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Systématique, biogéographie et diversification du genre *Crudia* (Leguminosae, Detarioideae)

par Boris Domenech

Département de Sciences Biologiques
Centre sur la Biodiversité
Institut de Recherche en Biologie Végétale
Faculté des Arts et des Sciences

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Résumé

Le genre *Crudia* Schreb. présente une distribution pantropicale et une richesse spécifique élevée, inhabituelles pour un genre appartenant à la sous famille des Detarioideae (Leguminosae). Les espèces de *Crudia*, réparties en Amérique du Sud, en Afrique de l'Ouest et en Asie du Sud Est, ont fait l'objet de plusieurs études de taxonomie indépendantes, réalisées par plusieurs auteurs successifs. En revanche, l'évolution et l'histoire biogéographique du genre sont inconnues à ce jour. Afin de mieux comprendre l'histoire évolutive de *Crudia*, nous proposons une approche pluridisciplinaire visant à mettre à jour les connaissances à propos de ce genre méconnu.

La première partie de cette étude a pour objectif de réaliser une révision taxonomique des espèces asiatiques du genre *Crudia*, les espèces africaines et américaines ayant déjà été traitées par d'autres auteurs. Nous avons pour cela utilisé des méthodes de taxonomie traditionnelle en compilant des données morphologiques sur un grand nombre de spécimens d'herbier. Sur les trente-cinq espèces initiales décrites en Asie, nous en avons retenu quatorze et avons ajouté une nouvelle espèce. Les autres espèces ont été mises en synonymie pour la plupart, exceptée l'une d'entre elle qui est à présent considérée comme douteuse. Suite à ces réassignations taxonomiques, les distributions géographiques respectives des espèces ont été réévaluées et des nouveaux statuts de conservation ont été proposés.

La seconde partie de cette étude a pour objectif de poser un cadre conceptuel afin d'étudier dans le détail l'évolution de ce genre, son histoire biogéographique et les relations entre espèces. Nous avons pour cela séquencé cinq régions nucléaires (ITS, ETS, *AGT1*, *CALTL*, *AIGP*) pour de nombreux spécimens, principalement prélevés sur des échantillons d'herbiers (K, US, P, L, WAG, U). Les phylogénies réalisées montrent que *Crudia* est monophylétique et possède une structure interne bien définie, avec un clade regroupant toutes les espèces asiatiques et un autre regroupant les espèces africaines et américaines, ces dernières formant elles-mêmes un clade clairement identifiable. La reconstruction de l'histoire biogéographique, associée à la datation à l'aide d'un macrofossile, montre que *Crudia* trouve son origine en Afrique au cours de l'Éocène, puis subit deux évènements indépendants de dispersion vers l'Amérique du Sud et vers l'Asie au cours de l'Éocène moyen.

La troisième partie de cette étude a pour objectif d'identifier si la richesse spécifique du genre *Crudia* pouvait être associée à un évènement de changement des taux de diversification au cours du temps, mais également savoir si les niches écologiques des différentes espèces étaient semblables à travers l'aire de distribution du genre au complet. Nous avons utilisé pour cela des données d'occurrences des espèces, ainsi que des données reliées au régime de précipitations et à la température. Parallèlement, les taux de diversification ont été étudiés à l'échelle du genre et à l'échelle des Detarioideae. Au final, il s'est avéré que les niches écologiques différaient d'un continent à l'autre, et qu'il n'existait pas de changement des taux de diversification dans le genre *Crudia* pouvant être relié précisément à la richesse spécifique. Le nombre élevé d'espèces au sein du genre *Crudia* pourrait en revanche être lié à un âge relativement plus vieux de ce genre, comparé aux autres genres évolutivement proches.

Mots-clés : *Crudia*, Detarioideae, révision taxonomique, phylogénie, évolution,
biogéographie, datation, systématique, niche écologique, diversification

Abstract

In the subfamily Detarioideae (Leguminosae), the genus *Crudia* Schreb. shows an unusual pantropical distribution and high species richness compared to closely related genera. *Crudia* species, spread throughout South America, West Africa and Southeastern Asia, have been the focus of independent taxonomic studies conducted by several consecutive authors. To date, however, the evolution and biogeographic history of this genus remain poorly understood. We propose a multidisciplinary approach to study this poorly known genus and to improve our understanding of its evolutionary history.

First, we conducted a taxonomic revision of Asian species within the genus *Crudia*, in accordance with the recent revisions of African and American species. We used traditional taxonomic methods by compiling morphological data based on the study of herbarium specimens. From an initial description of thirty five species from the literature, we retained fourteen species and synonymized the others except for one we consider as a doubtful species. A newly described species was also added. Species geographic distributions were reevaluated and new conservation statuses were suggested.

Second, we established a conceptual framework to study the evolution, biogeographic history, and relationship between species of this genus. We sequenced five nuclear regions (ITS, ETS, *AGT1*, *CALTL*, and *AIGP*) on numerous sampled herbarium specimens (K, US, P, L, WAG, U). The phylogenetic analyses resolve *Crudia* as monophyletic with a well-identified internal structure composed of one clade grouping all Asian species and one clade grouping both African and American species, with the American species grouped in a single clade. Reconstructions of biogeographic history and an associated divergence time analysis calibrated with macrofossils show *Crudia* originated in Africa during the Eocene and underwent two independent dispersal events during mid-Eocene: from Africa to South America and from Africa to Southeastern Asia.

Third, we tested if species richness in the genus *Crudia* is associated with changes in diversification rates through time and with ecological niche shifts throughout its global distribution. We used species occurrence data, carefully selected to avoid identification errors, associated with environmental data retrieved from the literature. Diversification rates were studied both at the scale of the genus *Crudia* and the Detarioideae subfamily. We conclude that ecological niches differ from one continent to another and no diversification rates changes were detected in the genus *Crudia*. Our finding suggest that the greater species richness in *Crudia* compared to sister genera may be the consequence of relatively older age of this genus.

Keywords: *Crudia*, Detarioideae, taxonomic revision, phylogeny, evolution, biogeography, divergence time, systematic, ecological niche, diversification

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Liste des abréviations et sigles

A : Harvard University Herbaria
AGT1 : peroxisomal photorespiratory enzyme that catalyzes transamination reactions with multiple substrates, involved in photorespiration
AIC : Akaike Information Criterion
AIGP : auxin independent growth
ANOVA : analysis of variance
BAMM : Bayesian Analysis of Macroevolutionnary Mixtures
BEAST : Bayesian Evolutionary Analysis Sampling Trees
BEAUti : Bayesian Evolutionary Analysis Utility
BioGeoBEARS : BioGeography with Bayesian (and likelihood) Evolutionary Analysis in R Scripts
BLAST : Basic Local Alignment Search Tool
BM : British Museum of Natural History
BO : Herbarium Bogoriense (Indonesian Institute of Science)
BRI : Queensland Herbarium
BSA : bovine serum albumine
CAL : Central National Herbarium, India
CALTL : Calreticulin
CANB : Australian National Herbarium
CTAB : Cetyltrimethyl Ammonium Bromide
D : Schoener's equivalency index
DBH : diameter at breast height
DEC : dispersal extinction cladogenesis model
DEC+J : dispersal extinction cladogenesis and jump model
DMSO : dimethyl sulfoxide
DNA : acide désoxyribonucléique
dNTPs : desoxynuceloside triphosphate
E : east
e.g. : exempli gratia

ENM : ecological niche modelling
etc. : et caetera
ETS : external transcribed spacer
ESS : effective sampling size
F : forward
FL : flowering specimen
FR : fruiting specimen
G : gamma
GBIF : Global Biodiversity Information Facility
GTR : generalized time-reversible model of molecular evolution
HKY : Hasegawa, Kishino and Yano model of molecular evolution
holo : holotype
HPD : highest probability density
I : invariant sites
I : Hellinger distance similarity index
i.e. : id est
IGS : intergenic spacer
iso : isotype
ITS : internal transcribed spacer
IUCN : International Union for Conservation of Nature
K : Royal Botanic Garden Kew
KEP : Forest Research Institute Malaysia
L : Naturalis Biodiversity Center (Nationaal Herbarium Nederland)
LPWG : Legume Phylogeny Working Group
Ma : million years
MAFFT : multiple sequence alignment based on fast Fourier transform
Maxent : Maximum entropy method
MCC : maximum clade credibility
MCMC : Markov Chain Monte Carlo
MH : Botanical Survey of India, Southern Regional Centre
N : north

NY : New York Botanical Garden
P : Museum National d'Histoire Naturelle
PC : principal component
PCA : principal component analysis
PCR : polymerase chain reaction
PEG : polyethylene glycol
pers. obs. : personal observation
PETM : Paleocene Eocene Thermal Maximum
PNH : Philippine National Herbarium
PP : posterior probability
R : reverse
S : south
SAN : Forest Research Center
SAR : Sarawak Herbarium
SING : Singapore Botanic Gardens
ST : sterile specimen
stdev : standard deviation
sp. nov. : species novae
syn. nov. : synonyme novae
U : Naturalis Biodiversity Center (Nationaal Herbarium Nederland)
US : United States National Herbarium, Smithsonian Institution
vol : volume
W : west
WAG : Naturalis Biodiversity Center (Nationaal Herbarium Nederland)

« Rien ne sert de courir, il faut partir à point »
Le lièvre et la tortue – Jean de La Fontaine (1668)

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Introduction

La diversité biologique n'est pas homogène à l'échelle de la planète

En observant les multiples organismes présents sur Terre, il est frappant de constater leur diversité en termes de taille, de forme, de fonction, d'interactions entre eux (prédation, parasitisme, mutualisme, etc.). Cette diversité est également variable dans le temps et l'espace : de nombreuses crises biologiques passées sont à l'origine de la disparition et de l'apparition des groupes d'organismes (Rosenzweig 1997). La diversité des organismes n'est pas distribuée de manière uniforme à la surface du globe : les tropiques abritent relativement plus d'organismes comparativement aux pôles et aux régions tempérées (Chown et al. 2000, Mittelbach et al. 2007, Brown 2014). D'autres régions restreintes du globe, enfin, rassemblent une diversité biologique encore plus élevée, représentée dans plusieurs taxons indépendants : c'est ce que l'on appelle des points chauds de biodiversité, et ceux-ci sont particulièrement vulnérables aux activités humaines (Myers et al. 2000, Brooks et al. 2002).

Afin d'appréhender la diversité du vivant d'une manière la plus appropriée possible, à des fins d'études, de protection ou de conservation, il est nécessaire de pouvoir caractériser les unités fondamentales qui composent le monde vivant, c'est-à-dire les espèces. D'un point de vue pratique, les biologistes s'accordent à classer les organismes connus en espèces distinctes, en se basant sur les caractères observés chez ces différents individus, permettant ainsi d'établir des limites entre les espèces (Mayr 1942, Mayden et al. 2013). Par la suite, l'étude des liens évolutifs, reliant les espèces entre elles, a permis de mettre en évidence que la diversité biologique n'était également pas homogène à l'échelle de l'arbre du vivant (Maddison et al. 2007, Scholl et al. 2016). Ainsi, certaines portions de l'arbre du vivant vont regrouper plus d'espèces que d'autres (e.g. insectes parmi les arthropodes (Gaston 1991) ; angiospermes parmi les embryophytes (Ricklefs et al. 1994, Soltis et al. 2014)).

