–	AY549897	AY535819-AY535806	–
Pomaria burchellii (DC.) B.B.Simpson & G.P.Lewis	Klepper 252/A/42 (PRU)	South Africa	–	–	–	AY549898	AF430744	–
Pomaria canescens (Fisher) B.B.Simpson	Turner et al. 93-128 (TEX)	Mexico	–	–	–	AY549899	AY535820-AY535807	–
Pomaria fruticosa (S. Watson) B.B.Simpson	Villareal 4439 (TEX)	Mexico	–	–	–	AY549901	AY535822-AY535809	–
Pomaria jamesii (Torr. & A.Gray) Walp.	Gagnon & Marazzi EG2010.020 (MT)	USA	KF522089	X	X	–	–	X
Pomaria jamesii (Torr. & A.Gray) Walp.	Higgins 17628 (NY)	USA	KF522090	KP003793	KP003736	KP003677	EU361830	EU362029
Pomaria lactea (Schinz) B.B.Simpson & G.P.Lewis	Pearson 9742 (MO)	South Africa	–	–	–	AY549904	AY535824-AY535811	–

Pomaria melanosticta S.Schauer	Simpson 92-06-23-1 (TEX)	USA	–	–	–	AY549905	AF430760	–
Pomaria multijuga (S.Watson) B.B.Simpson	Engard 649 (TEX)	Mexico	–	–	–	AY549906	AY535825-AY535812	–
Pomaria pilosa (Vogel) B.B.Simpson & G.P.Lewis	Wasum et al. 4571 (NY)	Brazil	–	–	–	AY549900	AY535821-AY535808	–
Pomaria pilosa (Vogel) B.B.Simpson & G.P.Lewis	Wasum & Bastos 8008 (NY)	Brazil	–	–	–	AY549907	AY535824-AY535813	–
Pomaria rubicunda (Vogel) B.B.Simpson & G.P.Lewis	Biganzoli & al. s.n. (NY)	Argentina	KF522085	KP003795	KP003738	KP003679	EU361775	–
Pomaria rubicunda (Vogel) B.B.Simpson & G.P.Lewis	Lima 463 (HUEFS)	Brazil	KP003642	KP003794	KP003737	KP003678	–	–
Pomaria rubicunda (Vogel) B.B.Simpson & G.P.Lewis var. *rubicunda*	Vanni & Marunak 3755 (NY)	Argentina	–	–	–	AY549909	AY535827-AY535814	–
Pomaria rubicunda var. *hauthalii* (Harms) B.B.Simpson & G.P.Lewis	Ibarrola 1750 (US)	Argentina	KF522087			AY549908	AF430723	
Pomaria sandersonii (Harv.) B.B. Simpson & G.P. Lewis	Hilliard & Burtt 9225 (MO)	South Africa				AY549910	AY535828-AY535815	

Pomaria stipularis (Vogel) B.B. Simpson & G.P. Lewis	Jönsson 1002a (A)	Brazil	KF522086			AY549911	AF430739	
Pomaria wootonii (Britton) B.B. Simpson	Johnston 4341 (TEX)	Mexico				AY549912	AY535829-AY535816	
Pterolobium R. Br. ex Wight & Arn (4/11 species)								
**Pterolobium* stellatum* (Forssk.) Brenan	Herendeen 17-XII-9709 (US)	Tanzania	KF522238	X	–	X	X	EU362032
**Pterolobium* stellatum* (Forssk.) Brenan	Briden & al. RNB219 (JRAU) BOLD rec. KNPA1387-09	South Africa	–	–	–	–	–	JF270908
**Pterolobium* stellatum* (Forssk.) Brenan	Albers 63080 (TEX)	Ethiopia	–	–	–	–	AF430783	–
Pterolobium hexapetalum (Roth) Santapau & Wagh	Grierson & Long 2075 (P)	Bhutan	X	–	X	X	–	–
Pterolobium integrum Craib	van Beusekom 4021 (P)	Thailand	–	X	–	–	–	–
***Pterolobium macropterum* Kurz**	**Grierson & Long 1624 (P)**	**Bhutan**	**X**	**X**	**X**	–	–	–
***Pterolobium macropterum* Kurz**	**Geesink & al. 5934 (P)**	**Thailand**	**X**	**X**	–	–	–	–
Stahlia Bello (1/1 species)								
**Stahlia* monosperma* (Tul.) Urb.	Gardner 7029 (E)	Dominican Republic	X	X	X	–	EU361838	EU362050

* *Stahlia monosperma* (Tul.) Urb.	Proctor 48543 (MO)	Puerto Rico	–	–	–	–	AF430787	–
Stenodrepanum Harms (1/1 species)									
* *Stenodrepanum bergii* Harms	Hick & Bertone 8 (CORD)	Argentina	–	–	–	–	JX219461	JX219467
**Stenodrepanum bergii* Harms	Hick & Bertone 16 (CORD)	Argentina	–	–	–	–	JX219462	–
Stuhlmannia Taub. (1/1 species)									
**Stuhlmannia moavi* Taub.	Luke 3710 (MO, K)	Tanzania	KF522061	X	X	X	–	–
**Stuhlmannia moavi* Taub.	Keraudren-Aymonin & Aymonin 25628 (MO)	Madagascar	KF522060	X	X	X	–	–
**Stuhlmannia moavi* Taub.	Tanner 2404 (NY)	Tanzania	–	–	–	–	AF430789	–
**Stuhlmannia moavi* Taub.	Luke & Robertson 2336 (K)	Kenya	KF522058	–	–	–	–	–
**Stuhlmannia moavi* Taub.	Robertson 7509 (K)	Kenya	KF522059	X	X	X	EU361839	X
**Stuhlmannia moavi* Taub.	Tanner 3167 (K)	Tanzania	AY899765	–	–	–	AY899707	–
Tara Molina (3/3 species)									
**Tara spinosa* (Molina) Britton & Rose	Eastwood & al. RJE36 (FHO)	Peru	KF522128	X	X	–	–	KF379250
**Tara spinosa* (Molina) Britton & Rose	Hughes 2360 (FHO)	Peru	KF522129	X	X	X	–	–

**Tara spinosa* (Molina) Britton & Rose	Nee 45494 (MO)	Australia, cultivated	KF522130	X	X	X	–	–
Tara spinosa (Molina) Britton & Rose	Lewis 2200 (K)	Ecuador	–	–	–	KF379235	X	–
**Tara spinosa* (Molina) Britton & Rose	Aronson 7756 (TEX)	Chile	–	–	–	–	AF430738	–
Caesalpinia cacalaco Humb. & Bonpl.	Gagnon & Marazzi EG2010.022 (MT)	USA, cultivated	KF522202	X	–	X	–	–
Caesalpinia cacalaco Humb. & Bonpl.	Soto Nuñez 13682 (MEXU)	Mexico	KF522312	–	–	–	–	–
Caesalpinia cacalaco Humb. & Bonpl.	Walker s.n., RBG Liv.Coll. 1986–6481 (K)	Mexico	KF522203	X	X	X	–	–
***Caesalpinia cacalaco* Humb. & Bonpl.**	**Lewis 1789 (K)**	**Mexico**	**–**	**–**	**–**	**–**	**AF430709**	**EU361898**
***Caesalpinia cacalaco* Humb. & Bonpl.**	**Lewis 1788 (K)**	**Mexico**	**–**	**–**	**–**	**X**	**–**	**–**
Caesalpinia vesicaria L.	Hawkins & Hughes 11 (FHO)	Nicaragua	KF522204	X	X	X	–	–
Caesalpinia vesicaria L.	Lewis & Hughes 1768 (K)	Mexico	KF522205	–	–	X	AF430742	–
Zuccagnia Cav. (1/1 species)								
**Zuccagnia punctata* Cav.	Fortunato 5545 (MO)	Argentina	KF522142	X	X	X	–	–
**Zuccagnia punctata* Cav.	Galleto & al. 171 (CORD)	Argentina	KF522141	KP003798	KP003742	KP003688	AF430791	X

**Zuccagnia punctata* Cav.	Guglianone & al. 1668 (K, SI)	Argentina	KF522143	X	X	X	–	–
**Zuccagnia punctata* Cav.	Lutz 136 (NY)	Argentina	KF522140	X	X	X	EU361842	–
**Zuccagnia punctata* Cav.	Tapia & al. s.n. (CORD)	Argentina	–	–	–	–	JX219463	JX219468
Unassigned Old World taxa (13/~20 species)								
Caesalpinia crista L.	Herendeen 1-V-99-3 (US)	Thailand	KF522073	X	X	X	X	EU361900
Caesalpinia crista L.	Wieringa & al. 4199 (WAG)	Australia, cultivated	KF522074	X	X	X	–	–
Caesalpinia crista L.	PS1367MT01 (retrieved from Genbank)	N.A.	–	–	–	–	–	HM049549
Caesalpinia decapetala (Roth) Alston	Marazzi BM137 (Z)	Switzerland, cultivated	AM086910	–	–	–	–	AM086828
Caesalpinia decapetala (Roth) Alston	Hughes & al. 2227 (FHO)	Peru, cultivated	KF522081	X	X	X	–	–
Caesalpinia decapetala (Roth) Alston	Hooper & Gandhi 2429 (US)	India, cultivated	KF522080	–	–	–	–	
Caesalpinia decapetala (Roth) Alston	Herendeen & Mbago 19-XII-97-1 (US)	Tanzania	KF522082	X	X	X	X	KF379248.
Caesalpinia decapetala (Roth) Alston	PS1589MT01 (retrieved from Genbank)	N.A.	–	–	–	GU217669	–	HM049555
Caesalpinia decapetala (Roth) Alston	Corby 2173; Krukoff coll. (K)	N.A.	–	–	–	–	AF430714	–

Caesalpinia decapetala (Roth) Alston	(retrieved from Genbank)	N.A.	–	–	–	JF708207	–	–
Caesalpinia digyna Rottler	van Beusekom & Phengklai 3036 (P)	Thailand	X	X				
Caesalpinia digyna Rottler	Maxwell 91-827 (P)	Thailand	X	X	–	X	–	–
Caesalpinia digyna Rottler	Parnell et al. 95-617 (K)	Thailand	X	X	–	–	–	–
Caesalpinia digyna Rottler	Cheng et al. CL 643 (P)	Cambodia	X	X	–	X	–	–
Caesalpinia godefroyana Kuntze	Cheng & al. CL642 (P)	Cambodia	X	X	X	X	–	–
***Caesalpinia mimosoides* Lam.**	**Larsen & al. 44653 (MO)**	**Thailand**	**KF522251**	**X**	**X**	**–**	**–**	**–**
***Caesalpinia mimosoides* Lam.**	**Clark RPC237 (K)**	**Thailand**	**X**	**X**	**X**	**–**	**X**	**–**
Caesalpinia oppositifolia Hattink	Lugas 607 (K)	Malaysia	KF522056	X	–	–	–	–
Caesalpinia oppositifolia Hattink	Lugas 921 (K)	Malaysia	KF522055	X	X	X	–	–
Caesalpinia parviflora Prain	van Beusekom & al. 3977 (K)	Thailand	KF522057	X	X	X	–	–
Caesalpinia pearsonii Bolus	Strey 2475 (K)	Namibia	X	X	X	X	–	X
Caesalpinia pearsonii Bolus	Kolberg & Loots, NAM2943-HK1399 (K)	Namibia	X	X	X	X	X	X
Caesalpinia milettii Hook. & Arn.	Ying 1639 (K)	China	–	X	–	–	–	–

***Caesalpinia sappan* L.**	**Jinawn 76 (K)**	**Sabah, Borneo**	**–**	**X**	**–**	**–**	**–**	**–**
***Caesalpinia sappan* L.**	**PS1370MT04, (retrieved from Genbank)**	**N.A.**	**–**	**–**	**–**	**GQ434751**	**–**	**–**
***Caesalpinia sappan* L.**	**PS1370MT05, (retrieved from Genbank)**	**N.A.**	**–**	**–**	**–**	**–**	**–**	**HM049952**
***Caesalpinia sappan* L.**	**Gillis 9548 (P)**	**India**	**–**	**X**	**–**	**–**	**–**	**–**
***Caesalpinia sappan* L.**	**(retrieved from Genbank)**	**N.A.**	**–**	**–**	**–**	**EU243573**	**–**	**–**
***Caesalpinia sappan* L.**	**PS1370MT01, (retrieved from Genbank)**	**N.A.**	**–**	**–**	**–**	**–**	**–**	**HM049551**
Caesalpinia tortuosa Roxb.	Lace 6332 (K)	Burma	–	X	–	X	–	–
Caesalpinia vernalis Benth.	Li Shi Jin 787 (CAS, IBSC)	China	KF522075	–	–	–	–	–
Caesalpinia welwitschiana (Oliv.) Brenan	Bidgood & al. 2913 (K)	Tanzania	KF522133	X	–	–	–	–
Caesalpinia welwitschiana (Oliv.) Brenan	Malaisse 13658 (K)	Zaire	KF522134	X	X	–	–	X

Annex 2.