L'unité de base pour étudier la diversité biologique : l'espèce

Le concept d'espèce en biologie a souvent été et est encore variable selon le groupe étudié, notamment par les méthodes envisagées pour poser les délimitations entre les espèces. Plusieurs courants de pensées ont pu cohabiter lorsqu'il s'agit de définir ce concept : une espèce chez les bactéries (Rossello-Mora et al. 2001) n'aura pas la même définition qu'une espèce chez les mammifères (Bradley et al. 2001) ou chez les champignons (Taylor et al. 2000). Le concept d'espèce utilisé jouera ainsi sur le nombre d'espèces reconnues (De Queiroz 2005b), et par conséquent influencera la manière de quantifier et de qualifier la diversité. Historiquement, le concept d'espèce biologique tel que décrit par Mayr (1942) expose l'idée qu'une espèce est constituée de diverses populations inter-fertiles et que deux espèces sont distinctes lorsqu'elles sont isolées génétiquement. Cette définition s'applique particulièrement bien chez la plupart des métazoaires ; en revanche, chez d'autres groupes d'organismes tels que les plantes, cette définition n'est pas toujours appropriée. En effet, il est reconnu que chez les plantes, il existe des phénomènes d'échanges de matériel génétique entre espèces distinctes, suite à l'introgression de gènes (Rieseberg et al. 1993).

Dans le cadre de cette thèse, nous avons préféré le concept d'espèce reformulé par De Queiroz (2007), c'est-à-dire qu'une espèce est constituée par une lignée regroupant des métapopulations évoluant séparément, montrant des flux de gènes réguliers entre les individus (Petit et al. 2009). Cette définition est toutefois à nuancer lorsqu'il s'agit d'étudier la diversité végétale : il faut souvent ajouter une dimension écologique au concept de l'espèce considérée comme une lignée méta-populationnelle. Ainsi, certaines espèces d'arbres répandues dans les milieux tropicaux secs n'auront pas la même structure en terme de populations et de flux de gènes, par comparaison avec d'autres espèces d'arbres localisées dans les zones tropicales humides (Pennington et al. 2015). De même, certaines espèces, bien que regroupant des individus séparés par des océans et des milliers de kilomètres, montrent une structure génétique homogène suite à l'échange constants de gènes, via des diaspores très efficaces (Takayama et al. 2013, Wee et al. 2014).

Une nouvelle délimitation des espèces, suite à la réexamination des caractères diagnostiques par exemple, peut entrainer une réévaluation du nombre desdites espèces au sein d'un groupe taxonomique donné (Agapow et al. 2004, Padial et al. 2009, Carstens et al. 2010, Shirley et al. 2014). Dans le cas des espèces cryptiques (Gagnon et al. 2014), celles ci peuvent être étudiées à l'aide de la taxonomie intégrative (Dayrat 2005) et nouvellement délimitées en utilisant des caractères moléculaires associés avec une réévaluation des caractères morphologiques diagnostiques jusqu'alors passés inaperçus. Avant de pouvoir statuer sur l'évolution d'un groupe taxonomique, il faut donc en connaitre davantage sur le nombre précis d'espèces qui le constituent.

Étudier la diversité des espèces d'un point de vue taxonomique et systématique

Si l'espèce constitue l'unité de base permettant de mesurer la diversité biologique sur Terre, cette diversité peut quant à elle être étudiée selon des approches différentes. Dans cette thèse, nous allons nous focaliser principalement sur l'étude de la diversité biologique grâce à la taxonomie, la systématique, la biogéographie et la diversification des espèces.

La taxonomie : des méthodes pour délimiter les espèces

L'espèce étant l'entité fondamentale sur laquelle se basent les études en biologie (De Queiroz 2005b), il est essentiel de circonscrire les limites de chacune, une fois un concept d'espèce en particulier retenu. Pour cela, il est essentiel d'en connaitre la taxonomie, qui a pour objectif de décrire et délimiter les espèces afin de pouvoir les classer de manière organisée et intelligible (Lecointre et al. 2006).

D'un point de vue pratique, plusieurs méthodes existent pour définir les barrières entre les espèces et attribuer l'appartenance des organismes observés à l'une ou l'autre, en fonction des caractères qu'ils portent. Rappelons qu'un caractère est représenté par tout attribut mesurable d'un organisme et que c'est sur l'observation desdits caractères que l'on se base pour délimiter les espèces. Ces caractères peuvent être de différente nature, allant des caractères morphologiques directement observables jusqu'aux caractères moléculaires accessibles uniquement après séquençage (Duminil et al. 2009), sans oublier d'autres caractères relevant du comportement (Isler et al. 1998, 1999) ou encore de l'environnement (Acanski et al. 2017).

Ces caractères sont tout particulièrement utilisés dans le cadre des révisions taxonomiques qui permettent de formaliser la délimitation des espèces. Différents critères sont applicables aux caractères qui doivent être choisis dans le cadre d'une telle révision (Maxted 1992) : idéalement, les caractères choisis doivent être discontinus à l'intérieur du groupe d'étude, tout en conduisant au regroupement de certains spécimens en entités clairement identifiables. Parmi ces caractères, certains doivent être diagnostiques, afin d'identifier un sous ensemble de spécimens correspondant à une espèce. L'exactitude d'une révision taxonomique est relative aux caractères sélectionnés, ainsi qu'au nombre de spécimens consultés : intégrer un nombre élevé de spécimens dans une révision taxonomique est donc une priorité, afin de prendre en compte le maximum de la variabilité des états de caractères, représentés chez les différents individus.

Enfin, une meilleure taxonomie permet d'avoir une idée plus exacte du nombre d'espèces présentes dans un milieu déterminé, et par conséquent, de connaître avec précision la diversité de ce milieu. Dans le cas par exemple des études de taxonomie environnementale, les méthodes de séquençage de nouvelle génération permettent de mieux estimer le nombre des espèces présentes dans un milieu donné et ainsi de pouvoir évaluer correctement la diversité des espèces (Sogin et al. 2006, von Mering et al. 2007, Huse et al. 2008).

La systématique phylogénétique : mettre de l'ordre dans le chaos biologique

La systématique est la science des classifications biologiques et des relations évolutives entre les organismes (Nelson et al. 1981, Lecointre et al. 2006). L'un de ses rôles majeurs (Wiens 2007) est de déterminer les relations phylogénétiques entre les espèces. Ainsi, la systématique se base sur l'étude comparative des caractères liés aux différents organismes, afin de trouver les relations de parenté qui existent entre les espèces. L'objectif de la systématique phylogénétique (Hennig 1965) est de classer les organismes selon leur degré de parenté et de chercher en priorité à regrouper les entités biologiques dans des clades, c'est-à-dire des lignées évolutives comprenant un ancêtre et tous ses descendants. Les clades sont formés sur la base des caractères dérivés et partagés par les organismes, ou synapomorphies.

Connaitre la systématique d'un groupe permet d'en étudier l'évolution des caractères : des innovations évolutives clés pourront être mises en évidence et être potentiellement reliées au succès évolutif de certains clades (e.g. apparition du vol chez les oiseaux, Brusatte et al. (2015)), sans oublier une meilleure compréhension de l'apparition de certains caractères et de leur transformation au cours du temps (e.g. précurseurs des nectaires extrafloraux chez les Légumineuses, Marazzi et al. (2012), Marazzi et al. (2013)). La connaissance de la systématique d'un groupe et les relations entre les différents taxons à l'intérieur de celui-ci pourra aussi mener à inférer des reconstructions de caractères ancestraux, essentiel pour comprendre l'origine des caractères actuellement observés chez les organismes (e.g. reconstruction de la fleur ancestrale des Angiospermes, Sauquet et al. (2017)). Enfin, connaitre la systématique d'un groupe permet d'étudier l'apparition successive des différents taxons, ce qui est essentiel dans le cas où l'on veut utiliser la systématique d'un groupe à des fins de reconstruction biogéographique.

Étudier les patrons de diversité à l'aide de la biogéographie historique

Établir la systématique d'un groupe taxonomique permet ensuite d'en étudier la diversité d'un point de vue temporel et spatial. Ainsi, en se basant sur le cadre systématique préétabli (i.e. la connaissance des liens de parenté entre les différentes espèces), il est possible de reconstruire l'histoire biogéographique du clade d'intérêt. Étudier la biogéographie d'un groupe d'organismes peut avoir plusieurs objectifs : émettre des conjectures à propos des migrations des lignées à la surface du globe (Azuma et al. 2001, de Boer et al. 2015) ; déterminer quels phénomènes (vicariance, dispersion longue distance) entrent en jeu pour expliquer les distributions observées des organismes (Korall et al. 2014, He et al. 2016) ; estimer les relations entre les différentes aires biogéographiques au cours du temps en effectuant des analyses comparatives de la biogéographie de plusieurs clades évolutivement éloignés (Turner et al. 2001, Linder et al. 2012, Ung et al. 2016).

La vicariance est un phénomène essentiel intervenant en biogéographie : il s'agit de la fragmentation des aires biogéographiques ancestrales, suite à des évènements de géographie physique (ouverture d'un océan, surrection d'une montagne, etc.), pour aboutir aux aires de distribution observées actuellement (Crisci et al. 2003, Baum et al. 2013). Ce phénomène est particulièrement relié à l'idée qu'une espèce est composée de méta-populations qui, une fois physiquement séparées et avec un flux génique interrompu entre elles, vont diverger pour former de nouvelles espèces (suite au phénomène de spéciation). La vicariance est surtout avérée pour des groupes anciens, ayant subi une séparation suite à la dérive continentale (McLoughlin 2001, Swenson et al. 2001, Mao et al. 2012) et qui possèdent une distribution terrestre actuelle disjointe, avec des aires séparées par les océans (e.g. Proteaceae, Milner et al. (2015); crocodiles, Turner (2004)). Particulièrement, on évoque le phénomène de vicariance gondwanienne, lié à la spéciation, pour expliquer la divergence de deux espèces sœurs présentes chacune sur deux continents séparés par une barrière physique, tels que l'Afrique et l'Amérique du Sud. Cette explication est aussi valable dans le cas de la distribution d'un taxon de rang élevé, comprenant des taxons frères répartis de part et d'autre d'une barrière infranchissable.

De nombreux groupes récents se sont formés après la séparation des masses continentales, mais présentent tout de même des patrons de distribution qui, à première vue, sont liés au résultat d'un phénomène de vicariance (e.g. la présence des singes en Afrique et en Amérique du Sud, postdatant l'ouverture de l'océan Atlantique, Houle (1999)). Les reconstructions biogéographiques actuelles tendent à favoriser les évènements de dispersion longue distance par rapport aux évènements de vicariance, lorsqu'il s'agit d'étudier des groupes terrestres apparus durant l'ère Tertiaire (Katinas et al. 2013). En effet, à cette période, les masses continentales étaient déjà séparées par les océans et avaient une configuration proche de celle retrouvée actuellement (Scotese 2004, 2014) : dans ces cas là, la vicariance gondwanienne invoquée comme explication ne s'applique plus (Trenel et al. 2007) ; la dispersion longue distance devient donc la seule et unique possibilité d'expliquer les distributions observées. Chez certains groupes présentant des patrons de distribution disjoints habituellement associés à la vicariance gondwanienne, les phénomènes de dispersion longue distance sont considérés comme étant à l'origine des patrons observés (e.g. migrations lentes au travers d'un continent pour atteindre les aires de distribution actuelles, Davis et al. (2002), Davis et al. (2004)). Il existe également certains groupes pour lesquels la vicariance ainsi que la dispersion longue distance ont joué un rôle dans la distribution des espèces : c'est le cas pour les groupes ayant une origine ancienne mais qui ont subit des évènements successifs de dispersion plus récents (Korall et al. 2014, Thomas et al. 2015, Wei et al. 2015). Afin de produire une reconstruction de l'histoire biogéographique des taxons la plus proche de la réalité, il est donc nécessaire de considérer à la fois les phénomènes de vicariance et de dispersion longue distance, sans oublier les phénomènes de diffusion lorsque cela s'applique, pour expliquer les distributions actuelles. Bien évidement, ces phénomènes seront à relier avec le climat et la géologie de la Terre qui auront changé au cours des différentes périodes successives (Cocks 1981).

Une dimension écologique de la diversité biologique

En plus d’être réparties de manière non homogène dans l’arbre du vivant, les espèces ne se retrouvent pas uniformément dispersées à la surface du globe. L’exemple le plus frappant est le gradient de diversité biologique existant entre l’équateur et les pôles (Chown et al. 2000, Mittelbach et al. 2007), avec nettement plus d’espèces dans les régions tropicales et subtropicales que dans les régions arctiques et subarctiques, jusqu’à atteindre des concentrations les plus élevées dans les points chauds de biodiversité (Myers et al. 2000, Brooks et al. 2002). Si certains groupes taxonomiques sont spécifiques des régions tropicales (e.g. Annonaceae, Chatrou et al. (2012), Thomas et al. (2015)), d’autres préfèrent les régions tempérées voire polaires (e.g. certains genres de conifères, Ran et al. (2006), Xiang et al. (2015). D’autres clades, retrouvés à la fois dans les milieux tropicaux à subarctiques, possèdent une diversité d’espèces plus élevée dans les latitudes proches de l’équateur (e.g. Orchidaceae, Dressler (1981)) ou même à des échelles géographiques plus restreintes (e.g. mammifères en Amérique du Nord, Simpson (1964)) : ce gradient de diversité peut être alors attribué non pas directement à l’histoire évolutive du clade considéré, mais plutôt à l’effet de l’environnement. Ainsi, de nombreux facteurs environnementaux influencent la richesse des espèces : ces facteurs peuvent être d’origine abiotique, telle que l’énergie apportée et directement associée à la durée d’ensoleillement (Davies et al. 2004), le régime des précipitations (O'Brien 1998), les caractéristiques édaphiques (Espeland et al. 2010), ou d’origine biotique telle que les interactions avec d’autres espèces (Lunau 2004, Valente et al. 2012). Ces différents facteurs vont contraindre la distribution des espèces et vont participer à accroitre ou diminuer la diversité de celles-ci, en agissant particulièrement sur les taux de spéciation et d’extinction : une région insulaire dépeuplée fournira de nombreux environnements exempts de prédateurs, favorables au développement de nombreuses espèces dans le cadre d’une radiation évolutive (Chap. 9, Howard et al. (1998)) ; de même, dans une région où les pressions de sélection sont plus élevées, la formation de nouvelles espèces pourra avoir lieu suite à des phénomènes de spéciation en sympatrie (Lande et al. 2001) ; enfin, si les pressions sont trop élevées, les espèces disparaîtront suite au phénomène d’extinction. En conséquence, les facteurs environnementaux jouent un rôle essentiel dans la diversification d’un groupe d’espèces, et donc participent à leur succès (ou échec) évolutif, matérialisé par un nombre d'espèces plus ou moins important. Ces facteurs environnementaux déterminent les niches écologiques des espèces. La définition d'une niche écologique pouvant être traitée de différentes manières (dont on trouvera un résumé dans l'étude de Donoghue et al. (2014)), nous retiendrons ici la celle donnée par Holt (2009) qui considère la niche écologique d'une espèce comme étant l'espace statistique, délimité par des paramètres environnementaux, au sein duquel une espèce peut se maintenir et prospérer.

Bien que les niches puissent diverger entre certaines espèces proches (Joly et al. 2014), le conservatisme de niches est présent la majorité du temps (Wiens et al. 2010). S'adapter à une nouvelle niche, un nouvel environnement, ne semble pas être un phénomène très répandu (Donoghue 2008, Donoghue et al. 2014) mais lorsque cela arrive, les groupes concernés montrent parfois une plus grande diversification que les autres taxons évolutivement proches : on pensera notamment aux espèces ayant colonisé des milieux insulaires et ayant pu occuper différentes niches vacantes (Losos et al. 2003, Velasco et al. 2016).

La famille des Légumineuses

Au sein de certaines familles de plantes à fleurs, il est possible d'observer des patrons biogéographiques et de diversité caractéristiques, matérialisés par l'abondance variable des espèces selon les clades et leur localisation géographique. Un exemple pertinent se retrouve dans la famille des Leguminosae, ou Fabaceae (couramment appelé légumineuses), qui est la troisième famille de plantes à fleurs la plus diversifiée en terme de nombre d'espèces (Lewis et al. 2005). On retrouve les espèces de cette famille réparties sur toute la surface du globe, exception faite des déserts secs (e.g. Sahara) et froids (e.g. Antarctique) (Raven et al. 1981, Schrire et al. 2005a). La diversité des légumineuses est maximale dans les forêts tropicales humides d'Afrique et d'Asie, ainsi que dans les forêts tropicales sèches (Doyle et al. 2003). Au sein de cette famille se retrouvent l'un des genres de plantes à fleurs comptant le plus grand nombre d'espèces, le genre *Astragalus* L. avec environ 2500 espèces (Wojciechowski 2005), mais également de nombreux genres monotypiques tels que *Tamarindus* Tourn. ex L. (Lewis et al. 2005), qui comporte la seule espèce *Tamarindus indica* L.

Les légumineuses sont actuellement organisées en six sous familles (LPWG 2017) : Duparquetioideae, Cercidioideae, Detarioideae, Dialioideae, Caesalpinioideae, Papilionoideae. Dans cette thèse, nous nous focaliserons spécifiquement sur la sous-famille des Detarioideae

(Mackinder 2005, de la Estrella et al. 2017, LPWG 2017), qui forment l'une des premières sous familles à diverger et comportent quelques 760 espèces, réparties dans 81 genres (de la Estrella et al. 2017). Ces espèces se retrouvent presque exclusivement dans le biome de forêt humide tropicale (Schrire et al. 2005a). La diversité d'espèces chez les Detarioideae est concentrée en Afrique (Mackinder 2005), qui serait par ailleurs le berceau (i.e. l'aire ancestrale) ayant vu apparaitre ce groupe (de la Estrella et al. 2017). Ainsi, il existe environ 58% des genres de Detarioideae qui se retrouvent uniquement en Afrique (e.g. *Schotia* Jacq., *Oxystigma* Harms, *Daniellia* Benn., etc.) tandis que 20% des genres sont distribués dans les Néotropiques, dans plusieurs types d'environnements allant de la forêt atlantique brésilienne (e.g *Brodriguesia* Cowan (Cowan 1981)) à la forêt amazonienne (e.g. *Brownea* Jacq. (Klitgaard 1991)). Quelques genres enfin (12%) se retrouvent en Asie tropicale, souvent présents dans les petites îles éparpillées dans l'océan pacifique (e.g. *Saraca* L. (Zuijderhoudt 1967), *Kingiodendron* Harms). Si la sous famille des Detarioideae possède une distribution très étendue, en revanche la plupart des genres possèdent des distributions restreintes à une zone précise au sein de chaque continent, avec des taux d'endémismes importants : certains genres se retrouvent uniquement sur quelques îles éparses dans le Pacifique (e.g. quelques espèces de *Kingiodendron* se retrouvent uniquement en Papouasie Nouvelle Guinée), ou même sont endémiques d'une zone géographique très restreinte au sein d'un continent (e.g. *Hardwickia* Roxb. en Inde) ou d'une île (e.g. *Brandzeia* Baill. à Madagascar). Ainsi, 92% des genres sont localisés dans une seule région continentale, Afrique, Asie ou Amérique du Sud (Schrire et al. 2005b). Cinq genres seulement possèdent des distributions disjointes entre au moins deux masses continentales : *Afzelia* Sm. (Afrique de l'Ouest et Asie du Sud Est), *Guibourtia* Benn. (Afrique et forêt sèche au Brésil), *Hymenea* L. (forêt Amazonienne et Afrique de l'Est), *Intsia* Thouars (Asie du Sud Est, Madagascar et Afrique de l'Est), *Sindora* Miq. (Asie du Sud Est et Afrique de l'Ouest). Enfin, seuls trois genres possèdent une distribution pantropicale : *Copaifera* L., *Cynometra* L. s.s. (incluant *Maniltoa* Scheff., Radosavljevic et al. (2017)) et *Crudia* Schreb.

Le genre *Crudia* Schreb.

Ce genre est strictement inféodé au biome de forêt tropicale humide et présente une distribution pantropicale, rarement rencontrée au niveau générique chez les Detarioideae. On retrouve des espèces de *Crudia* en Amérique du Sud, jusque dans les Caraïbes (Amshoff 1953, Vieira 1990) ; en Afrique, principalement dans la région Ouest tropicale le long des côtes (Breteler et al. 2008) ; en Asie, avec des espèces aussi bien présentes sur les masses continentales (De Wit 1950) que sur les îles éparses du Pacifique (Hosokawa 1938). L'histoire évolutive du groupe n'ayant jusqu'à présent jamais été élucidée, la présente thèse va chercher à en reconstruire l'évolution et les liens de parenté existant entre les espèces. En ayant un cadre évolutif résolu, il sera possible d'estimer les différents scénarios biogéographiques ayant menés aux patrons de distribution actuellement observés. En rendant ces patrons plus intelligibles, nous pourrons ensuite émettre différentes hypothèses à propos de la dynamique de la diversité des espèces dans le temps et l'espace. Étudier l'évolution spatio-temporelle du genre *Crudia* enseignera également à propos de l'influence des phénomènes géologiques et climatiques passés sur les patrons observés de la diversité de ces plantes tropicales.

Révision taxonomique des espèces asiatiques du genre *Crudia*

Avant de réaliser toute étude de systématique dans le but d'évaluer les relations de parenté entre les espèces, il est essentiel de s'assurer que la taxonomie du groupe étudié est fiable et solide. L'espèce étant l'unité de base pour travailler en biologie évolutive, il est donc nécessaire de connaitre avec précision les délimitations de chacune d'entre elles, pour plusieurs raisons : il est alors possible d'évaluer plus exactement le nombre d'espèces dans un groupe taxonomique (Breteler 2010, Mackinder et al. 2013) induisant directement une meilleure reconstruction des relations de parenté entre lesdites espèces nouvellement délimitées (Conceicao et al. 2009, Pirie et al. 2009) ainsi qu'une plus grande précision dans l'évaluation des statuts de conservation des espèces (Klitgaard 2005, Leache et al. 2009).