Accessions included in the study of chapter 3. Species of the Caesalpinia Group are classified sensu Gagnon & al. (in prep., chapter 2), and the number of species sampled over the total number of species recognized in the genus is given in parentheses. Type species for genera in the Caesalpinia Group are preceded by an asterisk (*). Collector names and numbers (and herbarium acronym) of voucher specimens are listed for all material that was taken from herbarium specimens and for the voucher specimens of seed collections and silica-dried leaf samples, if known. Accession numbers are provided for published sequences downloaded directly from Genbank; The majority of the sequences downloaded from Genbank come from the following published studies: Bruneau & al. (2001), Simpson & al. (2003), Haston & al. (2005), Simpson & al. (2005), Marazzi & al. (2006), Simpson & al. (2006), Marazzi & Sanderson (2010), Babineau & al. (2013), Gagnon & al. (2013, chapter 1), and Gagnon & al. (2015, chapter 4). In bold are accessions that were concatenated togheter in the phylogenetic matrix. GenBank accession numbers will be provided upon acceptance of the manuscript.

Genus (no. of species sampled/total no. species) ***Species***	**Voucher specimen (Herbarium)**	**Collection Locality**	***rps16***	***trnD-trnT***	***ycf6-psbM***	***ITS***	***trnL-trnF***	***matK***
OUTGROUP								

Cassia javanica L.	Fougère-Danezan 6 (MT)	Singapore, cultivated	KF522255	X	X	X	EU361782	EU361910
Colvillea racemosa **Bojer ex Hook.**	**Haston V200303 (RNG)**	**Madagascar**	**AY899794**	**–**	**–**	**–**	**AY899739**	**–**
Colvillea racemosa **Bojer ex Hook.**	**Bruneau 1397 (MT)**	**Madagascar**	**–**	**KF379366**	**–**	**KF379221**	**–**	**KF379241**
Conzattia multiflora **(B.L. Rob.) Standl.**	**Du 600 (K),Haston V200303 (RNG)**	**Mexico**	**AY899785**	**–**	**–**	**–**	**–**	**–**
Conzattia multiflora **(B.L. Rob.) Standl.**	**Hughes 1815 (NY)**	**Mexico**	**–**	**KF379378**	**–**	**KF379219**	**–**	**–**
Conzattia multiflora **(B.L. Rob.) Standl.**	**Simpson 17-XI-97 (TEX)**	**Mexico**	**–**	**–**	**–**	**–**	**AF430770**	**–**
Conzattia multiflora **(B.L. Rob.) Standl.**	**Werling 399 (ASU)**	**Mexico**	**–**	**–**	**–**	**–**	**–**	**AY386918**
Gymnocladus chinensis **Baill.**	**Herendeen II-V-02-1 (US)**	**USA, cultivated**	**KF522308**	**X**	**X**	**X**	**X**	**–**
Gymnocladus chinensis **Baill.**	**Herendeen 8-V-2003-1 (US)**	**USA, cultivated**	**–**	**–**	**–**	**–**	**–**	**AY386928**
Pterogyne nitens **Tul.**	**Pennington 244 (FHO)**	**Brazil**	**AY899747**	**–**	**–**	**–**	**AY899689**	**–**
Pterogyne nitens **Tul.**	**Herendeen 13-XII-97-1 (US)**	**Tanzania**	**–**	**X**	**X–**	**X**	**–**	**EU362031**
Senna covesii **(A. Gray) H.S. Irwin & Barneby**	**Marazzi BM297 (ARIZ)**	**USA, cultivated**	**HM236885**	**–**	**–**	**–**	**–**	**–**
Senna covesii **(A. Gray) H.S. Irwin & Barneby**	**Wojciechowski 876 (ASU)**	**USA**	**–**	**–**	**–**	**X**	**EU361835**	**AY386850**

***Senna spectabilis* (DC.) H.S. Irwin & Barneby**	**Marazzi et al. BM029 (PY, CTES, Z)**	**Paraguay**	**AM086983**	**–**	**–**	**–**	**–**	**AM086900**
***Senna spectabilis* (DC.) H.S. Irwin & Barneby**	**Herendeen & Pooma 24–IV–99–6 (US)**	**Thailand**	**–**	**X**	**X**	**X**	**–**	**–**
Senna alata (L.) Roxb.	Bruneau 1076 (MT)	Cameroun, cultivated	–	X	X	X	AF365091	EU362042
***Tetrapterocarpon geayi* Humbert**	**Noyes 1049 (K)**	**Madagascar**	**AY899742**	**–**	**–**	**–**	**AY899684**	**–**
***Tetrapterocarpon geayi* Humbert**	**Bruneau & Ranaivojaona 1395 (WAG)**	**Madagascar**	**–**	**X**	**X**	**X**	**–**	**GU321972**
CAESALPINIA GROUP								
Arquita E.Gagnon & al. (5/5 species)								
* *Arquita mimosifolia* (Griseb.) E.Gagnon & al.	Gagnon & al. EG203 (MT)	Argentina	KF522160	KP003760	KP003707	KP003654	–	X
* *Arquita mimosifolia* (Griseb.) Gagnon & al.	Gagnon & Atchison EG211 (MT)	Argentina	KF522159	KP003759	KP003706	KP003653	–	X
* *Arquita mimosifolia* (Griseb.) E.Gagnon & al.	Särkinen et al. 2006 (FHO)	Argentina	KF522161	KP003761	KP003708	KP003655	–	KF379244
* *Arquita mimosifolia* (Griseb.) E.Gagnon & al.	Chumley 7387 (TEX)	Argentina	–	–	–	AY549893	AY535818-AY535805	–
Arquita ancashiana (Ulibarri) E.Gagnon & al.	Hughes & al. 3021 (MT, Z)	Peru	KF522164	KP003747	KP003696	KP003643	–	X

Arquita ancashiana (Ulibarri) E.Gagnon & al.	Hughes & al. 3070 (MT, Z)	Peru	KF522167	KP003749	KP003698	KP003644	–	–
Arquita ancashiana (Ulibarri) E.Gagnon & al.	Lewis & Klitgaard 2266 (K)	Ecuador	KF522170	KP003753	KP003792	KP003647	X	–
Arquita celendiniana (G.P. Lewis & C.E. Hughes) E.Gagnon & al.	Hughes & al. 2210 (FHO)	Peru	KF522148	KP003756	KP003703	KP003650	X	X
Arquita celendiniana (G. P. Lewis & C.E. Hughes) E.Gagnon & al.	Hughes & al. 3097 (MT, Z)	Peru	KF522149	KP003757	KP003704	KP003651	–	X
Arquita celendiniana (G.P. Lewis & C.E. Hughes) E.Gagnon & al.	Hughes & al. 3102 (MT, Z)	Peru	KF522147	KO003758	KP003705	KP003652	–	X
Arquita trichocarpa var. *trichocarpa* (Griseb.) E.Gagnon & al.	Lewis & Klitgaard 2166 (K)	Argentina	KF522163	KP003762	KP003709	KP003659	AF430740	X
Arquita trichocarpa var. *boliviana* E.Gagnon & al.	Hughes & al. 2442 (FHO)	Bolivia	KF522162	KP003764	KP003711	KP003657	–	X
Arquita grandiflora E.Gagnon & al.	Särkinen & al. 2225 (FHO)	Peru	KF522151	KP003763	KP003710	KP003656	–	X
Arquita grandiflora E.Gagnon & al	Hughes & al. 3047 (K, MT)	Peru	KF522150	KP003774	KP003719	KP003668	–	–
Arquita grandiflora E.Gagnon & al	Hughes & al. 3155 (K, MT)	Peru	KF522153	KP003779	KP003724	KP003673	–	–
Arquita grandiflora E.Gagnon & al	Hughes & al. 3156 (K, MT)	Peru	KF522156	KP003778	KP003723	KP003672	–	–
Balsamocarpon Clos (1/1 species)								
*_Balsamocarpon brevifolium_ Clos.	Baxter DCI 1869 (E)	Chile	KF522135	KP003801	KP003743	KP003689	EU361739	EU361864

**Balsamocarpon brevifolium* Clos.	Taylor 745 (K)	Chile	KF522136	X	X	X	–	–
Biancaea Tod. (6/6 species)								
**Biancaea decapetala* (Roth) O.Deg	Marazzi BM137 (Z)	Switzerland, cultivated	AM086910	–	–	–	–	AM086828
**Biancaea decapetala* (Roth) O.Deg	Hughes & al. 2227 (FHO)	Peru, cultivated	KF522081	X	X	X	–	–
**Biancaea decapetala* (Roth) O.Deg.	Herendeen & Mbago 19-XII-97-1 (US)	Tanzania	KF522082	X	X	X	X	KF379248.
**Biancaea decapetala* (Roth) O.Deg.	PS1589MT01 (retrieved from Genbank)	N.A.	–	–	–	GU217669	–	HM049555
Biancaea godefroyana (Kuntze) E.Gagnon & al.	Cheng & al. CL642 (P)	Cambodia	X	X	X	X	–	–
Biancaea milettii (Hook. & Arn.) E.Gagnon & al.	Ying 1639 (K)	China	–	X	–	–	–	–
Biancaea oppositifolia (Hattink) E.Gagnon & al.	Lugas 607 (K)	Malaysia	KF522056	X	–	–	–	–
Biancaea oppositifolia (Hattink) E.Gagnon & al.	Lugas 921 (K)	Malaysia	KF522055	X	X	X	–	–
Biancaea parviflora (Prain) E.Gagnon & al.	van Beusekom & al. 3977 (K)	Thailand	KF522057	X	X	X	–	–
***Biancaea sappan* (L.) E.Gagnon & al.**	**Gillis 9548 (P)**	**India**	–	**X**	–	–	–	–
***Biancaea sappan* (L.) E.Gagnon & al.**	**(retrieved from Genbank)**	**N.A.**	–	–	–	**EU243573**	–	–
***Biancaea sappan* (L.) E.Gagnon & al.**	**PS1370MT01, (retrieved from Genbank)**	**N.A.**	–	–	–	–	–	**HM049551**

Caesalpinia L. sensu stricto (7/~8 species)								
**Caesalpinia brasiliensis* L.	Leonard & Leonard 13904 (US, K)	Haiti	KF522092	X	X	X	–	–
Caesalpinia anacantha Urb.	Liogier 16639 (P)	Dominican Republic	X	X	–	X	–	–
Caesalpinia bahamensis Lam.	Baker B27 (K)	Bahamas	KF522091	X	–	X	–	–
Caesalpinia bahamensis Lam	Pollard & al. 1295 (K)	Tuks & Caicos Islands	X	X	–	X	–	–
Caesalpinia barahonensis Urb.	Ekman 5965 (K)	Haiti	KF522094	X	–	X	–	–
Caesalpinia cassioides Willd.	Hughes & al. 2023 (FHO)	Peru	KF522097	X	X	X	–	–
Caesalpinia cassioides Willd.	Hughes & al. 2228 (FHO)	Peru	KF522098	X	X	X	–	–
Caesalpinia cassioides Willd.	Hughes & al. 2641 (FHO)	Peru	KF522095	X	X	X	–	–
Caesalpinia cassioides Willd.	Pennington & al. 789 (E)	Peru	KF522096	X	X	X	X	
Caesalpinia nipensis Urb.	Marie-Victorin & al. 21509 (MT)	Cuba	X	X	–	X	–	–
Caesalpinia nipensis Urb.	Lewis 1838 (K)	Cuba	X	X	X	X	–	X
Caesalpinia pulcherrima (L.) Sw.	Cox 1, RBG Liv.Coll. 1975-3028 (K)	cultivated	KF522174	–	–	–	–	–
Caesalpinia pulcherrima (L.) Sw.	Fougère-Danezan 19 (MT)	Singapore, cultivated	KF522172	X	X	X	X	KF379245

Caesalpinia pulcherrima (L.) Sw.	Lewis & Hughes 1715 (K)	Guatemala	KF522171	X	–	X	AF430733	–
Caesalpinia pulcherrima (L.) Sw.	Montreal Botanical Garden 7089-92 (MT)	Canada, cultivated	KF522173	X	X	X	–	–
Cenostigma Tul. (11/14 species)								
*_Cenostigma macrophyllum_ Tul.	Coradin & al. 6306 (K)	Brazil, Bahia	KF522053	X	X	–	–	–
*_Cenostigma macrophyllum_ Tul.	Thomas 9615 (K)	Brazil, Piaui	KF522069	–	X	–	–	–
*_Cenostigma macrophyllum_ Tul.	de Queiroz 9147 (HUEFS)	Brazil, Bahia	KF522037	X	X	–	–	–
Cenostigma bracteosa (Tul.) E.Gagnon & al.	Carvalho–Sobrinho 218 (HUEFS)	Brazil	KF522035	X	X	–	–	–
Cenostigma bracteosa (Tul.) E.Gagnon & al.	de Queiroz 10085 (HUEFS)	Brazil	KF522079	X	–	–	–	–
Cenostigma bracteosa (Tul.) E.Gagnon & al.	de Queiroz 7845 (HUEFS)	Brazil	KF522036	X	X	–	–	–
Cenostigma eriostachys (Benth.) E.Gagnon & al.	Hughes 1832 (K)	Mexico	AY899751	–	–	–	AY899693	–
Cenostigma eriostachys (Benth.) E.Gagnon & al.	Lewis & al. 1799 (K)	Mexico	KF522029	X	X	X	AF430715	–
Cenostigma gaumeri (Greenm.) E.Gagnon & al.	Hughes 492 (K)	Mexico	KF522034	X	–	–	–	–
Cenostigma gaumeri (Greenm.) E.Gagnon & al.	Lewis & Hughes 1762 (K)	Mexico	KF522044	KP003799	KP003739	KP003692	–	–

Cenostigma laxiflora (Tul.) E.Gagnon & al.	de Queiroz 7063 (HUEFS)	Brazil	KF522051	X	–	X	–	–
Cenostigma marginata (Tul.) E.Gagnon & al.	Dubs 1746 (K)	Brazil	KF522045	–	–	X	–	–
Cenostigma marginata (Tul.) E.Gagnon & al.	Wood & al. 26514 (K)	Bolivia	KF522048	X	X	X	–	–
Cenostigma marginata (Tul.) E.Gagnon & al.	Wood & al. 26561 (K)	Bolivia	KF522046	X	X	X	–	X
Cenostigma microphylla (Mart. ex. G.Don) E.Gagnon & al.	de Queiroz 9060 (HUEFS)	Brazil	KF522039	X	X	X	–	–
Cenostigma pellucida (Vogel) E.Gagnon & al.	Ekman 4999 (K)	Haiti	–	X	–	–	–	–
Cenostigma pluviosa (DC.) E.Gagnon & al.	de Queiroz 12795 (HUEFS)	Brazil	KF522049	KP003800	KP003735	KP003687	–	–
Cenostigma pluviosa (DC.) E.Gagnon & al.	Wood & al. 26552 (K)	Bolivia	KF522047	X	X	X	–	–
Cenostigma pluviosa (DC.) E.Gagnon & al. var. *pluviosa*	Wood 8838 (K)	Bolivia	KF522052	X	–	X	–	–
Cenostigma pluviosa (DC.) E.Gagnon & al. var. *pluviosa*	Nee 40000 (K)	Bolivia	KF522054	–	–	X	–	–
Cenostigma pluviosa var. *maraniona* (G.P.Lewis & C.E.Hughes) E.Gagnon & al.	Hughes & al. 2215 (FHO)	Peru	KF522033	X	X	X	X	–
Cenostigma pluviosa var. *maraniona* (G.P.Lewis & C.E.Hughes) E.Gagnon & al.	Hughes & al. 3105 (MT)	Peru	KF522032	X	X	X	–	X

Cenostigma pluviosa var. *maraniona* (G.P.Lewis & C.E.Hughes) E.Gagnon & al.	Pennington & al. 793 (E, K)	Peru	KF522031	X	X	X	–	–
Cenostigma pluviosa var. peltophoroides (DC.) E.Gagnon & al.	Lewis & al. 1632 (K, NY)	Brazil	–	–	–	X	–	–
Cenostigma pluviosa var. *sanfranciscana* (G.P.Lewis) E.Gagnon & al.	Lewis & Andrade 1896 (K)	Brazil	KF522050	X	X	X	–	–
Cenostigma pyramidalis (Tul.) E.Gagnon & al.	Dorea 117 (HUEFS)	Brazil	KF522041	X	X	X	–	–
Cenostigma pyramidalis (Tul.) E.Gagnon & al.	de Queiroz 9020 (HUEFS)	Brazil	KF522042	X	X	X	–	–
Cenostigma tocantinum Ducke	Klitgaard & de Lima 88 (K)	Brazil, cultivated	KF522071	KP003803	KP003740	KP003694	–	X
Cenostigma tocantinum Ducke	Klitgaard s.n. (INPA)	Brazil	KF522070	X	X	X	–	–
Cordeauxia Hemsl. (1/1 species)								
**Cordeauxia edulis* Hemsl.	Hassan 232 (FHO, K)	Somalia	AY899748	–	–	–	AY899690	–
**Cordeauxia edulis* Hemsl.	Kuchar 17803 (K)	Somalia	KF522084	X	X	X	X	X
Coulteria Kunth (7/7 species)								
**Coulteria mollis* Kunth	Way NMLW 28 (K)	Venezuela	KF522187	X	X	X	–	–

Coulteria platyloba (S.Watson) N.Zamora	Gagnon & Marazzi, EG2010.007 (MT)	USA, cultivated	KF522175	X	X	X	–	–
Coulteria platyloba (S.Watson) N.Zamora	MacQueen 178 (K)	Mexico	KF522178	X	X	X	–	–
***Caesalpinia colimensis* F.J.Herm.**	**Sousa 6163 (K)**	**Mexico**	**KF522176**	**X**	**X**	**X**	–	–
***Caesalpinia colimensis* F.J.Herm.**	**Sousa 7659 (TEX)**	**Mexico**	–	–	–	–	**AF430713**	–
***Caesalpinia pringlei* (Britton & Rose) Standl.**	**Cruz Duran 926 (MEXU)**	**Mexico**	**KF522180**	–	–	–	–	–
***Caesalpinia pringlei* (Britton & Rose) Standl.**	**Panero 4037 (TEX)**	**Mexico**	–	–	–	–	**AF430732**	–
Caesalpinia pumila (Britton & Rose) F.J.Herm.	Gagnon & Marazzi EG 2010.014 (MT)	USA, cultivated	KF522182	X	X	X	–	–
Caesalpinia pumila (Britton & Rose) F.J.Herm.	Lewis & al. 2067 (K)	Mexico	KF522177	X	X	X	KF379385	KF379247
Caesalpinia velutina (Britton & Rose) Standl.	Hughes & al. 2087 (FHO)	Mexico	KF522189	X	X	X	–	–
Caesalpinia velutina (Britton & Rose) Standl.	Lewis 1797 (NY)	Mexico	KF522179	X	X	X	–	–
Caesalpinia velutina (Britton & Rose) Standl.	Way & al. JIC 22176 (K)	Mexico	KF522190	X	X	X	–	–
Caesalpinia velutina (Britton & Rose) Standl.	Hughes 255 (FHO)	Guatemala	AY899752	–	–	–	AY899694	–
Caesalpinia violacea (Mill.) Standl.	Lewis & al. 1763 (NY)	Mexico	KF522188	X	X	–	X	JX099334

Denisophytum R.Vig. (7/8 species)								
****Denisophytum madagascariense*** **R.Vig**	**Bruneau 1348 (MT)**	**Madagascar**	**KF522119**	**X**	**X**	**X**	**–**	**KF379246**
****Denisophytum madagascariense*** **R.Vig**	**Lewis & al. 2158 (K)**	**Madagascar**	**KF522120**	**X**	**X**	**X**	**AF430726**	**–**
Denisophytum buchii (Urb.) E.Gagnon & al.	Acevedo-Rodriguez & al. 8522 (US, K)	Dominican Republic	KF522115	X	X	X	–	–
Denisophytum erianthera (Chiov.) E.Gagnon & al.	Friis & al. 4698 (K)	Somalia	KF522123	X	X	X	–	–
Denisophytum erianthera (Chiov.) E.Gagnon & al.	Radcliffe-Smith 5518 (K)	Oman	KF522122	X	X	X	–	–
Denisophytum erianthera (Chiov.) E.Gagnon & al.	Thulin & Mohamed 6941 (K)	Somalia	KF522125	X	X	X	–	–
Denisophytum erianthera var. *pubescens* (Brenan) E.Gagnon & al.	Boulos & al. 17000 (K)	Yemen	KF522117	X	X	X	–	–
Denisophytum pauciflora (Griseb.) E.Gagnon & al.	Ekman 9703 (K)	Cuba	KF522124	X	X	X	–	–
Denisophytum pauciflora (Griseb.) E.Gagnon & al.	Liogier & Liogier 20521 (NY)	Hispaniola	KF522116	X	X	–	X	–
Denisophytum pauciflora (Griseb.) E.Gagnon & al.	Lewis 1854 (K)	Cuba, cultivated	–	X	–	X	–	–
Denisophytum rosei Urb.	Ekman H13620 (K, TEX)	Dominican Republic	X	X		X	AF430735	
Denisophytum sessilifolia **(S.Watson) E.Gagnon & al.**	**Palmer 533 (K, MO)**	**Mexico**	**X**	**X**	**X**	**X**	**–**	**–**