Dans le cadre du genre *Crudia*, des études taxonomiques poussées et exhaustives ont été conduites sur les espèces d'Amérique du Sud (Amshoff 1939, 1953, Vieira 1990) et d'Afrique (Breteler et al. 2008), mais les espèces asiatiques n'ont été que peu étudiées (De Wit 1950). Aucune révision taxonomique des espèces asiatiques du genre *Crudia* n'existe à l'heure actuelle. Cela s'explique probablement par le fait que les espèces asiatiques possèdent une aire de distribution très étendue, étirée sur plusieurs milliers de kilomètres, comparativement à leurs homologues africains et américains : réaliser une seule campagne de collecte exhaustive pour le genre *Crudia* en Asie s'avère difficilement envisageable. En effet, on retrouve des espèces depuis le Sri Lanka (Dassanayake et al. 1980) jusqu'à l'Australie du Nord (Bean 2010) avec des présences notées sur de toutes petites îles du Pacifique telles que l'île de Palau (Hosokawa 1938). De plus, les rares monographies à propos des espèces de *Crudia* en Asie se focalisent essentiellement sur des zones géographiques restreintes, souvent limitées par des frontières politiques, et non pas à l'échelle d'un continent ou d'une zone climatique : De Wit (1950) et Hou et al. (1996) (qui ont réalisé les deux études majoritaires à propos des espèces de *Crudia* en Asie) ne traitent que des espèces présentes sur l'archipel malais (réunissant une partie de Bornéo et de la péninsule malaise), ce qui exclut toute la diversité des espèces présentes en Océanie et au Nord de la péninsule malaise. D'autre part, la délimitation des espèces peut souffrir du manque de données, lié à un défaut de collectes de spécimen : certaines espèces ne sont connues que par un unique spécimen (i.e. le spécimen type) ou seulement quelques spécimens (e.g. *Crudia cauliflora* Merr.), ce qui restreint l'observation de la diversité et de la variabilité des caractères au sein d'une espèce et peut influer sur la révision taxonomique du groupe.

Notre hypothèse de départ est que le nombre d'espèces de *Crudia* dans la zone asiatique a été surévalué, suite aux descriptions réalisées successivement par différents auteurs, sans nécessairement tenir compte de l'ensemble des espèces présentes dans cette région du globe. Le premier objectif de cette thèse est donc le suivant : réviser la taxonomie des espèces asiatiques en utilisant des méthodes de taxonomie traditionnelle basée sur la morphologie. Cette révision servira à valider ou non les délimitations des espèces telles que décrites par des auteurs précédents ; puis nous évaluerons les statuts de conservation des espèces nouvellement délimitées afin de connaitre les menaces environnementales qui pèsent sur elles.

Ces étapes de description et délimitation des espèces sont décisives car elles permettront de mieux évaluer la diversité spécifique du genre *Crudia* : par la suite, les unités taxonomiques que sont les espèces seront intégrées à d'autres études, tout particulièrement concernant la systématique moléculaire et la biogéographie, afin de proposer une reconstruction de l'histoire évolutive du genre au complet.

Systématique et biogéographie historique du genre *Crudia*

L'existence d'espèces correctement délimitées ne permet pas nécessairement d'inférer des relations de parenté entre elles. A cette fin, les études de systématique phylogénétique permettent d'y voir plus clair dans l'histoire évolutive d'un groupe taxonomique. Une fois la systématique du genre connue, celle-ci peut à son tour être utilisée comme support à plusieurs types d'études, allant de l'inférence de l'évolution des caractères (Bruneau et al. 2014), jusqu'à l'estimation de scénarios de biogéographie historique (Buerki et al. 2011, Olmstead 2013, Yang et al. 2017). C'est ce dernier point qui nous intéresse ici : en effet, la distribution actuelle des espèces du genre *Crudia* est pantropicale, et soulève des questions quant aux évènements et processus qui se sont déroulés pour aboutir à la répartition observée de ce genre.

Il n'existe à ce jour aucune étude de phylogénie sur l'ensemble de *Crudia* incluant plus de six espèces, la plupart du temps elles-mêmes incluses dans des études plus larges (Bruneau et al. 2008, de la Estrella et al. 2017), souvent basées sur des marqueurs chloroplastiques qui apportent peu de résolution à des niveaux infragénériques (Wolfe et al. 1987, Clegg et al. 1994). L'un des objectifs présentés dans ce chapitre est donc de connaitre la systématique phylogénétique du genre, en utilisant non seulement l'échantillonnage le plus exhaustif à ce jour (125 spécimens provenant de l'Asie, l'Amérique et l'Afrique, correspondant à 79% des espèces échantillonnées), mais également cinq marqueurs nucléaires, dont un nouvellement utilisé pour cette étude.

L'autre objectif de ce chapitre est de reconstruire l'histoire biogéographique du genre *Crudia*, afin de déterminer quels phénomènes passés pourraient être responsables des distributions actuelles observées. Nous avons pour cela utilisé des analyses de datation, afin d'estimer l'âge des différentes lignées au sein de *Crudia*, ainsi que la nature et le nombre d'évènements liés à l'occupation actuelle des trois continents (i.e. vicariance, dispersion longue distance...). Nous avons évalué la possibilité pour les différentes lignées d'avoir emprunté des ponts continentaux et des détroits situés à des latitudes élevées mais possédant des climats favorables à l'époque aux plantes tropicales (Erkens et al. 2009, Brikiatis 2014) pour occuper leur distribution actuelle, ainsi que la dispersion longue distance via les océans (Renner 2004).

Interprétation des patrons de diversité du genre *Crudia* : changement de taux de diversification et/ou influence des paramètres environnementaux ?

Dans certains groupes taxonomiques, si à première vue les niches écologiques occupées par des espèces évolutivement proches se ressemblent, il existe parfois des groupes pour lesquels on constate un changement de préférences écologiques entre certaines espèces (Aguirre-Gutierrez et al. 2015, Acanski et al. 2017). Dans la majorité des cas, les niches écologiques restent semblables, suite au phénomène de conservatisme de niche (Wiens et al. 2010). On peut alors se demander si les espèces du genre *Crudia* ont effectivement conservé la même niche au cours de l'évolution, ou bien si les espèces ont subit des changements de niches au cours des dispersions successives. En effet, il est remarquable de constater que toutes les espèces de *Crudia* sont inféodées au milieu de forêt tropicale humide, peu importe le continent considéré. Partant ce constat, nous avons émis l'hypothèse que toutes les niches écologiques des espèces de *Crudia* étaient semblables. Pour cela, nous avons utilisé un corpus de données constitué de 233 occurrences de spécimens appartenant à 26 espèces différentes, principalement extraites des bases de données en ligne, et 19 variables bioclimatiques. Ces données ont été étudiées à l'aide d'analyses multivariées.

Parallèlement aux études de niches, nous sommes partis d'un autre constat : parmi les Detarioideae, le genre *Crudia* est l'un des genres possédant la richesse spécifique la plus élevée. Au sein du monde vivant, un nombre d'espèces plus élevé dans un groupe précis, peut être parfois lié à un changement dans les taux de diversification (avec, entre autre, une accélération des taux de spéciation) (Alfaro et al. 2009, Steeman et al. 2009). Nous avons émis l'hypothèse que *Crudia* avait une richesse spécifique plus élevée au sein des Detarioideae, suite à la présence de taux de diversification plus important que chez les autres genres. Nous avons pour cela analysé l'histoire évolutive du genre *Crudia* et des Detarioideae en général, à l'aide de méthodes bayésiennes, dans le but de tester si les taux de diversification étaient variables pour le genre *Crudia* ou s'ils variaient également à d'autres périodes de l'histoire évolutive des Detarioideae.

Chapitre I : Taxonomic revision of the Asian species of *Crudia* Schreb. (Leguminosae, Detarioideae)

Boris Domenech[1], Gwilym P. Lewis[2], Ruth Clarke[3], Anne Bruneau[1]

[1]Institut de Recherche en Biologie Végétale and Département de sciences biologiques, Université de Montréal, 4101 Sherbrooke Est, Montréal, Québec, H1X2B2, Canada

[2]Comparative Plant and Fungal Biology Department, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, U.K.

[3]Identification and Naming Department, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, U.K.

Résumé

Crudia (Leguminosae, Detarioideae) possède une distribution pantropicale, avec des espèces en Afrique de l'Ouest, en Amérique du Sud et Centrale, en Asie du Sud Est et Océanie. Alors que les espèces africaines et américaines sont bien définies, aucune étude ne s'est penchée sur la délimitation et la circonscription des espèces asiatiques considérées dans leur ensemble. Nous avons réalisé la révision des espèces asiatiques de *Crudia*. La variation morphologique inhérente à chaque espèce a été prise en compte suite à l'étude de nombreux spécimens provenant de diverses localités en Asie du Sud-Est et en Océanie. De nouveaux caractères diagnostiques, tels que la courbure de la nervure centrale ou le contour et la forme du limbe des folioles, ont été développés afin de discriminer les espèces ; tandis que d'autres caractères utilisés dans des études antérieures, tels que l'indumentum, ne sont plus considérés comme étant les uniques caractères diagnostiques permettant de discriminer les espèces. Nous présentons une clé d'identification, à l'aide des caractères essentiels à la délimitation de barrières taxonomiques précises entre les espèces. En tout, quinze espèces sont validées, comparativement aux trente-cinq espèces considérées auparavant comme valides en Asie. Une nouvelle espèce est décrite, *Crudia curvosa* Domenech, G. P. Lewis & R. Clark, quatorze espèces sont maintenues et dix-huit espèces sont mises en synonymie. En utilisant des données de présence de spécimens, couplées à des données environnementales et des outils permettant de qualifier les statuts de conservation des espèces, nous proposons de nouveaux statuts IUCN pour chaque espèce.

Mots clés : Leguminosae, *Crudia*, taxonomie, Asie du Sud Est, folioles, *Crudia curvosa*

Abstract

Crudia (Leguminosae, Detarioideae) displays a disjunct pantropical distribution pattern, with species in West Africa, South and Central America, and Southeastern Asia and Oceania. Although species delimitation is well-documented for Africa and America, no study has focused on the delimitation of all Asian species together throughout their range. Here, we provide a revision of the Asian species of *Crudia.* The morphological variation among species was studied using herbarium specimens from numerous locations in Southeastern Asia and Oceania. New diagnostic characters, such as leaflet midvein curvature and lamina outline and shape, have been used to discriminate species, whereas some characters such as indumentum are no longer considered as the only diagnostic characters used for species delimitation. A key to the species is presented, with critical characters highlighted. A total of fifteen species are recognized: this is a significant reduction from the c. 35 species previously recorded from Asia. One new species is described (*Crudia curvosa* Domenech, G. P. Lewis & R. Clark) and eighteen binomials are placed in synonymy. Using specimen occurrences, as well as environmental data and measuring tools for conservation status of species, we propose new IUCN conservation status for each species.

Key words: Leguminosae, *Crudia*, taxonomy, Southeastern Asia, leaflets, *Crudia curvosa*

I.1 – Introduction

The genus *Crudia* Schreb. belongs to the Leguminosae subfamily Detarioideae (de la Estrella et al. 2017, LPWG 2017) and is nested in the tribe Amherstieae (de la Estrella et al. 2018). The genus has a pantropical distribution, with all species restricted to the tropical rainforest habitat. Recent molecular phylogenetic analyses strongly support *Crudia* as a monophyletic genus (de la Estrella et al. 2017)(Chap II). Within *Crudia*, the Asian species cluster together in a strongly supported clade that is sister to a clade of African and American species in which the American taxa form a well-identified subclade derived from African species. Taxonomic studies of the African (Breteler et al. 2008) and American species (Amshoff 1939, 1953, Vieira 1990) have accepted ten species in Africa and nine in America. These taxonomic revisions are consistent with results obtained in our recent phylogenetic analyses of the genus for these two groups (Chap II). However, no taxonomic revision is available for the Asian clade.

Over 35 Asian species have been described, ranging in distribution from Sri Lanka in the west to North Australia in the east. Previous taxonomic treatments, undertaken at regional or local levels by at least 16 different authors, have clearly resulted in an over-estimate of species number and diversity. Because of the insular nature of the Asian and Pacific area, many independent species have been repeatedly described from distinct localities, but some of these represent morphological variants of more widely distributed species. Our recent phylogenetic analysis of *Crudia* (Chap II) demonstrated weak phylogenetic boundaries between Asian species, highlighting the need for a full taxonomic revision.

Several taxonomic studies (Table I.1) have published independent descriptions of *Crudia* species, but were geographically focused on narrowly circumscribed Asian and Pacific areas (e.g., the small island of Palau (Hosokawa 1938), Papua New Guinea (Verdcourt 1978, 1979), the Malay Peninsula (King 1897), and the Philippine Islands (Rolfe 1884)) and lack integration into the systematics or classification of the whole genus. Additional floristic studies have likewise focused on specific regions within Asia, e.g. Larsen et al. (1984), Hou et al. (1996). In addition, some *Crudia* species, e.g. *Crudia cauliflora* Merr., are known only from the type collection (Hou et al. 1996). Recently, new species have been described for the Great Nicobar Island (Sanjappa 1994) and Northern Australia (Bean 2010). Additionally, De

Wit (1950) proposed an infrageneric treatment for the genus, but his classification focused solely on species from Malaysia.

Given that the Asian species are now known to form a strongly unified assemblage (Chap II), but that there has been no published broad-scale overview of the Asian species to date, we here present a taxonomic revision of the group. We focused only on Asian and Oceanian species, and considered their observed morphological diversity relative to the diversity observed across the genus worldwide. Our study here has the following objectives: 1) to reevaluate species boundaries and distinguish accepted names from those that should be placed in synonymy; 2) to produce an identification key based on the diagnostic characters for each species; and 3) to provide an up-to-date assessment of the conservation status (last updated in 1998) of Asian species.

I.2 – Material and methods

I.2.1 – Observation protocols

Quantitative data was measured from specimens in the Kew herbarium (K) with an electronic calipers (Neiko tools, model 01408A), giving a 0.1 mm precision. Flowers on herbarium sheets were rehydrated and dissected to add flower morphological data to descriptions. All type specimens at Kew were consulted and supplemented by studying images of types online (https://plants.jstor.org/).

I.2.2 – Species concept and delimitation

Species were considered as separately evolving metapopulation lineages (De Queiroz 2007), gathering individuals with sometimes highly variable characters. Because rare phenotypic variants can still be part of given species (Moritz 2002) it might sometimes be difficult to identify clear species boundaries. Here, we focused mainly on vegetative features to evaluate species barriers and find conserved diagnostic characters able to distinguish specimen groups as suggested by Maxted (1992). We examined successive lists of potentially diagnostic morphological characters, based on what we could find in previous works (De Wit 1950, Hou et al. 1996) and on reccuring observed features on several specimens, to build empirical species delimitation (Lee 2003). For example, we noted that several variable characters (e.g. leaflets number, leaflet outline shape, surfaces hairiness) allowed to unite many morphologically variable specimens under one unique species, rather than splitting many specimens in many extremelly homogenous species.

I.2.3 – Morphological characters

Because many of the studied specimens were collected in the mid-20th century or earlier, some morphological elements (fruits or flowers) were often lacking and were accompanied by sparse field notes. In consequence, species identification, diagnosis and delimitation have been largely based on vegetative characters. In addition, the small, petal-less flowers of *Crudia*, easily fall off or lose their parts during collection, making them difficult to observe. For the same reasons, Breteler et al. (2008) also focused on vegetative characters (e.g. stipule morphology) in their revision of the African species. Many vegetative characters are also considered diagnostic for the American species (Amshoff 1939, 1953, Vieira 1990). Because one of our goals is also to facilitate identification of Asian species, we added an illustrated glossary (Figs. I.2 to I.4) based on our own illustrations and on the Kew Plant Glossary (Beentje 2016). The following list explains the terms we have used in more detail.

<u>Leaflet number</u>: Asian *Crudia* species differ in the number of leaflets per leaf. For each specimen, we counted leaflet number of the leaves with the highest number of leaflets; among-species variation in leaflet number ranged between one to more than ten leaflets per leaf.

<u>Leaflet size</u>: To assess leaflet size, we consistently measured the largest leaflet on each specimen. Leaflet length was measured from the lamina base (excluding the petiolule) to its apex and leaflet width was measured at the widest point of the leaflet lamina, perpendicular to the midvein. Leaflet size is highly variable across the whole genus, but is relatively constant within most but not all species.

<u>Midvein curvature</u>: We included the curvature of leaflets (Fig. I.1) as a new character for *Crudia* species. Curvature may be assessed only when the leaflets and their lamina margin are not damaged or distorted. The midvein is considered as “curved” when the angle between its base and its apex exceeds 20 degrees (and usually closer to 30 degrees). The curvature must be

observable throughout the length of the midvein and on more than one leaflet per specimen. In contrast, a leaflet midvein is considered to be straight when the angle between the base and the apex is less than 20 degrees.

Leaflet shape: As leaflet shape is variable within specimens, we generally considered every leaflet on each specimen. Leaflet shape is described along two axes: *proximal* VS *distal* and *right* VS *left* seen from above. All shapes used in the descriptions are illustrated in Fig. I.2 to I.4.

Leaflet lamina symmetry: We also measured leaflet blade symmetry, a feature that is constant within a species. Leaflet symmetry describes the condition where the left and right portions of the lamina on either side of the midvein are equal or nearly equal. When the midvein is curved, the leaflet lamina is, in consequence, asymmetrical. In the case of *Crudia*, whose leaflets are always slightly asymmetrical, it is possible to have both a straight midvein (see previous character) and a strongly asymmetrical lamina. Symmetry variability is illustrated in Fig. I.4.

Indumentum: Some species have previously been diagnosed and delimitated based on the indumentum on different parts of the plant. De Wit (1950), in particular, considered indumentum as “a highly valuable character for specific distinction”. However, we observe that indumentum is highly variable even at the individual level, and that this variability is age-dependent: aging leaflets tend to be glabrescent, with young leaflets displaying a dense indumentum while older leaflets are often glabrous.

Characters not used: When available, we described characters associated with stipules. However, because stipules are early caducous, we did not use those characters to discriminate species despite being considered useful distinguishing characters for the African species (Breteler et al. 2008). Indeed, stipules are generally absent on herbarium specimens, and thus not useful taxonomically when trying to identify herbarium specimens. It is quite possible that field work and the collection of juvenile foliage will yield more reliable stipule characters.

Seeds number: Because fruits were often closed on herbarium sheets, or missing, we did not have access to seed number. Data concerning ovules and seeds number were only retrieved from the literature.

I.2.4 – Conservation status

We extracted specimen distributions of *Crudia* species from the GBIF database (GBIF 2017), as well as location data from the literature and personal records of observations associated with herbarium specimens. When available, we used conservation status described in the literature (e.g. Sanjappa (1994), Bean (2010)). Then, we used the online tool GeoCAT (Geospatial Conservation Assessment Tools) to facilitate the process of Red Listing and identify threatened species (Bachman et al. 2011). This tool uses the extent of occurrence (EOO) and the area of occupancy (AOO) of species to determine their conservation status. We used data location of species as presented in the Table I.2, with a cell size of 2 km² as basic unit to evaluate AOO, as recommended by IUCN Standards and Petitions Subcommitte (2010). We also consulted literature on general conservation politics in the country where the specimens were found on the basis that mentioning of conservation issues in local governmental objectives may be reflective of the general level of environmental threat.

I.2.5 – Poorly known species

We were unable to access herbarium sheets for a few Asian species known only from the type collection. For this reason the following names were included in the taxonomic treatment (as synonyms), based primarily on original descriptions and online specimen images available in Jstor Plants (http://plants.jstor.org/): *Crudia acuta* De Wit; *Crudia balachandrae* Sanjappa; *Crudia cauliflora* Merr.; *Crudia cynometroides* Hosok.; *Crudia mansonii* Prain; *Crudia mutabilis* De Wit; *Crudia sparei* Whitmore; *Crudia viridiflora* De Wit; and *Crudia splendens* De Wit.

I.3 – Description of Asian clade of the genus *Crudia* Schreb.

Habits: shrub, tree, rarely climbing, 2-30 m height, 10-120 cm DBH. Stipules: usually caducous, but when present, linear subulate, 2-8 x 1-2mm, hairy. Leaves: 1 to 12-13, alternate leaflets, petiole and rachis together 1.9-13.6 cm long, glabrous or hairy, rachis sometimes extending beyond the upper petiolule into a short tip. Leaflets: lanceolate, oblanceolate, elliptic, subovate, ovate, obovate, sometimes subcordate, midvein straight or curved, 2.0-25.2 x 1.4-7.9 cm, upper and lower surface glabrous or hairy, base rounded, obtuse, cuneate, apex acute, obtuse, acuminate, subfalcate, obtuse, attenuate with a short rounded terminal protrusion, lateral veins 4-10 pairs, petiolule 1.2-6.9 mm long, glabrous or hairy. Inflorescence: a raceme, 2.0-31.3 cm long, glabrous or hairy, with or without numerous showy bracts at the base, pedicel 1-16.5 mm long, glabrous or hairy, basal pedicel bracts absent or inconspicuous or present, orbicular, lanceolate, oblanceolate, linear, rounded, triangular, crescent-shaped, 0.1-10.7 mm long, glabrous or hairy, pedicel bracteoles absent, inconspicuous or present, elliptic, lanceolate, linear, triangular, 0.1-6.8 mm long, glabrous or hairy. Flower: hypanthium 0.3-2.9 mm long, glabrous or hairy; sepals 4, oblong, elliptic, lanceolate, suborbicular 1.7-4.9 x 1.5-3.3 mm, glabrous or hairy on inner and outer surface; petals absent; stamens 9-10; gynoecium stipe 0.2-2.7 mm long, glabrous or hairy, ovary 2-10.1 mm long, hairy, style 0.8-8.7 mm long, glabrous, sometimes with a few hairs at the base. Legume: dehiscent, swollen-inflated or flattened, ovoid, elliptic, lanceolate, oblanceolate, 3.0-12.7 x 1.6-5.5 cm, surface smooth or with prominent reticulate veins, apex acuminate and sometimes mucronate, glabrous or hairy. Seeds: one or two, sometimes four.

The description of the genus provided here is only for the Asian clade. Despite forming a well-supported clade in the molecular analyses (Chap II), no obvious morphological synapomorphies support the uniqueness of the Asian species compared to the American and African ones. Nevertheless, as noted by Herendeen et al. (1990), *Crudia* species in Asia bear petiolules with a less pronounced twist (sometimes the twist is not noticeable) than those in Africa and America; also, fruits are generally smaller in Asian species compared to African and American species (Vieira 1990, Breteler et al. 2008).