***Denisophytum sessilifolia* S.Watson E.Gagnon & al.**	**Neff 8–24–91–4 (TEX)**	**Mexico**	**–**	**–**	**–**	**–**	**AF430737**	**–**
Denisophytum stuckertii (Hassl.) E.Gagnon & al.	Beck 9443 (NY)	Bolivia	KF522126	X	X	X	X	–
Erythrostemon (Hook.) Klotzsch (30/31 species)								
**Erythrostemon gilliesii* Klotzsch	Marazzi & al. BM131 (CTES, Z)	Argentina	AM086914	–	–	–	–	AM086829
**Erythrostemon gilliesii* Klotzsch	Spellenberg 12701 (MT)	USA, cultivated	KF522296	KP003786	KP003729	KP003681	JX073265	JX099328
Erythrostemon acapulcensis (Standl.) E.Gagnon & al.	MacQueen & al. 406 (K)	Mexico	KF522235	X	X	–	–	–
Erythrostemon angulata (Hook & Arn.) E.Gagnon & al.	Brownless & al. 591 (E)	Chile	KF522288	X	X	X	–	–
Erythrostemon argentina (Burkart) E.Gagnon & al.	Hughes & al. 2460 (FHO)	Bolivia	KF522289	X	X	X	–	–
Erythrostemon argentina (Burkart) E.Gagnon & al.	Pennington & al. 13323 (K)	Bolivia	KF522290	X	X	X	–	–
***Erythrostemon caladenia* (Standl.) E.Gagnon & al.**	**Contreras 2818 (MEXU)**	**Mexico**	–	–	–	–	**EF177383**	–
***Erythrostemon caladenia* (Standl.) E.Gagnon & al.**	**Lewis & al. 2072 (K)**	**Mexico**	**KF522228**	**X**	**X**	**–**	**–**	**–**
Erythrostemon calycina (Benth) L.P.Queiroz	Giuletti 2045 (HUEFS)	Brazil	KF522304	X	X	–	–	–
Erythrostemon calycina (Benth) L.P.Queiroz	Lewis & Andrade 1885 (K)	Brazil	KF522303	–	X	X	X	X

***Erythrostemon caudata* (A.Gray) E.Gagnon & al.**	**Simpson I-IV-01-3 (TEX)**	**USA**	**KF522298**	**X**	**X**	**–**	**–**	**–**	
***Erythrostemon caudata* (A.Gray) E.Gagnon & al.**	**Neff 99-3-16-1 (TEX)**	**USA**	**–**	**–**	**–**	**–**	**AF430712**	**–**	
Erythrostemon coccinea (G.P.Lewis & J.L.Contr.) E.Gagnon & al.	Lewis 1802 (K)	Mexico	KF522225	X	–	X	–	–	
Erythrostemon coccinea (G.P.Lewis & J.L.Contr.) E.Gagnon & al.	Lewis 1803 (K)	Mexico	KF522226	–	–	–	EF177386	–	
Erythrostemon coluteifolia (Griseb.) E.Gagnon & al.	Gagnon et al. EG207 (MT)	Argentina	KF522291	X	X	X	–	–	
Erythrostemon coluteifolia (Griseb.) E.Gagnon & al.	Gagnon &Atchison EG223 (MT)	Argentina	KF522292	X	X	X	–	–	
Erythrostemon coulterioides (Griseb. emend. Burkart) E.Gagnon & al.	Gagnon &Atchison EG209 (MT)	Argentina	KF522285	X	X	X	–	–	
***Erythrostemon epifanioi* (J.L.Contr.) E.Gagnon & al.**	**Contreras 2039 (K)**	**Mexico**	**KF522278**	**KP003787**	**KP003733**	**KP003682**	**–**	**–**	
***Erythrostemon epifanioi* (J.L.Contr.) E.Gagnon & al.**	**Sotuyo & al. 63 (MEXU)**	**Mexico**	**–**	**–**	**–**	**–**	**DQ208901**	**–**	
Erythrostemon exilifolia (Griseb.) E.Gagnon & al.	Gagnon & al. EG201 (MT)	Argentina	KF522295	X	X	X	–	–	
Erythrostemon exilifolia (Griseb.) E.Gagnon & al.	Gagnon & Atchison EG219 (MT)	Argentina	KF522293	X	X	X	–	–	

***Erythrostemon exilifolia* (Griseb.) E.Gagnon & al.**	**Gagnon &Atchison EG222 (MT)**	**Argentina**	**X**	**X**	**X**	**X**	**–**	**–**
***Erythrostemon exilifolia* (Griseb.) E.Gagnon & al.**	**Galleto 167 (CORD)**	**Argentina**	**–**	**–**	**–**	**–**	**AF430716**	**–**
Erythrostemon exostemma (DC.) E.Gagnon & al. subsp. *exostemma*	Lewis & Hughes 1712, RBG Liv.Coll. 1989–3073 (K)	Guatemala	KF522224	X	–	–	AF430717	–
Erythrostemon exostemma (DC.) E.Gagnon & al. subsp. *exostemma*	Lewis & Hughes 1753 (K)	Guatemala	KF522222	X	X	–	–	–
Erythrostemon fimbriata (Tul.) E.Gagnon & al.	Hughes et al. 2441 (FHO)	Bolivia	KF522284	KP003785	KP003728	KP003680	–	–
Erythrostemon fimbriata (Tul.) E.Gagnon & al.	Hughes et al. 2466 (FHO)	Bolivia	KF522286	X	X	X	–	–
Erythrostemon fimbriata (Tul.) E.Gagnon & al.	Solomon & Nee 16062 (NY)	Bolivia	KF522297	X	X	X	X	–
Erythrostemon glandulosa (DC.) E.Gagnon & al.	Ekman 9838 (K)	Haiti	X	X	–	–	–	–
Erythrostemon hintonii (Sandwith.) E.Gagnon & al.	Sotuyo 46 (MEXU)	Mexico	KF522270	X	X	X	DQ208882	–
Erythrostemon hughesii (G.P.Lewis) E.Gagnon & al.	Lewis & al. 1795 (K)	Mexico	KF522223	X	X	–	AF430725	–
Erythrostemon laxa (Benth.) E.Gagnon & al.	Delgado 2337 (MEXU)	Mexico	KF522274	–	–	–	–	–
Erythrostemon macvaughii (J.L.Contr. & G.P.Lewis) E.Gagnon & al.	Sotuyo & al. 8 (MEXU)	Mexico	KF522299	X	X	X	DQ208918	–

Erythrostemon macvaughii (J.L.Contr. & G.P.Lewis) E.Gagnon & al.	Steinmann 3175 (INIREB, K, MEXU)	Mexico	KF522268	X	–	–	DQ208916	–
Erythrostemon melanadenia (Rose) E.Gagnon & al.	Hughes & al. 2091 (FHO)	Mexico, Oaxaca	KF522275	X	X	–	–	–
***Erythrostemon melanadenia* (Rose) E.Gagnon & al.**	**Hughes & al. 2074 (FHO)**	**Mexico, Puebla**	**KF522276**	**X**	–	**X**	–	–
***Erythrostemon melanadenia* (Rose) E.Gagnon & al.**	**Sotuyo & Gonzalez s.n. (MEXU)**	**Mexico, Puebla**	–	–	–	–	**DQ208904**	–
Erythrostemon mexicana (A.Gray) E.Gagnon & al.	Hughes & al. 1606 (NY, FHO)	Mexico	KF522218	X	X	–	EU361772	EU361904
Erythrostemon mexicana (A.Gray) E.Gagnon & al.	Delgado 01-2114 (MEXU)	Mexico	KF522219	–	–	–	EF177387	–
Erythrostemon mexicana (A.Gray) E.Gagnon & al.	Lewis s.n., Kew Living Coll. 1973-21714 (K)	Mexico	KF522215	KP03788	KP003730	KP00383	–	–
Erythrostemon mexicana (A.Gray) E.Gagnon & al.	Mason s.n. (K)	USA	–	–	–	AY549892	AF430727	–
Erythrostemon nelsonii (Britton & Rose) E.Gagnon & al.	Contreras & Sotuyo s.n. (MEXU)	Mexico	KF522300	X	X	–	–	–
Erythrostemon nelsonii (Britton & Rose) E.Gagnon & al.	Sotuyo, s.n., RBG Liv.Coll. 2002–3577 (K)	Mexico	KF522301	KP003789	KP003731	KP003684	EF177385	–
Erythrostemon nicaraguensis (G.P.Lewis) E.Gagnon & al.	Hawkins & Hughes 4 (K)	Nicaragua	KF522302	–	–	X	–	–

Erythrostemon oyamae (Sotuyo & G.P.Lewis) E.Gagnon & al.	Hawkins & Hughes 23 (FHO, MEXU, TEX)	Mexico	KF522210	X	X	–	AF430724	–	
Erythrostemon palmeri (S.Watson) E.Gagnon & al.	Gagnon & al. EG2010.010 (MT)	USA, cultivated	KF522230	X	X	–	–	–	
Erythrostemon palmeri (S.Watson) E.Gagnon & al.	Lewis & al. 2065 (K)	Mexico	KF522231	KP003790	KP003732	KP003685	X	KF379243	
Erythrostemon pannosa (Standl.) E.Gagnon & al.	Lewis 2051 (K)	Mexico	KF522282	KP003791	KP003734	KP003686	X	–	
Erythrostemon phyllanthoides (Standl.) E.Gagnon & al.	Nee 32666 (K)	Mexico	KF522220	X	X	–	–	–	
*Erythrostemon placida (*Brandegee) E.Gagnon & al.	Lewis & al. 2032 (K)	Mexico	KF522273	KP003792	KP003735	KP003687	–	–	
*Erythrostemon placida (*Brandegee) E.Gagnon & al.	Lewis 2046 (K)	Mexico	KF522272	X	X	X	X	–	
Erythrostemon standleyii (Britton & Rose) E.Gagnon & al.	Contreras 2745 (K)	Mexico	KF522236	X	X	–	–	–	
Erythrostemon yucatanensis (Greenm.) E.Gagnon & al. subsp. *yucatanensis*	Lewis 1765 (K)	Mexico	KF522280	X	X	–	AF430743	–	
Erythrostemon yucatanensis subsp. *chiapensis* (G.P.Lewis) E.Gagnon & al.	Hughes 1353 (FHO)	Mexico	KF522271	X	X	X	–	–	

Gelrebia E.Gagnon & al. (7/8 species)								
**Gelerbia rubra* (Engl.) E.Gagnon & al.	de Winter 3164 (K)	South Africa	KF522260	–	–	–	–	–
**Gelrebia rubra* (Engl.) E.Gagnon & al.	Oshikoto 1917BD (K)	Namibia	KF522259	–	–	–	–	–
Gelrebia bracteata (Germish.) E.Gagnon & al.	Van Hoepen 2018 (K)	South Africa	KF522258	X	X	X	–	–
Gelrebia dauensis (Thulin) E.Gagnon & al.	Gilbert & al. 7695 (K)	Ethiopia	KF522266	X	X	X	–	–
Gelrebia glandulosopedicellata (R.Wilczek) E.Gagnon & al.	Bamps & Malaisse 8647 (K)	Zaire	KF522261	X	X	X	X	X
Gelrebia oligophylla (Harms.) E.Gagnon & al.	Hassan 70 (FHO, K)	Somalia	KF522262	X	–	X	–	–
Gelrebia rostrata (N.E.Br.) E.Gagnon & al.	ILC6-5 (PRE)	South Africa, cultivated	X	X	X	X	X	–
Gelrebia trothae subsp. *erlangeri* (Harms) E.Gagnon & al.	Beckett & White 1711 (K)	Somalia	KF522263	X	X	X	–	X
Gelrebia trothae subsp. *erlangeri* (Harms) E.Gagnon & al.	Thulin & Warfa 5816 (K)	Somalia	KF522267	X	–	–	–	–
Gelrebia trothae subsp. *trothae* (Harms) E.Gagnon & al.	Bidgood et al. 559 (K)	Tanzania	KF522265	X	X	–	X	X
Gelrebia trothae subsp. *trothae* (Harms) E.Gagnon & al.	Gillettt 21088 (K)	Kenya	–	X	–	X	–	–

Guilandina L. (6/7–18 species)								
**Guilandina bonduc* L.	Bruneau 1342 (MT)	Madagascar	KF522062	X	X	X	–	KF379242
**Guilandina bonduc* L.	van Balooy s.n., Krukoff coll. (K)	Malaysia	KF522063	–	–	–	AF430708	–
**Guilandina bonduc* L.	Herendeen 9-XII-97-3 (US)	Tanzania	–	–	–	KF379229	X	–
Guilandina ciliata Wikstr.	Walker 51 (K)	British Virgin Islands	X	X	–	X	–	–
Guilandina major L.	Herendeen & Pooma 30-IV-1999-1 (US)	USA, cultivated	KF522253	X	X	–	X	–
Caesalpinia minax Hance	Li Shi Jin 802 (CAS, IBSC)	China	KF522131	X	–	X	–	–
Caesalpinia minax Hance	PS1368MT01, Genbank	N.A.	–	–	–	GU217664	–	HM049550
Caesalpinia murifructa Gillis & Proctor	Gillis 13096 (K)	Bahamas	KF522064	X	X	X	–	–
Caesalpinia volkensii Harms	Archbold 2861 (K)	Tanzania	KF522065	–	–	–	–	–
Caesalpinia volkensii Harms	Friis & al. 3516 (K)	Ethiopia	KF522066	X	X	X	–	–
Caesalpinia volkensii Harms	Somers s.n., RBG Liv.Coll. 1978-891 (K)	Kenya	KF522067	X	X	X	–	–
Haematoxylum L. (3/5 species)								

**Haematoxylum* campechianum* L.	Bruneau 1313 (MT)	Mexico	KF522200	X	X	–	–	–
**Haematoxylum* campechianum* L.	Hughes 1273 (FHO)	Guatemala	AY899754	–	–	–	AY899697	–
**Haematoxylum* campechianum* L.	Miller & Morello 8849 (MO)	Dominica	KF522201	X	X	X	–	–
Haematoxylum brasiletto H.Karst.	Bernandes et al. 891 (MO)	Colombia	KF522209	X	X	X	–	–
Haematoxylum brasiletto H.Karst.	Gagnon & Marazzi EG2010.011 (MT)	USA, cultivated	KF522207	X	X	X	–	–
Haematoxylum brasiletto H.Karst.	Gagnon & Marazzi EG2010.013 (MT)	USA, cultivated	KF522206	X	X	X	–	–
***Haematoxylum dinteri* Harms**	**Sucheach s.n. (OFI), Haston V200308 (RNG)**	**Namibia**	**AY899755**	**–**	**–**	**–**	**AY899698**	**–**
***Haematoxylum dinteri* Harms**	**Millenium seed bank project, HK2728 (K)**	**Namibia**	**X**	**X**	**X**	**X**	**–**	**–**
Hererolandia E.Gagnon & al. (1/1 species)								
**Hererolandia pearsonii* (Bolus) E.Gagnon & al.	Kolberg & Loots, NAM2943-HK1399 (K)	Namibia	X	X	X	X	X	X
Hoffmannseggia Cav. (23/23 species)								

**Hoffmannseggia glauca* (Ortega) Eifert	Gagnon & Marazzi EG2010.05 (MT)	USA	KF522214	X	X	X	–	–
**Hoffmannseggia glauca* (Ortega) Eifert	Spellenberg 12699 (MT)	USA	KF522213	KP003796	KP003744	KP003690	AF365069	EU361969
**Hoffmannseggia glauca* (Ortega) Eifert	Hick & Bertone 5 (CORD)	Argentina	–	–	–	–	JX219459	JX219465
**Hoffmannseggia glauca* (Ortega) Eifert	Cocucci 15-VI-1991 (CORD)	Argentina	–	–	–	X	AF430747	–
**Hoffmannseggia glauca* (Ortega) Eifert	Simpson 91-VII-22-1 (TEX)	Mexico	–	–	–	X	AY308488	–
Hoffmannseggia aphylla (Phil.) G.P.Lewis & Sotuyo	Gardner & Knees 6503 (E)	Chile	KF522146	X	X	X	–	–
Hoffmannseggia arequipensis Ulibarri	Simpson 20-II-00-1 (TEX)	Peru	–	–	–	AY308550	AY308483	–
Hoffmannseggia doelli Philippi	Simpson 11-II-00-2 (TEX)	Chile	–	–	–	AY308552	AY308485	–
Hoffmannseggia doelli subsp. *argentina* Ulibarri	Gagnon & Atchison EG220 (MT, K)	Argentina	X	X	X	X	–	–
Hoffmannseggia drepanocarpa A.Gray	Simpson 29-V-89 (TEX)	Mexico	–	–	–	AY308553	AF430745	–
Hoffmannseggia drummondii Torr. & A.Gray	Simpson 05-15-92-2 (TEX)	Mexico	–	–	–	AY308554	AF430747	–
Hoffmannseggia erecta Philippi	Chumley 7379 (TEX)	Argentina	–	–	–	AY308555	AY308486	–
Hoffmannseggia eremophila (Phil.) Ulibarri	Aranoi & Sequeo 10334 (CORD)	Chile	–	–	–	AY308556	AY308487	–

Hoffmannseggia humilis (M.Martens & Galeotti) Hemsl.	Mayfield et al. 898 (TEX)	Mexico	–	–	–	AY308559	AF430748	–
Hoffmannseggia intricata Brandegee	Irwin 2371 (TEX)	Mexico	–	–	–	AY308560	AY308489	–
Hoffmannseggia microphylla Torr.	Holmgrenn 6505 (NY)	USA	KF522145	X	X	X		–
Hoffmannseggia microphylla Torr.	Simpson 03-15-03-1 (TEX)	Mexico	–	–	–	AY308561	AF430749	–
Hoffmannseggia minor (Phil.) Ulibarri	Simpson 1-II-00-9 (TEX)	Argentina	–	–	–	AY308562	AY308534	–
Hoffmannseggia miranda Sandwith	Hughes & Daza 2358 (FHO)	Peru	KF522240	X	X	X	–	–
Hoffmannseggia miranda Sandwith	Simpson 21-II-00-1 (TEX)	Peru	–	–	–	AY308564	AY308491	–
Hoffmannseggia oxycarpa subsp. *arida* (Rose) B.B.Simpson	Simpson 91-VII-21-2 (TEX)	Mexico	–	–	–	AY308566	AF430751	–
Hoffmannseggia peninsularis (Britton) Wiggins	Simpson 03-15-93-5 (TEX)	Mexico	–	–	–	AY308567	AF430752	–
Hoffmannseggia prostrata DC.	Hughes & Daza 2359 (FHO)	Peru	KF522241	X	X	X	–	–
Hoffmannseggia prostrata DC.	Dillon & Dillon 5926 (F)	Chile	–	–	–	AY308568	AF430753	–
***Hoffmannseggia pumilio* (Griseb.) B.B.Simpson**	**Gagnon & Atchison EG221 (MT, K)**	**Argentina**	**X**	**X**	**–**	**X**	**–**	**–**
***Hoffmannseggia pumilio* (Griseb.) B.B.Simpson**	**Simpson 1-II-00-1 (TEX)**	**Argentina**	**–**	**–**	**–**	**AY308549**	**AF430791**	**–**
Hoffmannseggia repens (Eastw.) Cockerell	Simpson 27-V-89-7 (TEX)	USA	–	–	–	AY308569	AF430755	–

Hoffmannseggia tenella Tharp & L.O.Williams	Neff 4-XI-88 (TEX)	USA	–	–	–	AY308570	AF430755	–
Hoffmannseggia ternata DC.	Dillon & Dillon 3746 (F)	Peru	–	–	–	AY308571	AF430756	–
Hoffmannseggia ternata DC.	Simpson 15-II-00-1 (TEX)	Chile	–	–	–	AY308572	AY308493	–
Hoffmannseggia ternata DC.	Simpson 22-II-00-3 (TEX)	Peru	KF522139	–	–	AY308575	AY308496	–
Hoffmannseggia trifoliata Cav.	Simpson 21-I-00-3A (TEX)	Argentina	–	–	–	AY308576	AY308497	–
Hoffmannseggia viscosa Hook. & Arn.	Eastwood & al. RJE35 (FHO)	Peru	KF522138	X	X	X	–	–
Hoffmannseggia viscosa Hook. & Arn.	Sagastegui 11465 (MO)	Peru	–	–	–	AY308577	AY308498	–
Hoffmannseggia watsonii (Fisher) Rose	Hunter 25354 (TEX)	Mexico	–	–	–	AY308579	AY308500	–
Hoffmannseggia yaviensis Ulibarri	Simpson 30-I-00-1 (TEX)	Argentina	–	–	–	AY308580	AY308501	–
Hultholia E.Gagnon & al. (1/1 species)								
***_Hultholia mimosoides_ (Lam.) E.Gagnon & al.**	**Larsen & al. 44653 (MO)**	**Thailand**	**KF522251**	**X**	**X**	**–**	**–**	**–**
***_Hultholia mimosoides_ (Lam.) E.Gagnon & al.**	**Clark RPC237 (K)**	**Thailand**	**X**	**X**	**X**	**–**	**X**	**–**
Libidibia (DC.) Schltdl. (7/7–8 species)								
**Libidibia coriaria* (Jacq.) Schltdl.	Fougère–Danezan 20 (MT)	Singapore, cultivated	KF522109	X	X	–	–	–
***_Libidibia coriaria_ (Jacq.) Schltdl.**	**Hughes 1495 (K)**	**Mexico**	**AY899750**	**–**	**–**	**–**	**AY899692**	**–**

***Libidibia coriaria* (Jacq.) Schltdl.**	**Hughes & al. 2163 (FHO)**	**Mexico**	**KF522107**	**KP003797**	**KP003745**	**KP003691**	**–**	**–**
Libidibia ferrea (Mart. ex Tul.) L.P.Queiroz	Fougère-Danezan 21 (MT)	Singapore, cultivated	KF522105	X	X	–	JX073260	EU361901
Libidibia glabrata (Kunth) Castellanos & G.P. Lewis	Eastwood & al. RJE84 (FHO)	Peru	KF522102	X	X	X	–	–
Libidibia glabrata (Kunth) Castellanos & G.P. Lewis	Lewis & Lozano 3043 (K)	Ecuador	KF522101	X	X	–	X	–
Libidibia monosperma (Tul.) E.Gagnon & al.	Gardner 7029 (E)	Dominican Republic	X	X	X	–	EU361838	EU362050
Libidibia paraguariensis (Parodi) E.Gagnon & al.	Hughes & al. 2307 (FHO)	Bolivia	KF522110	X	X	–	–	–
Libidibia paraguariensis (Parodi) E.Gagnon & al.	Hughes & al. 2475 (FHO)	Bolivia	KF522111	X	X	–	–	–
Libidibia paraguariensis (Parodi) E.Gagnon & al.	Lewis & Klitgaard 2170 (K)	Argentina	KF522112	X	X	KF379233	AF365062	EU361905
Libidibia punctata (Willd.) E.Gagnon & al.	Cardenas 4071 (K)	Venezuela	KF522106	X	X	–	–	–
***Libidibia sclerocarpa* (Standl.) E.Gagnon & al.**	**Lewis & Hughes 1778 (K)**	**Mexico**	**KF522108**	**X**	**X**	–	–	–
***Libidibia sclerocarpa* (Standl.) E.Gagnon & al.**	**Kew seed collection s.n.**	**Mexico**	–	–	–	–	**AF430736**	–
Lophocarpinia Burkart (1/1 species)								
**Lophocarpinia aculeatifolia* (Burkart) Burkart	Fortunato 8639 (BAB)	Argentina	–	–	–	–	JX219460	JX219466
Mezoneuron Desf. (11/26 species)								