I.4 – Key to the Asian species

1. Leaflets seven or more ……..………………………………………………………………………………..……**2**

2. Pedicels at least 3-4 times the length of the ovary; leaflet blade symmetrical to slightly aymmetrical; inflorescences with 15-30 flowers; legumes 5-10 cm long, flat pubescent, with slightly prominent veins; Southern Malay Peninsula ……........***C. curtisii***

2. Pedicels about the length of the ovary; leaflet blade highly asymmetrical; inflorescence with 40-50 flowers; legumes 3-3.5 cm long, ovoid and swollen, velutinous, without veins; Northern Philippines ……………………………………..…***C. blancoi***

1. Leaflets one to six ………………………………………………………………………..……………………**3**

3. Leaflets one to three ………………………………………..**4**

4. Leaflet midvein curved; blade asymmetrical ……………………………………………………………….**5**

5. Leaflets two, apex elongated, acuminate to subfalcate; inflorescence less than 5 cm long; legumes laterally compressed, glabrescent; Borneo (Sarawak) …….. ***C. curvosa***

5. Leaflets three, apex shortened, acuminate; inflorescence more than 5 cm long; legumes subglobose, densely pubescent; Borneo (Kalimantan)……………………………………………………………….... ***C. tenuipes***

4. Leaflet midvein straight; blade symmetrical to slightly asymmetrical ……………………………….………..**6**

6. Base of the inflorescence (and sometimes base of the branchlets) with persistent, numerous, filiform (from 1 to 11-13 mm long) bracts; stipules sometimes persistent (often filiform to subulate) ……………….…………….…...**7**

7. Inflorescences cauliflorous; Philippines …………………………………………………...***C. cauliflora***

7. Inflorescences axillary or terminal on branches ……………………………………………………..**8**

8. Leaflets one to two (when mature), apex acuminate, long, sometimes less pronounced; legumes pubescent or glabrous; Borneo and Java …………………………………..……………***C. bantamensis***

8. Leaflets one to three, apex attenuate; legumes densely brown velvety; Great Nicobar Island ………………………………………………………………………………………… ***C. balachandrae***

6. Base of the inflorescence and of the branchlet without bract; stipules caducous …..…………………………........**9**

9. Leaflets three, clearly alternate (not subopposite), membranaceous, lanceolate to oblanceolate, apex acuminate to rounded; petiolule slightly darker than the leaflet blade; flowers sessile to sub-sessile; widespread in Borneo, Philippines, Malay Peninsula, New Guinea, Thailand, Java ..……………….. ***C. gracilis***

9. Leaflets two, opposite to subopposite, coriaceous, elliptic lanceolate, apex obtuse to acute; petiolule much darker than the leaflet blade; pedicel length equaling the corolla ……...**10**

10. Legumes pubescent, with laxly prominent reticulate veins; Solomon Islands, New Guinea, Papua, Northern Australia ………………………………………………………………………..….***C. papuana***

10. Legumes glabrous, without veins; Palau Island …………………...………….. ***C. cynometroides***

3. Leaflets four to six …………………………………………………………………………………..…**11**

11. Pedicel bracts or bracteoles absent; pedicel less than twice the ovary length; ovary 2-3 mm ……………..……..….......**12**

12. Leaflets five, blade asymmetrical; leaflets small (2 to 9 cm long), ovate to sub-ovate, base rounded, apex obtuse with a short rounded terminal protrusion; pedicel as long as the ovary and extending at anthesis; Cambodia, Thailand, Sri Lanka ………………………………………………………………………………………..***C. zeylanica***

12. Leaflets four to six, sometimes seven, blade symmetrical; leaflets large (5 to 25 cm long), lanceolate to oblanceolate, base obtuse, apex thin elongating; pedicel shorter than or equaling the ovary length at anthesis; Borneo (Kalimatan), Malay Peninsula, Thailand ……………………………….…………………………***C. penduliflora***

11. Pedicel bracts and bracteoles persistent, sometimes small and inconspicuous; pedicels twice as long or even longer than the ovary length; ovary 1.5-5 mm ……..…..**13**

13. Leaf rachis and petiolules densely pubescent; leaflet midvein canaliculate on the upper surface, prominently raised on the lower surface; bracts and bracteoles showy, persistent, pubescent; Malay Peninsula, Thailand and Borneo (Sarawak) ……………………………………………………………..……...……………….. ***C. caudata***

13. Leaf rachis and petiolules glabrous to glabrescent; leaflet midvein slightly canaliculate on the upper surface, raised on the lower surface mostly from petiolule to midlamina; bracts inconspicuous to showy, pubescent ……......**14**

> **14.** Leaflets six, 3 to 10 cm long, ovate to lanceolate, asymmetrical; inflorescence with c. 30 flowers and more; corolla (including pedicel) 7–9 mm long; ovary 1.5-3 mm; style equaling the ovary; Northern Australia ……….…………………………………………………………………………………….……***C. abbreviata***
>
> **14.** Leaflets four to six, 7 to 15 cm long, lanceolate to oblanceolate, symmetrical; inflorescences with 10-20 flowers; corolla (including pedicel) 12–19 mm long; ovary 4-5 mm; style equaling or longer than the ovary; Borneo (Sabah) ………………………………...……………………………………………….. ***C. ornata***

I.5 – Taxonomy

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***Crudia abbreviata* A.R.Bean.** Austrobaileya 8(2): 151-154 (2010). *Type*: Australia, Queensland, *Sankowsky 1631* (holo: BRI; iso: CNS)

Description from Bean (2010).

Habit: tree to 27 m height, unknown DBH. Stipules: caducous, when present subulate, linear to narrowly-deltate, 2-3mm long. Leaves: Sometimes three, mostly four to seven alternate leaflets, petiole and rachis together 4-7.5 cm long, sparsely hairy, rachis tip extending up to 5 mm beyond terminal leaflet, but rarely seen (caducous). Leaflets: thin, chartaceous or membranous, ovate, midvein straight, 2.8-9.8 x 1.2-4.1 cm, upper surface glabrous, lower surface hairy, base obtuse to broadly cuneate, more or less symmetric, apex acute to acuminate, lateral veins 7-8 pairs, petiolule 2-4 mm long, hairiness unknown. Inflorescence: a raceme, 3-5.5 cm long, densely puberulous, bearing 70-100 flowers, bracts basal absent, pedicel 5.5–7 mm long at anthesis, articulated at the base, glabrous or with sparse antrorse to patent hairs, basal pedicel bracts narrowly-deltate, 0.9–1.3 mm long, with dense, rusty antrorse hairs, pedicel bracteoles opposite to sub-opposite, ovate to deltate, 0.4–1 mm long, with dense, rusty antrorse hairs, attached to the proximal one-third of the pedicel, persistent at least to anthesis. Flower: hypanthium 1.5-2 mm long, glabrous; sepals 4, elliptic, cymbiform, glabrous 2.5-3.5 x 1.8-2.8 mm; petals absent; stamens (8-)10; gynoecium stipe 1.2 mm long, glabrous except distally, ovary 1.5-2 mm long, hairy, style 1.2-2 mm long, glabrous. Legume: obliquely oblong, 3.7-4 x 3-3.3 cm, transversely wrinkled, flat, not beaked, densely rusty-hairy. Seeds: not seen.

Specimens studied (by Domenech, in complement with specimens studied by Bean (2010))

Australia. Queensland, Archer River, 13°25’S 142°10’ E, 16 sep 1974 (st.), *Hyland 3079* (K); Queensland, Archer River, 12°27’19”S 142°38’27”E, 10 jun 2004 (st.), *Gray B08932*.

Diagnostic features

Crudia abbreviata is mainly recognizable by its elongated and narrow leaflets with asymmetrical bases, and by its short densely flowered inflorescences (30 flowers and more).

Related species:

Crudia abbreviata may be closely related to *Crudia blancoi* as suggested in the molecular phylogenetic analysis (Chap II) and by Bean (2010): the two species differ mostly by inflorescence size, which is longer in *Crudia blancoi*. Bracts are also inconspicuous in both species.

Synonyms

No synonym is known for *Crudia abbreviata*.

Conservation status

Description from Bean (2010):

"*Crudia abbreviata* is known from at least five populations, and some of these have subpopulations that may behave as components of genetic metapopulations. At the known sites, the species is locally common, but the number of mature individuals is unknown. The area of occurrence of known populations is c. 7000 km^2. There are considerable areas of riverine gallery forest that have never been botanically explored in the area of occurrence and the species is likely to be much more widespread than currently known. However, the area of occupancy is unlikely to exceed 40 km^2. The species has been recorded from the Conservation Reserve Estate in Mungkan Kandju National Park (formerly Archer Bend N.P.) and on the Australian Wildlife Conservancy property 'Piccaninny Plains'. The suggested conservation status is Near Threatened based on the criterion D of IUCN (2001)"

Distribution and habitat

Northern Australia. The species is found in "well-developed semi-deciduous notophyll rainforest along riverbanks and flood-channels" (Bean 2010).

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Crudia balachandrae **Sanjappa** Kew Bulletin, 49(3): 565-568 (1994). *Type*: Great Nicobar Island, *Sanjappa 18137* (holo: CAL; iso: PBL, MH)

Description from Sanjappa (1994)

Habit: tree, 6-8m height, unknown DBH. Stipules: linear-subulate, connate at base, 3 mm long. Leaves: one to three alternate leaflets, petiole and rachis together 6-9.5 cm long, glabrous, rachis produced beyond the upper petiolule into a long, subulate, caducous tip which ultimately leaves a minute persistent point. Leaflet: elliptic oblong, midvein straight, 10-19 x 3.5-6.5 cm, upper surface glabrous, lower surface hairy, base obtusely cuneate to rounded, apex obtusely acuminate to caudate, lateral veins 4-10 pairs, petiolule unknown. Inflorescence: a raceme, 5-8 cm long, glabrous to glabrescent, with a few brown basal sterile bracts, pedicel 6-12 mm long, puberulous, basal pedicel bracts ovate acute, less than 1 mm long, hairy (puberulous-ciliate), pedicel bracteoles, similar to bracts. Flower: hypanthium 1.5-2 mm long, puberulous; sepals 4, broadly ovate, obtuse, 4-4.5 x 3-3.5 mm, puberulous ciliate; petals absent; stamens 10; gynoecium stipe 1.5-2 mm long, glabrous lower half, ovary 2.5-3 mm long, densely wooly-hirsute, style 7-8 mm long, glabrous. Legume: dehiscent, somewhat trapezoidal with subligneous valves, 3.8 x 2.8 cm, base rounded, compressed, apex oblique and abruptly acuminate, densely brown velvety. Seeds: One.

Specimen studied

No specimen was available for this species.

Diagnostic features

As described in Sanjappa (1994), *Crudia balachandrae* has "small scale-like peduncular bracts, pedicellar bracts and bracteoles, and long, slender pendulous racemes", quite similar to what is found in *Crudia bantamensis*. Unlike *Crudia bantamensis*, *Crudia balachandrae* has numerous leaflets. These characters (numerous bracts and several leaflets) in combination are diagnostic for *Crudia balachandrae*. The particular geographic location (i.e. Great Nicobar Island) is also characteristic for this species.

Related species

We did not have access to any material of *Crudia balachandrae*, but this species appears morphologically similar to *Crudia bantamensis*, based on the original description by Sanjappa (1994). The specimen *Sanjappa 18137*, on which the *Crudia balachandrae* diagnosis and description are based, has "a few brown basal sterile bracts", which is one of the diagnostic characters for *Crudia bantamensis*. The overall shape of the leaflets (lanceolate to oblanceolate) is also characteristic and resembles the shape of *Crudia bantamensis*. However, the fruit of *Crudia balachandrae* is described as "densely brown velvety" whereas the specimens examined in describing *Crudia bantamensis* are mostly glabrous or rarely glabrescent. The overall shape of the fruits of *Crudia bantamensis* is somewhat variable, but always has a sharp or mucronate apex, similar to the fruit of *Crudia balachandrae*. Lastly, the fruit surface is smooth in *Crudia bantamensis* compared to "smooth or impressed with veins" in *Crudia balachandrae*.

Sanjappa (1994) also mentioned that "the specimens from Great Nicobar Island prove to represent a new species allied to *C. gracilis* Prain and *C. velutina* Ridley."

Synonyms

Although we consider that *Crudia balachandrae* must be closely related to *Crudia bantamensis*, it is not a synonym.

Conservation status

This species has a vulnerable status based on the criterion D2 of the IUCN redlist (IUCN 2017). It is also qualified as a "rare species".

Distribution and habitat

Endemic to Great Nicobar Island. The species habitat is described as "slopes of hills in tropical rain forests" (Sanjappa 1994).

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***Crudia bantamensis* (Hassk.) Benth** Trans. Linn. Soc. 25:315 (1865); *Touchiroa bantamensis* Hassk., Retzia 1:202 (1855); *Pryona bantamensis* (Hassk.) Miq., Fl. Ned. Ind. 1(1): 1081

(1855); *Apalatoa bantamensis* (Hassk.) Baill. Hist. Pl. 2:103-104 (1870). *Type*: Java, *Hasskarl s.n.* March 1925, (holo K; iso: L), cult., Bot Gard Bogor, under nr. I-i-38

Crudia reticulata Merr., Philipp. J. Sc., Bot. 13(2):73-74 (1918); De Wit, Bull. Bot. Gard. Buitenzorg III, 18:426 (1950), emend. *Type* : Sabah, *Villamil 393* (holo: K; iso: K; photo: L), **syn. nov.**

Habit: shrub, tree, 5-20 m, 5-90 cm DBH. Stipules: caducous. Leaves: one or two alternate leaflets, often one when mature, petiole and rachis together 0.28-2.32 cm long, glabrous or hairy, prolonged beyond the terminal petiolule into a short tip. Leaflets: lanceolate, oblanceolate, 12.2-22.3 x 3.7-7.9 cm, midvein straight, upper surface glabrous, lower surface glabrous or sparse glabrescent, base rounded, obtuse, sometimes slightly cuneate, apex obtuse, acute sometimes acuminate, secondary veins in 6-10 pairs, petiolule 2.2-5.1 mm long, glabrous or hairy. Inflorescence: 4.9-10 cm long, glabrous or hairy, bracts numerous at the base, pedicels 1.3-4.5 mm long, glabrous or hairy, pedicel bracts, rounded to triangular, 0.3 mm long, glabrous or hairy, pedicel bracteoles, linear, 0.2-0.8 mm long, hairy. Flower: hypanthium 1-1.8 mm long, glabrous to hairy; sepals 4, elliptic, lanceolate, 2.1-3.6 x 1.3-2.5 mm, glabrous on inner surface, glabrous or with few sparse hairs on outer surface; stamens 10; gynoecium stipe, 2-2.7 mm long, hairy, ovary 1.9-2.7 mm long, hairy, style 3.5-7.5 mm long, glabrous with sometimes very few hairs at the base. Legume: lanceolate, 4.3-7.2 x 2.7-3.7 cm, pubescent or sometimes glabrous, surface smooth (no veins noticeable). Seeds: One to four.

Specimens studied

Java. cult. Java, Bot Gard Bogor, under nr. I-i-38, March 1925 (fl., st.)*, Hasskarl s.n.* (K, BO, L); location unknown, date unknown (fl., st.) collector unknown *629* (K); Herb. Hort. Bogor 1858, (fl., st.), *Marten 3674* (K); Foot of Mt. Hondje, 30 Dec. 1961 (st.), *Kostermans 19328* (K, BO).

Borneo. Sabah, Maliau Basin Conservation Area, upstream from Agathis Camp, 04 Apr. 2000, (fl., st.), *Sidkan MB6* (K); East Borneo, Kutei Reserve, Segata and Mentoko R. North of Samararinda, 14 June 1971 (fr., st.), *Soegeng Reksodihardjo 713* (K); Sepilok Forest Res., Sandakan, 8 Apr. 1954 (fl., st.), *Wood 1954A* (K); East Kalimantan, Wanariset Samboja UUCD area, 117°E 1°S, 14 Oct. 1996, (fr., st.), *Ambriansyah and Hamdi AA2056* (K, L);

North Borneo, Sepilok, 17 March 1949, (fl., st.), *North Borneo Forestry Department A2534* (K); East Borneo, Loa Djanan, Region west of Samarinda, 6 Sept. 1954, (fl., st.), *Kostermans 9962* (K, BO); Sabah, Sandakan, Mostyn, Kalumpang forest reserve, 22 Feb. 1966, (fl., st.), *Nordin and Ali 54441* (K); Sabah, Sandakan, Sepilok Forest Reserve, 6 Sept 2004, (fr., st.), *Diwol, Lynma, Tawadong and Umbin SAN110748* (K); Sabah, Lahad Datu District, 1 March 1985 (st.) *Argent, Ratter, Leopold, Dongop and Kumin 108294* (K); Sabah, Sandakan, Sg. Lamag, 12 Feb. 1979 (fl., st.), *Aban G. and Dewol S. SAN89938* (K, L, SAR, US); Sabah, Sandakan, Bukit Mengalas-Kalas, Kunatong, 9 March 1981, (fl., st.), *Dewol Sundaling SAN93136* (K, L, SAR, US); Sabah, Sandakan, Keningau district, unknown date, (fl., st.), *Fidilis SAN127551* (K).

Diagnostic features

One diagnostic characters of this species is the presence of numerous showy bracts at the base of the inflorescence. Bracts are usually persistent even after leaves have fallen (except when the herbarium specimen is too degraded). Leaves are often unifoliolate, with some of the longest leaflets among Asian species. The generally lanceolate to oblanceolate leaflet shape with a slight distal broadening is also characteristic of this species. Leaflets usually have prominent veins on the lower surface.

Related species

De Wit (1950) hypothesized *Crudia bantamensis* was related to *C. penduliflora* (at the time known under the names of *Crudia acuta, C. mutabilis, C. ripicola*) and *C. gracilis* (at the time known under the name of *C. subsimplicifolia*) and he organized them in the same section. However, these species have divergent leaflet morphologies: *Crudia bantamensis* has large leaflets (more than 10 cm long), compared to the other species, as well as a different number of leaflets, and may be unrelated. Numerous bracts at the base of the inflorescences are also diagnostic of *Crudia bantamensis* and are not found in the other species.

Synonyms

Every specimen of *Crudia reticulata* studied had numerous bracts at the base of the inflorescence, as well as unifoliolate or bifoliolate leaves with pronounced prominent veins on the lower leaflet surface. These morphological features are typical of *Crudia bantamensis*, and we therefore consider *Crudia reticulata* as synonymous with *Crudia bantamensis*.

Conservation status

Based on the GeoCAT analysis, the conservation status of *Crudia bantamensis* is endangered (EN). It is also known that human activities in Borneo are responsible for biodiversity erosion, particularly forest surface loss (e.g. Curran et al. (2004)). This is especially the case in North Borneo which practices intensive oil palm culture (e.g. Fitzherbert et al. (2008)). Thus the environment where *Crudia bantamensis* grows is threatened, consistent with its endangered status. However, because we only had 14 occurrences available in our dataset, the endangered status of *Crudia bantamensis* might be overestimated and could benefit from other supplementary occurrence data.

Distribution and habitat

Borneo, Java. This species is found in "lowland primary forest, dipterocarp forest, marshy, periodically inundated, seasonal or peat swamp, sandy soil, moderately drained ground, loam soil with coral limestone" (Hou et al. 1996).

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Crudia blancoi **Rolfe** J. Linn. Soc. Bot. 21:309 (1884). *Type*: Luzon, *Ahern's coll. 2956* (holo: K) [originally identified as *Apalatoa blancoi* Merr. on the specimen sheet]

Habit: tree, height unknown, unknown DBH. Stipules: caducous. Leaves: Seven to eight alternate leaflets, relatively numerous compared to other *Crudia* species, petiole and rachis together 6-10 cm long, glabrous, glabrescent or hairy. Leaflets: ovate to lanceolate, midvein straight, 5-7 x 2-3 cm, upper surface glabrous, lower glabrescent, base rounded to sometimes obtuse, apex acute, lateral veins 4-7 pairs, petiolule 2.4-3.2 mm long, glabrescent. Inflorescence: 5.5-10.0 cm long, hairy, basal bracts absent, pedicel 1.7-4.8 mm long, hairy, pedicel bracts 0.2 mm long, hairy, pedicel bracteoles 0.1-0.4 mm long, hairy. Flower: hypanthium 0.5-0.7 mm long, glabrous; sepals 4, elliptic, oblong, 3-3.4 x 1.6-1.8 mm, hairy on inner surface, glabrous on outer surface; stamens 10; gynoecium stipe 1.8-2.3 mm long, glabrous, ovary, 2.2-2.4 mm long, hairy, style 0.8-2.9 mm long, glabrous. Legume: ovoid, swollen, 3.0-3.3 x 1.6-1.7 cm, velutinous. Seeds: One.

Specimens studied

Philippines. Luzon, Rizal Province, date unknown, (fl., st.), *Merrill 882* (K); Luzon central, Rio de Montalban, 5 may 1993, (fr., st.), *Loher 2199* (K); Bulacan, Malolos, (fl., st.), *Loher 2200* (K); Luzon, Rizal Province, feb 1907, (fl., st.), *Ramos 2142* (K); Luzon, Province of Rizal, feb 1905, (fl., st.), *Ahern's Coll 2661* (K); Luzon, Rizal Province, Apr 1905, (fr., st.), *Ahern's coll 2956* (K); Luzon, Province of Rizal, may/jun 1905, (fl., st.), *Ahern's coll 3136* (K); Luzon, Province of Rizal, may/jun 1905, (fr., st.), *Ahern's coll 3074*.

Diagnostic features

Crudia blancoi has some of the smallest leaflets among Asian species (as well as *Crudia zeylanica*) but is also characterized by straight midveins with clearly asymmetrical leaflet blades, especially at the base of the lamina. The dense inflorescences with clustered flowers borne by small pedicels are also diagnostic. Legumes are swollen, not flattened, and usually pubescent.

Related species

Based on leaflets size, *Crudia blancoi* could be related to *Crudia zeylanica*. However, these two species have clearly disjunct distributions, and so are considered two distinct ensembles.

Synonyms

No synonym is known for *Crudia blancoi*.

Conservation status

The Philippines are one of several biodiversity hotspots threatened by human activities (Brooks et al. 2002, Brooks et al. 2006) though some studies show natural area loss is dissimilar throughout the country (e.g. Long et al. (2014)) and some local conservation politics are conducted to protect what biodiversity remains (Posa et al. 2008). This species is located essentially in the North Philippines; a few herbarium records show collections from Luzon

Island. Unfortunately we did not have access to any precise specimen location (e.g. GPS coordinates) and thus could not use GeoCAT. Given available data, we are not able to precisely evaluate the conservation status for this species. However, knowing the area is threatened but that conservation efforts are sensibly increasing, this species could be considered as critically endangered (CR) to endangered (EN).

Distribution and habitat

Northern Philippines, Luzon. De Wit (1950) described the habitat of *Crudia blancoi* as a "shore in never inundated, clayey soil in primary forest on a gentle slope".