Mezoneuron andamanicum Prain	Herendeen 29-IV-1999-1 (US)	Thailand	KF522305	–	X	X	–	AY386931
Mezoneuron angolense Welw. ex Oliv.	Herendeen 12-XII-97-1 (US)	Tanzania	–	–	–	–	AF365068	EU361897
Mezoneuron benthamianum Baill.	Ern 2602 (K)	Togo	KF522196	X	X	X	–	–
Mezoneuron benthamianum Baill.	Morton & Jarr SL3295 (K)	Sierra Leone	KF522195	X	X	X	–	–
Mezoneuron benthamianum Baill.	Vigne 3487 (FHO)	Ghana	KF522197	–	–	–	–	–
Mezoneuron cucullatum (Roxb.) Wight & Arn.	Grierson & Long 3623 (K)	Bhutan	KF522194	X	–	X	–	–
Mezoneuron deverdiana Guillaumin	McPherson 6211 (K)	New Caledonia	KF522078	–	–	–	–	–
Mezoneuron hildebrandtii Vatke	Lewis & al. 2137 (K)	Madagascar	KF522198	X	X	X	X	X
Mezoneuron hildebrandtii Vatke	Simpson 17-XI-97 (TEX)	Madagascar	–	–	–	–	AF430780	–
Mezoneuron hymenocarpum Prain	Larsen &Larsen 34232 (K)	Thailand	–	X	X	X	–	–
Mezoneuron kauaiensis (H. Mann) Hillbr.	Lorence & Wagner 8904 (NTBG)	Hawaii, USA	KF522192	X	X	X	EU361770	EU361903
Mezoneuron kauaiensis (H. Mann) Hillbr.	Melville 71/1033 (K)	Hawaii, USA				X		
Mezoneuron scortechinii F. Muell.	Wieringa et al. 4195 (WAG)	Australia	KF522077	X	X	KF379231	X	KF379249
Mezoneuron sumatranum (Roxb.) Wight & Arn.	Beaman 9642 (NY, MO)	Malaysia	KF522199	–	–	X	–	–
Mezoneuron sp.	Pullen 7619 (K)	New Guinea	KF522193	–	–	–	–	–

Caesalpinia erythrocarpa Pedley	Schodde 2246 (K)	Papua New Guinea	KF522257	X	X	X	–	–
Caesalpinia nitens (F.Muell ex Benth.) Pedley	Bean 18033 (MO)	Australia	KF522076	X	X	X	–	–
Moullava Adans. (1/1 species)								
*_Moullava spicata_ (Dalzell) Nicolson	Critchett 11/79 (K)	Zambia, cultivated	KF522252	X	–	X	JX073267	JX099331
*_Moullava spicata_ (Dalzell) Nicolson	Hutchison 2784 (TEX)	Sri Lanka	–	–	–	–	AF430782	–
Moullava digyna (Rottler) E.Gagnon & al.	Maxwell 91-827 (P)	Thailand	X	X	–	X	–	–
Moullava digyna (Rottler) E.Gagnon & al.	Cheng et al. CL 643 (P)	Cambodia	X	X	–	X	–	–
Moullava tortuosa (Roxb.) E.Gagnon & al.	Lace 6332 (K)	Burma	–	X	–	X	–	–
Moullava welwitschiana (Oliv.) E.Gagnon & al.	Bidgood & al. 2913 (K)	Tanzania	KF522133	X	–	–	–	–
Moullava welwitschiana (Oliv.) E.Gagnon & al.	Malaisse 13658 (K)	Zaire	KF522134	X	X	–	–	X
Paubrasilia E.Gagnon & al. (1/1 species)								
*_Paubrasilia echinata_ (Lam.) E.Gagnon & al.	Filgueiras 3391 (NY)	Brazil, cultivated	KF522099	KP003802	KP003746	KP003695	X	
*_Paubrasilia echinata_ (Lam.) E.Gagnon & al.	Lewis & al. 1624 (K)	Brazil	KF522072	X	X	X		X
*_Paubrasilia echinata_ (Lam.) E.Gagnon & al.	Miranda 76 (HUEFS)	Brazil	KF522100	X	X	X	X	X
Pomaria Cav. (15/16 species)								

**Pomaria glandulosa* Cav.	Ventura & López 9294 (TEX)	Mexico	KF522088	–	–	AY549901	AY535823-AY535810	–
Pomaria austrotexana B.B.Simpson	Simpson 1-IV-01-2 (TEX)	USA	–	–	–	AY549895	AF430757	–
Pomaria brachycarpa (A. Gray) B.B.Simpson	Simpson 92-06-22-3 (TEX)	USA	–	–	–	AY549896	AF430758	–
Pomaria burchellii (DC.) B.B.Simpson & G.P.Lewis	Mott 766 (MO)	South Africa	–	–	–	AY549897	AY535819-AY535806	–
Pomaria burchellii (DC.) B.B.Simpson & G.P.Lewis	Klepper 252/A/42 (PRU)	South Africa	–	–	–	AY549898	AF430744	–
Pomaria canescens (Fisher) B.B.Simpson	Turner et al. 93-128 (TEX)	Mexico	–	–	–	AY549899	AY535820-AY535807	–
Pomaria fruticosa (S. Watson) B.B.Simpson	Villareal 4439 (TEX)	Mexico	–	–	–	AY549901	AY535822-AY535809	–
Pomaria jamesii (Torr. & A.Gray) Walp.	Gagnon & Marazzi EG2010.020 (MT)	USA	KF522089	X	X	–	–	X
Pomaria jamesii (Torr. & A.Gray) Walp.	Higgins 17628 (NY)	USA	KF522090	KP003793	KP003736	KP003677	EU361830	EU362029
Pomaria lactea (Schinz) B.B.Simpson & G.P.Lewis	Pearson 9742 (MO)	South Africa	–	–	–	AY549904	AY535824-AY535811	–

Pomaria melanosticta S.Schauer	Simpson 92-06-23-1 (TEX)	USA	–	–	–	AY549905	AF430760	–
Pomaria multijuga (S.Watson) B.B.Simpson	Engard 649 (TEX)	Mexico	–	–	–	AY549906	AY535825-AY535812	–
Pomaria pilosa (Vogel) B.B.Simpson & G.P.Lewis	Wasum et al. 4571 (NY)	Brazil	–	–	–	AY549900	AY535821-AY535808	–
Pomaria pilosa (Vogel) B.B.Simpson & G.P.Lewis	Wasum & Bastos 8008 (NY)	Brazil	–	–	–	AY549907	AY535824-AY535813	–
Pomaria rubicunda (Vogel) B.B.Simpson & G.P.Lewis	Biganzoli & al. s.n. (NY)	Argentina	KF522085	KP003795	KP003738	KP003679	EU361775	–
Pomaria rubicunda (Vogel) B.B.Simpson & G.P.Lewis	Lima 463 (HUEFS)	Brazil	KP003642	KP003794	KP003737	KP003678	–	–
Pomaria rubicunda (Vogel) B.B.Simpson & G.P.Lewis var. *rubicunda*	Vanni & Marunak 3755 (NY)	Argentina	–	–	–	AY549909	AY535827-AY535814	–
Pomaria rubicunda var. *hauthalii* (Harms) B.B.Simpson & G.P.Lewis	Ibarrola 1750 (US)	Argentina	KF522087			AY549908	AF430723	
Pomaria sandersonii (Harv.) B.B.Simpson & G.P.Lewis	Hilliard & Burtt 9225 (MO)	South Africa				AY549910	AY535828-AY535815	

Pomaria stipularis (Vogel) B.B.Simpson & G.P.Lewis	Jönsson 1002a (A)	Brazil	KF522086			AY549911	AF430739	
Pomaria wootonii (Britton) B.B.Simpson	Johnston 4341 (TEX)	Mexico				AY549912	AY535829-AY535816	
Pterolobium R. Br. ex Wight & Arn (4/11 species)								
**Pterolobium* *stellatum* (Forssk.) Brenan	Herendeen 17-XII-97-09 (US)	Tanzania	KF522238	X	–	X	X	EU362032
Pterolobium hexapetalum (Roth) Santapau & Wagh	Grierson & Long 2075 (P)	Bhutan	X	–	X	X	–	–
Pterolobium integrum Craib	van Beusekom 4021 (P)	Thailand	–	X	–	–	–	–
***Pterolobium macropterum* Kurz**	**Grierson & Long 1624 (P)**	**Bhutan**	**X**	**X**	**X**	–	–	–
***Pterolobium macropterum* Kurz**	**Geesink & al. 5934 (P)**	**Thailand**	**X**	**X**	–	–	–	–
Stenodrepanum Harms (1/1 species)								
* *Stenodrepanum bergii* Harms	Hick & Bertone 8 (CORD)	Argentina	–	–	–	–	JX219461	JX219467
Stuhlmannia Taub. (1/1 species)								
**Stuhlmannia moavi* Taub.	Luke 3710 (MO, K)	Tanzania	KF522061	X	X	X	–	–
**Stuhlmannia moavi* Taub.	Keraudren-Aymonin & Aymonin 25628 (MO)	Madagascar	KF522060	X	X	X	–	–

**Stuhlmannia moavi* Taub.	Robertson 7509 (K)	Kenya	KF522059	X	X	X	EU361839	X
Tara Molina (3/3 species)								
**Tara spinosa* (Molina) Britton & Rose	Eastwood & al. RJE36 (FHO)	Peru	KF522128	X	X	–	–	KF379250
**Tara spinosa* (Molina) Britton & Rose	Hughes 2360 (FHO)	Peru	KF522129	X	X	X	–	–
Tara spinosa (Molina) Britton & Rose	Lewis 2200 (K)	Ecuador	–	–	–	KF379235	X	–
Tara cacalaco (Humb. & Bonpl.) E.Gagnon & al.	Gagnon & Marazzi EG2010.022 (MT)	USA, cultivated	KF522202	X	–	X	–	–
Tara cacalaco (Humb. & Bonpl.) E.Gagnon & al.	Walker s.n., RBG Liv.Coll. 1986–6481 (K)	Mexico	KF522203	X	X	X	–	–
***Tara cacalaco* (Humb. & Bonpl.) E.Gagnon & al.**	**Lewis 1789 (K)**	**Mexico**	**–**	**–**	**–**	**–**	**AF430709**	**EU361898**
***Tara cacalaco* (Humb. & Bonpl.) E.Gagnon & al..**	**Lewis 1788 (K)**	**Mexico**	**–**	**–**	**–**	**X**	**–**	**–**
Tara vesicaria (L.) E.Gagnon & al.	Hawkins & Hughes 11 (FHO)	Nicaragua	KF522204	X	X	X	–	–
Tara vesicaria L.	Lewis & Hughes 1768 (K)	Mexico	KF522205	–	–	X	AF430742	–
Zuccagnia Cav. (1/1 species)								
**Zuccagnia punctata* Cav.	Fortunato 5545 (MO)	Argentina	KF522142	X	X	X	–	–

**Zuccagnia punctata* Cav.	Galleto & al. 171 (CORD)	Argentina	KF522141	KP003798	KP003742	KP003688	AF430791	X
**Zuccagnia punctata* Cav.	Guglianone & al. 1668 (K, SI)	Argentina	KF522143	X	X	X	–	–
**Zuccagnia punctata* Cav.	Lutz 136 (NY)	Argentina	KF522140	X	X	X	EU361842	–
**Zuccagnia punctata* Cav.	Tapia & al. s.n. (CORD)	Argentina	–	–	–	–	JX219463	JX219468
***Ticanto* clade** (2/~10 species)								
Caesalpinia crista L.	Herendeen 1-V-99-3 (US)	Thailand	KF522073	X	X	X	X	EU361900
Caesalpinia crista L.	Wieringa & al. 4199 (WAG)	Australia, cultivated	KF522074	X	X	X	–	–
Caesalpinia vernalis Benth.	Li Shi Jin 787 (CAS, IBSC)	China	KF522075	–	–	–	–	–

Annex 3.

References used to score the Geographical Areas, Biomes and Habit characters.

I) Hererolandia

References: Bolus (1920); Roux (2003); Curtis & Mannheimer (2005: 227);

II) Lophocarpinia

References: Burkart (1957); Ulibarri (2008); Nores & al. (2012);

III) Haematoxylum

References: Standley & Steyemark (1946); Ross (1977:122-114); Roux (2003); Curtis & Mannheimer (2005: 215); Durán & Ramírez (2008); Durán & Sousa (2014); Barreto Valdés (2013);

IV) Paubrasilia

References: Lewis (1998: 152-158). Cardoso & al. (2005).

V) Caesalpinia

References: Britton & Rose (1930); MacBride (1943: 191, 194-195); Ulibarri (1996); Barreto Valdés (2013);

VI) Denisophytum

References: Britton & Rose (1930); Burkart (1936: 84-86); Viguier (1948); Roti-Michelozzi, G. (1957); Brenan (1967); Capuron (1967); Thulin (1983: 16-18; 1993: 344-347); Ulibarri (1996); Du Puy & Rabevohitra (2002); Barreto Valdés (2013)

VII) Tara

References: Britton & Rose (1930); Sprague (1931); MacBride (1943); Ulibarri (1996); Barreto Valdés (2013)

VIII) Coulteria

References: Kunth (1824); Britton & Rose (1930: 320-322); Zamora Villalobos (2010); Sotuyo, Gagnon & Lewis (in prep.)

IX) Gelrebia

Wilczek (1951); Roti-Michelozzi, G. (1957); Brenan (1963); Brenan (1967); Ross (1977: 122-130); Thulin (1980, 1983: 16-18; 1993: 344-347); Germishuizen (1991); Roux (2003); Curtis & Mannheimer (2005: 226-228); Brummitt & al. (2007);

X) Hultholia

References: Vidal & Hul Thol (1976); Chen & al. (2010a: 42-43).

XI) Guilandina

References: Britton & Rose (1930: 336-341); Wilczek (1951); Brenan (1967); Gillis & Proctor (1974); Hattink (1974); Vidal & Hul Thol (1976); Heald (1994); Du Puy & Rabevohitra (2002: 46-48); Chen & al. (2010a);

XII) Moullava

References: Brenan (1963); Brenan (1967); Hattink (1974); Vidal & Hul Thol (1976); Nicolson (1980); Ansari (1990); Sanjappa (1992: 33); Brummitt & al. (2007, see both *Moullava* and *Mezoneuron welwitschianum*); Chen et al. (2010a);

XIII) Biancaea

References: Hattink (1974); Vidal & Hul Thol (1976); Jansen (2005); Brummitt & al. (2007); Chen & al. (2010a);

XIV) Pterolobium

References: Roti-Michelozzi (1957); Brenan (1967: 40-42); Vidal & Hul Thol (1974, 1976); Hul Thol & Hideux (1977); Hou (1996: 654-700); Chen & al. (2010b).

XV) Mezoneuron

References: Brenan (1967: 38-40); Hattink (1974); Vidal & Hul Thol (1976); Verdcourt (1979: 18-20); Lock (1989: 25); Herendeen & Zarucchi (1990); Pedley (1997); George (1998a: 59-67); Wagner & al. (1999); Du Puy & Rabevohitra (2002: 48-49); Brummitt & al. (2007); Clark & Gagnon (2015);

XVI) Cordeauxia

References: Brenan (1967); Roti-Michelozzi (1957); Thulin (1983: 20-21; 1993: 348); Brink (2006);

XVII) Stuhlmannia

References: Brenan (1967: 45-47); Capuron (1967, under *Caesalpinia insolita*); Lewis (1996); Du Puy & Rabevohitra (2002: 48, 50, under *Caesalpinia insolita*); Lemmens (2010);

XVIII) Cenostigma

References: Lewis (1987: 34-35); Freire (1994); Ulibarri (1996); Lewis (1998); de Queiroz (2009: 129-130, see also as *Poincianella,* 121-128) Warwick & Lewis (2009); Lewis & al. (2010);

XIX) Libidibia

References: Britton (1927); Britton & Rose (1930: 221, 318-319); Burkart (1936, *Caesalpinia melanocarpa:* 78-82); Macbride (1943, *Caesalpinia paipai*: 193-194); Little & Wadsworth (1964); Ford (1995); U.S. Fish and Wildlife Service (1995); Ulibarri (1996); de Queiroz (2009: 130-133); Borges & al. (2012); Barreto Valdés (2013)

XX) Balsamocarpon

References: Burkart (1940: 162); Ulibarri (1996); Ulibarri (2008); Nores & al. (2012);

XXI) Zuccagnia

References: Burkart (1952: 184-185); Ulibarri (in Kiesling & al. 1994: 286), Ulibarri (2008); Nores & al. (2012); Ulibarri (2005)

XXII) Stenodrepanum

References: Ulibarri (1978; in Kiesling & al., 1994: 285); Ulibarri (2008); Caponio & al. (2012); Nores & al. (2012);

XXIII) Hoffmannseggia

References: Britton & Rose (1930, under *Larrea* & *Moparia*); Burkart (1936); Macbride (1943); Ulibarri (1979, 1996); Simpson (1999); Simpson & al. (2004, 2005); Lewis (1998, *see Caesalpinia pumilio:* 171-173); Simpson & Ulibarri (2006); Lewis & Sotuyo (2010);

XXIV) Arquita

References: Burkart (1936); Ulibarri (1996); Lewis (1998: 167-171, 174-179); Lewis & al. (2010); Gagnon & al. (2015, in press);

XXV) Pomaria

References: Burkart (1936: 86-90); Brummitt & Ross (1974, as *Hoffmannseggia*); Ulibarri (1996); Simpson (1998); Simpson & Lewis (2003); Simpson & al. (2006); Ulibarri (2008);

XXVI) Erythrostemon

References: Britton & Rose (1930); Burkart (1936: 82-84, 97-108); Ulibarri (1996); Lewis (1998); de Queiroz (2009: 120-121);

XXVII) Ticanto clade

References: Hattink (1974); Vidal & Hul Thol (1976);

Annex 4.

Herbarium and voucher specimens used for morphological and phylogenetic analyses, for Gagnon & al. 2015 (chapter 4).

Species	**Collectors (Herbaria)**	**Country**	**Province /Department**	**Locality**	**Leaves**	**Flowers**	***rps16***	***trnDT***	***ycf6***	**ITS**
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Gagnon & al. EG204 (K, MT)	Argentina	Jujuy	dpto. Tilcara	(2)	(2)	KP003634	KP003767	KP003713	KP003661
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Gagnon & al. EG205 (K, MT)	Argentina	Jujuy	dpto. Tilcara	(2)	(2)	KP003635	KP003768	KP003726	KP003662
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Lewis & Klitgaard 2166 (K)	Argentina	Jujuy	dpto. Tumbaya : Pumamarca	-	-	KF522163	KP003762	KP003709	KP003659
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Gagnon & Atchison EG213 (K, MT)	Argentina	Salta	dpto. La Poma	(2)	(2)	KP003636	KP003769	KP003714	KP003663
Arquita trichocarpa (Griseb.)	Gagnon & Atchison	Argentina	Salta	dpto. Cachi	(2)	(2)	KP003637	KP003770	KP003715	KP003664

E.Gagnon & al.	EG216 (K, MT)									
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Gagnon & Atchison EG218 (K, MT)	Argentina	Salta	dpto. Molinos	(2)	(2)	KP003638	KP003771	KP003716	KP003665
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Gagnon & al. EG200 (K, MT)	Argentina	Tucumán	dpto. Tafí del Valle	(2)	(2)	KP003633	KP003766	KP003712	KP003660
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Jörgensen 1745 (US)	Argentina	Catamarca	dpto. Andalgalá	(1)	-	-	-	-	-
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Balls B6058 (K, US)	Argentina	Jujuy	dpto. Tilcara	(2)	(2)	-	-	-	-
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Clarke 109-03 (MO)	Argentina	Jujuy	dpto. Humahuaca	(2)	(1)	-	-	-	-
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Dillon & Rodriguez 586 (MO)	Argentina	Jujuy	dpto. Tilcara	-	(1)	-	-	-	-

Arquita trichocarpa (Griseb.) E.Gagnon & al.	Fortunato & al. 7421(MO)	Argentina	Jujuy	dpto. Humahuaca	-	(1)	-	-	-	-
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Saravia Toledo & Day 15185 (NY)	Argentina	Jujuy	dpto. Humahuaca	(1)	(1)	-	-	-	-
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Venturi 4881 (US)	Argentina	Jujuy	dpto. Tilcara	(1)	(2)	-	-	-	-
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Venturi 7485 (US)	Argentina	Jujuy	dpto. Tilcara	-	(1)	-	-	-	-
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Hayward 2155 (US)	Argentina	Salta	dpto. Cafayate	(2)	-	-	-	-	-
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Novara 2584 (MO)	Argentina	Salta	dpto. Molinos	(2)	-	-	-	-	-
Arquita trichocarpa	Planchuel 993 (US)	Argentina	Salta	Between Cachi	(1)	-	-	-	-	-

(Griseb.) E.Gagnon & al.				and Cafayte						
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Simpson 5-II-00-1 (MO)	Argentina	Salta	dpto. Cafayate	(1)	(1)	-	-	-	-
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Venturi 8542 (US)	Argentina	Salta	dpto. Rosario de Lerma	(1)	(1)	-	-	-	-
Arquita trichocarpa (Griseb.) E.Gagnon & al.	Burkart 5358 (K)	Argentina	Tucumán	dpto. Tafí del Valle	(1)	-	-	-	-	-
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Venturi 4275 (NY)	Argentina	Tucumán	dpto. Tafí del Valle	(2)	-	-	-	-	-
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Wood 17692 (K)	Bolivia	Cochabamba	prov. Capinota	(1)	(1)	KP003641	KP003783	KP003727	KP003675

Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Wood & al. 21342 (K)	Bolivia	Cochabamba	prov. Esteban Arce	(1)	(1)	-	KP003784	-	KP003676
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Beck 114PG94 (K)	Bolivia	La Paz	prov. Loayza: valle de Luribay	(1)	-	KP003639	KP003780	KP003725	KP003674
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Beck 3014 (NY)	Bolivia	La Paz	prov. Murillo	(2)	-	-	KP003782	-	-
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Hughes 2442 (K)	Bolivia	La Paz	prov. Murillo	(1)	-	KF522162	KP003764	KP003711	KP003657
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Wood 9556 (K)	Bolivia	Chuquisaca	prov. Sud Cinti	(1)	-	KP003632	KP003765	-	KP003658
Arquita trichocarpa	Beck & Panigua	Bolivia	Tarija	prov. José	(2)	-	KP003640	KP003781		

var. *boliviana* (Griseb.) E.Gagnon & al.	27049 (K, MO)			María Avilėz						
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Thomas ET244 (K)	Bolivia	Cochabamba	prov. Capinota	(1)	(1)	-	-	-	-
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Wood & al. 19278 (K)	Bolivia	Cochabamba	prov. Esteban Arce	(1)	(1)	-	-	-	-
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Fiebrig 2981 (K)	Bolivia	Chuquisaca	prov. Nor Cinti: Camargo	(1)	-	-	-	-	-
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Wood 8742 (K)	Bolivia	Chuquisaca	prov. Oropeza	(1)	(1)	-	-	-	-
Arquita trichocarpa var. *boliviana* (Griseb.)	Vuilleumier 409 (NY)	Bolivia	Chuquisaca	prov. Sud Cinti	(2)	(1)	-	-	-	-

E.Gagnon & al.										
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Fueurer & Menhofer 10140a (K)	Bolivia	La Paz	prov. Murillo	(1)	(1)	-	-	-	-
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Ortuño 244 (K)	Bolivia	La Paz	prov. Loayza	(1)	(1)	-	-	-	-
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Solomon 5090 (MO)	Bolivia	La Paz	prov. Murillo	(2)	-	-	-	-	-
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Solomon 7412 (MO	Bolivia	La Paz	prov. Murillo	(2)	(1)	-	-	-	-
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Solomon & Nee 16058 (K, MO)	Bolivia	La Paz	prov. Murillo	(2)	(1)	-	-	-	-

Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Wood 9151 (K)	Bolivia	La Paz	prov. Murillo	(1)	-	-	-	-	-
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Torrico & Peca 306 (K)	Bolivia	Potosi	prov. José M. Linares	(1)	(1)	-	-	-	-
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Fiebrig 3112a (K)	Bolivia	Potosi	Rencillo nr. Tupiza	(1)	(2)	-	-	-	-
Arquita trichocarpa var. *boliviana* (Griseb.) E.Gagnon & al.	Brother Julio 152 (US)	Bolivia	-	La Granja	-	(1)	-	-	-	-
Arquita grandiflora (Griseb.) E.Gagnon & al.	Hughes & al. 3156 (K, MT)	Peru	Ancash	prov. Antonio Raymondi: Llamellín	(2)	(2)	KF522153	KP003779	KP003724	KP003673

Arquita grandiflora (Griseb.) E.Gagnon & al.	Hughes & al. 3041 (K, MT)	Peru	Ancash	dist. Pueblo Libre	(2)	(1)	KF522152	KP003772	KP003717	KP003666
Arquita grandiflora (Griseb.) E.Gagnon & al.	Hughes & al. 3042 (K, MT)	Peru	Ancash	dist. Pueblo Libre	(2)	(2)	KF522154	KP003773	KP003718	KP003667
Arquita grandiflora (Griseb.) E.Gagnon & al.	Hughes & al. 3047 (K, MT)	Peru	Ancash	dist. de Shupluy	(2)	(2)	KF522150	KP003774	KP003719	KP003668
Arquita grandiflora (Griseb.) E.Gagnon & al.	Hughes & al. 3056 (K, MT)	Peru	Ancash	dist. de Mato	(2)	(2)	KF522158	KP003775	KP003720	KP003669
Arquita grandiflora (Griseb.) E.Gagnon & al.	Hughes & al. 3057 (K, MT)	Peru	Ancash	dist. de Mato	(2)	(2)	KF522155	KP003776	KP003721	KP003670
Arquita grandiflora (Griseb.) E.Gagnon & al.	Hughes & al. 3063 (K, MT)	Peru	Ancash	Huaylas	(2)	(2)	KF522157	KP003777	KP003722	KP003671

Arquita grandiflora (Griseb.) E.Gagnon & al.	Särkinen & al. 2225 (K, NY)	Peru	Ancash	Huaylas	(2)	(2)	KF522151	KP003763	KP003710	KP003656
Arquita grandiflora (Griseb.) E.Gagnon & al.	Hughes & al. 3155 (K, MT)	Peru	Huanuco	Huacaybamba	(2)	-	KF522156	KP003778	KP003723	KP003672
Arquita ancashiana (Ulibarri) E.Gagnon & al.	Hughes & al. 3065 (K, MT)	Peru	Catamarca	prov Contumazá: Chilete-Contumazá			KF522168	KP003750	KP003699	KP003645
Arquita ancashiana (Ulibarri) E.Gagnon & al.	Hughes & al. 3070 (K, MT)	Peru	Cajamarca	prov. Contumazá: Contumazá-Cascas			KF522167	KP003749	KP003698	KP003644
Arquita ancashiana (Ulibarri) E.Gagnon & al.	Hughes & al. 3021 (K, MT)	Peru	Ancash	prov. Recuay: dist. De Marca			KF522164	KP003747	KP003696	KP003643
Arquita ancashiana (Ulibarri)	Hughes & al. 3025 (K, MT)	Peru	Ancash	prov. Recuay: dist. de Marca			KF522166	KP003748	KP003697	-

E.Gagnon & al.										
Arquita ancashiana (Ulibarri) E.Gagnon & al.	Hughes & al. 3026 (K, MT)	Peru	Ancash	prov. Recuay: dist. de Cajacay			KF522165	KP003752	KP003701	-
Arquita ancashiana (Ulibarri) E.Gagnon & al.	Hughes & al. 3027 (K, MT)	Peru	Ancash	prov. Recuay: dist. de Cajacay			KF522169	KP003751	KP003700	KP003646
Arquita ancashiana (Ulibarri) E.Gagnon & al.	Lewis & al. 2266 (K, NY, MO)	Ecuador	Loja	Montaña Tarapo, Catacocha			KF522170	KP003753	KP003702	KP003647
Arquita ancashiana (Ulibarri) E.Gagnon & al.	Lewis & Lozano 3073 (K, NY, MO)	Ecuador	Loja	Catacocha-Catamayo			-	KP003754	-	KP003648
Arquita ancashiana (Ulibarri) E.Gagnon & al.	Lewis & al. 3815 (K, NY, MO)	Ecuador	Azuay	Saraguro-Cuenca			-	KP003755	-	KP003649
Arquita celendiniana (G.P.Lewis & C.E.Hughes)	Hughes & al. 3102 (K, MT)	Peru	La Libertad	Balsas to Bolivar: valley of rio Pusac			KF522147	KP003758	KP003705	KP003652

E.Gagnon & al.										
Arquita celendiniana (G.P.Lewis & C.E. Hughes) E.Gagnon & al.	Hughes & al. 3097 (K, MT)	Peru	Cajamarca	Celendín to Balsas			KF522149	KP003757	KP003704	KP003651
Arquita celendiniana (G.P.Lewis & C.E.Hughes) E.Gagnon & al.	Hughes & al. 2210 (K)	Peru	Cajamarca	Celendín to Balsas			KF522148	KP003756	KP003703	KP003650
Arquita mimosifolia (Griseb.) E.Gagnon & al.	Gagnon & al. EG203 (K, MT)	Argentina	Salta	dpto. La Viña : Alemania			KF522160	KP003760	KP003707	KP003654
Arquita mimosifolia (Griseb.) E.Gagnon & al.	Gagnon & Atchison EG211 (K, MT)	Argentina	Salta	dpto. Chicoana			KF522159	KP003759	KP003706	KP003653
Arquita mimosifolia (Griseb.) E.Gagnon & al.	Särkinen & al. 2006 (FHO)	Argentina	Catamarca	dpto. Valle Viejo			KF522161	KP003761	KP003708	KP003655

Arquita mimosifolia (Griseb.) E.Gagnon & al.	Chumley 7387 (TEX)	Argentina	La Rioja	dpto. Capital			-	-	-	AY549893
OUTGROUP										
Balsamocarpon brevifolium Clos.	Baxter DCI 1869 (E)	Chile					KF522135	KP003801	KP003743	KP003689
Caesalpinia echinata Lam.	Filgueiras 3391 (NY)	Brazil, cultivated					KF522099	KP003802	KP003746	KP003695
Cenostigma tocantinum Ducke	Klitgaard & de Lima 88 (K)	Brazil, cultivated					KF522071	KP003803	KP003740	KP003694
Erythrostemon gilliesii Klotzsch	Spellenberg 12701 (MT)	USA, cultivated					KF522296	KP003786	KP003729	KP003681
(Erythrostemon) Caesalpinia fimbriata Tul.	Hughes & al. 2441 (FHO)	Bolivia					KF522284	KP003785	KP003728	KP003680
Hoffmannseggia glauca (Ortega) Eifert	Spellenberg 12699 (MT)	USA					KF522213	KP003796	KP003744	KP003690
Libidibia coriaria (Jacq.) Schltdl.	Hughes & al. 2163 (FHO)	Mexico					KF522107	KP003797	KP003745	KP003691
(Poincianella) Caesalpinia epifanioi J.L.Contr.	Contreras 2039 (K)	Mexico					KF522278	KP003787	KP003733	KP003682

Poincianella gaumeri (Green.) Britton & Rose	Lewis & Hughes 1762 (K)	Mexico					KF522044	KP003799	KP003739	KP003692
Poincianella mexicana (A.Gray) Britton & Rose	Lewis s.n., Kew Living Coll. 1973-21714 (K)	Mexico					KF522215	KP003788	KP003730	KP003683
Poincianella nelsonii Britton & Rose	Sotuyo, s.n., RBG Liv.Coll. 2002-3577 (K)	Mexico					KF522301	KP003789	KP003731	KP003684
Poincianella palmeri (S. Watson) Britton & Rose	Lewis & al. 2065 (K)	Mexico					KF522231	KP003790	KP003732	KP003685
Poincianella pannosa (Standl.) Britton & Rose	Lewis & al. 2051 (K)	Mexico					KF522282	KP003791	KP003734	KP003686
Poincianella placida (Brandegee) Britton & Rose	Lewis 2046 (K)	Mexico					KF522272	KP003792	KP003735	KP003687
Poincianella pluviosa (DC.) L.P.Queiroz	de Queiroz 12795 (HUEFS)	Brazil					KF522049	KP003800	KP003741	KP003693
Pomaria burchellii	Mott 766 (MO)	South Africa					-	-	-	AY549897

(DC.) B.B.Simpson & G.P.Lewis										
Pomaria burchellii (DC.) B.B.Simpson & G.P.Lewis	Klepper 252/A/42 (PRU)	South Africa					-	-	-	AY549898
Pomaria glandulosa Cav.	Ventura & López 9294 (TEX)	Mexico					KF522088	-	-	AY549901
Pomaria jamesii (Torr. & A.Gray) Walp.	Higgins 17628 (NY)	USA					KF522090	KP003793	KP003736	KP003677
Pomaria lactea (Schinz) B.B.Simpson & G.P.Lewis	Pearson 9742 (MO)	South Africa					-	-	-	AY549904
Pomaria rubicunda (Vogel) B.B.Simpson & G.P.Lewis	Biganzoli & al. s.n. (NY)	Argentina					KF522085	KP003795	KP003738	KP003679
Pomaria rubicunda (Vogel) B.B.Simpson & G.P.Lewis	Lima 463 (HUEFS)	Brazil					KP003642	KP003794	KP003737	KP003678

Pomaria sandersonii (Harv.) B.B.Simpson & G.P.Lewis	Hilliard & Burtt 9225 (MO)	South Africa					-	-	-	AY549910
Zuccagnia punctata Cav.	Galleto & al. 171 (CORD)	Argentina					KF522141	KP003798	KP003742	KP003688