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***Crudia caudata* Prain** J. As. Soc. Beng. 66:219 (1897). *Type*: Malay Peninsula, Johore, *Ridley 6399* (holo: K; iso: BM)

Habit: shrub, tree 5-7 m high, 6-10cm DBH. Stipules: persistent, linear subulate, 4.4-8.1 x 1.2-1.7 mm, hairy. Leaves: four to six alternate leaflets, petiole and rachis together 4.4-9.3 cm long, hairy. Leaflet: ovate, lanceolate, 2.0-19.6 x 2.3-4.3 cm, upper surface glabrous, lower surface densely hairy, pubescent, base rounded (basal leaflet) or obtuse (terminal leaflet), apex acuminate to elongated, 6-10 pairs of lateral veins, petiolule 1.5-3.1 mm long, hairy. Inflorescence: 8.3-10.7 cm long, hairy, basal bracts absent, pedicels 8.9-11.3 mm long, hairy, pedicel bracts lanceolate, 5.7-6.3 mm long, hairy, pedicel bracteoles elliptic, lanceolate, 5.9-6.1 mm long, hairy, enclosing completely the flower bud when young. Flower: hypanthium 1.2 mm long, hairy; sepals 4, elliptic suborbicular (but almost spherical, concave), 4.8 x 1.6 mm, glabrous on inner surface, hairy on outer surface; stamens 10; gynoecium stipe unknown, ovary, 2-3.8 mm long, hairy, style, 3.1-4.6 mm long, glabrous. Legume: oblong, inflated, 3.5-10.5 x 1.6-3.0 cm, pubescent, surface smooth, sometimes with a few slightly prominent veins. Seeds: one.

Specimens studied

Malay Peninsula. Bukit Bauk forest reserve, compartment 13, +/- 5 miles S of Dungun, 8 Aug. 1977, (fr., st.), *Lewis 119* (K); Johore, Tanjung Kupang, 1894, (fr., st.), *Ridley 6399* (K); Johore, Sungai Endau, 5 July 1931, (fr., st.), *Holttum SFN24905* (K); Johore, Kanga Sedili Kechil, 19 June 1934 (st.) *Corner SFN28606* (K)

Thailand. Narathiwat, Su Ngai Pa Dee, 15 July 1984, (fr., st.), *Premvasmi & Niyomdham 6* (K); Narathiwat, Tak Bai District, Bang Khun Thong, 14 Feb. 1984, (fl., st.), *Niyomdham 769* (K); Narathiwat, Su Ngi Paadee, Paa Wai, 10 Feb. 1988, (fl., st.), *Niyomdham 1664* (K); Narathiwat Province, 8 March 1974(st.) *Larsen & Larsen 33061* (K); Narathiwat Province, 2 May 1999 (st.) *Herendeen & Pooma 2-V-1999-3* (K)

Borneo. Sarawak, May/June 1908, (fr., st.), *Foxworthy 306* (K), Sarawak, May 1872?, (fr., st.), *Beccari 1763* (K)

Diagnostic features

Crudia caudata displays a characteristic indumentum on the petiole, rachis and leaflet lower surface with densely clustered hairs and a velvety touch. This indumentum is diagnostic of the species. Base leaflets range from rounded in the most basal leaflets to more obtuse in the distal ones. The relative size of the leaflets also increases from the basal to the distal portion of the leaf.

Related species

Crudia caudata and *Crudia penduliflora* share large, lanceolate leaflets, with acuminate apex and a similar outer shape. This may indicate an evolutionary link between them, though no supporting evidence is given by the molecular analysis (Chap. II).

Synonyms

No synonym is known for *Crudia caudata*

Conservation status

We only have three reliable occurrences for *Crudia caudata* (see Table I.2) which may lead to some bias in the evaluation of its conservation status. However, specimen records are spread on two mainland parts (Borneo and Malay Peninsula), giving a better grasp of the distribution area of the species. By using GeoCAT (Bachman et al. 2011), we reconstructed the conservation status of the species as endangered (EN), but this evaluation must be improved by adding new occurrence records of the species.

Distribution and habitat

Malay Peninsula, Thailand and North Borneo (Sarawak). “Freshwater swamp forest” (Larsen et al. 1984) to “alluvial, peaty or sandy level grounds, along a tidal river in primary forest on temporarily inundated areas.” (De Wit 1950).

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Crudia cauliflora **Merr.** J. Arnodl. Arbor. 35:136-137 (1954). *Type*: Philippines, *Ramos & Pascasio BS 34921* (holo: A)

Description from Merrill (1954) and Hou et al. (1996)

Habit: small tree, height unknown, DBH unknown. Stipules: unknown. Leaves: one single leaflet, rachis and petiolule together less than 1 cm long, glabrous. Leaflet: oblong-elliptic, 15-15 x 6-7 cm, upper surface hairiness unknown, lower surface hairiness unknown, base rounded, apex clearly obtuse, acuminate, 7 pairs of lateral veins, petiolule less than 1 cm long, glabrous. Inflorescence: cauliflorous, about 10 cm, glabrous to slightly pubescent. Flower: unknown. Legume: oblong-elliptic, laterally compressed, slightly asymmetrical, 8 x 4 cm, densely shortly pubescent. Seeds: Two or three.

Specimen studied (online)

Philippines. Siargao Island, June 1918, (fr., st.), *Ramos & Pascasio BS 34921* (holo: A)

Diagnostic features

Crudia cauliflora is the only known species possessing cauliflorous inflorescences among the genus *Crudia*.

Related species

Crudia cauliflora, found in the Philippine Islands, appears morphologically similar to *Crudia bantamensis*, found in Borneo and Java, based on the description of Merrill (1954) and the study of online type specimen *Ramos & Pascasio 34921* (found on http://plants.jstor.org). The original description by Merrill (1954) also mentions that *Crudia cauliflora* "resembles several Malaysian species, such as *Crudia bantamensis* (Hassk.) Benth., *C. beccarii* Ridl., *C. curtisii* Prain, *C. reticulata* Merr. and even *C. subsimplicifolia*". Fruit shape on *Ramos & Pascasio 34921*, is also similar to that of *Crudia bantamensis*. However, inflorescences of *Crudia cauliflora* are cauliflorous, whereas those of *C. bantamensis* are not cauliflorous. Cauliflorous inflorescences are unusual in *Crudia*. Based on this distinctive character, we choose to keep *Crudia cauliflora* as a separate species. Moreover, geographic features indicate the two species are distinct: *Crudia bantamensis* specimens are geographically clustered in Borneo and Java, whereas the only record for *Crudia cauliflora* comes from the Philippine Islands.

Synonyms:

No synonym is known for *Crudia cauliflora*

Conservation status

As no location record is available for *Crudia cauliflora*, we cannot use GeoCAT to estimate the conservation status. However, the only record for this species comes from the Siargao Island, the most eastward island of the Philippines, now a protected area (GOVPH 1996). Even though this territory is monitored and protected by law, it is still threatened by human activities like tourism (Catibog-Sinha 2011). Therefore, the conservation status of *Crudia cauliflora*, directly linked with environmental threats, may be considered either as endangered (EN) or critically endangered (CR).

Distribution and habitat

Philippines islands, Siargao Island. Habitat unknown.

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***Crudia curtisii* Prain** J. As. Soc. Beng. 66(2): 220 (1897). *Type*: Malacca, *Curtis 3007* (holo: K)

Crudia scortechinii Prain J. As. Soc. Beng. 66(2):220 (1897). *Type*: Malay Peninsula, *Scortechini 2029* (holo: K), **syn. nov.**

Habit: tree 15-30 m high, 60-100 cm DBH. Stipules: caducous. Leaves: seven to thirteen alternate leaflets, petiole and rachis together 8.7-13.6 cm long, glabrous or hairy. Leaflets: lanceolate or slightly obovate with a straight midvein, 3.3-11.2 x 1.7-2.9 cm, upper surface glabrous or with sparse hairs, lower surface hairy, discolorous, the lower surface greyish, base rounded to obtuse, apex acute to obtuse, sometimes acuminate, 6-8 pairs of lateral veins, petiolule 2.2-4.8 mm long, sparsely to densely hairy. Inflorescence: 4.8-10.9 cm long, hairy, pedicel, 8.5-14.6 mm long, hairy, basal bracts absent, pedicel bracts and pedicel bracteoles minute, inconspicuous, often absent. Flower: hypanthium, 0.9-1.4 mm long, hairy; sepals 4, elliptic lanceolate, 3.4 x 1.5 mm, glabrous to hairy on inner surface, hairy on outer surface; stamens 10; gynoecium stipe, 0.5-1 mm, glabrous, ovary, 2.5-4.8 mm long, hairy, style glabrous. Legume: flat, elliptic, oblong, or suborbicular, 3.5-10.0 x 3.0-4.7 cm, pubescent. Seeds: One to sometimes two.

Specimens studied

Malay Peninsula. Kepong, Selangor, 21 May 1966 (st.) *Whitmore FRI0293* (K); Perak, date unknown (fl., st.), *Scortechinii s.n.* (K); Pulau Penang, Apr. 1893 (fl., st.), *Curtis 3007* (K); Pahang, 2 Apr. 1919, (fr., st.), *Yeob 3207* (K); Perak, Apr. 1885, (fl., st.), *King's Coll 7467*; Perak, Sept. 1885, (fr., st.), *King's Coll 8175* (K); Perak, Feb. 1886, (fl., st.), *King's Coll 8574* (K); Selangor, 1909, (fr., st.), *Murdock 14440* (K); Johore, Labis Forest Reserve, near Pahang, 19 Feb. 1971, (fr., st.), *Suppiah FRI14778* (K); Lesong Forest Reserea, Pahang, 25 June 1972, (fr., st.), *Chan FRI20000* (K); Kepong, Selangor, Templer Park, 16 Aug. 1975, (fr., st.), *Kochummen FRI023123* (K); Perak, Parit Forest Reserve, 21 Dec. 1940, (fr., st.), *Tronoh KEP50907* (K); Kepong, Selangor, Field 31 Forest Research Plantation, 30 Apr. 1951, (fr., st.), *Budin 70366* (K)

Diagnostic features

A higher number of leaflets per leaf compared to other species of *Crudia* is generally characteristic for this species, although leaflet number can be quite variable (between 7 and 13 per leaf); overall, *Crudia* species with higher number of leaflets per leaf are observed to have greater variation in leaflet number than species with fewer leaflets. The shape of the leaflets is typical of the species, slightly obovate or oblanceolate, with an almost symmetrical lamina, and a straight midvein.

Related species

Both *Crudia curtisii* and *C. scortechinii* were listed in the study by King (1897) who distinguished between the two species based on indumentum color ("tawny" for *C. scortechinii* and "grey" for *C. curtisii*), leaflet number, and legume indumentum (denser for *C. scortechinii* than for *C. curtisii*). Due to high inter and intraspecies variation of these characters, we recognize only a single species and consider *C. scortechinii* as a synonym of *C. curtisii*.

Synonyms

We synonymized *Crudia scortechinii* with *C. curtisii* based on morphological features. Priority name rule applies here and *Crudia curtisii* is the name retained.

Conservation status

We do not have precise GPS location for any *Crudia curtisii* specimen, and could not consequently use GeoCAT. *Crudia scortechinii* was previously considered as Vulnerable B1 based on the IUCN criteria (IUCN 2017), and there is no previous information about the conservation status of *C. curtisii*. However, due to environmental threats in the Malay Peninsula leading to deforestation (Wilcove et al. 2013) such as oil palm agriculture (Koh et al. 2011) and timber exploitation (Brookfield et al. 1990), we propose to keep the vulnerable status (VU), as suggested by IUCN redlist for *Crudia scortechinii*.

Distribution and habitat

Southern Malay Peninsula. This species is not widespread. Hou et al. (1996) described the species as growing in "forests of lowland, riverbank, and undulating seasonal swamp".

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Crudia curvosa **Domenech, G. P. Lewis & R. Clark spec. nov.** *Type*: Sarawak, *Yii S52109* (holo: K; iso: AAU, L, KEP)

Diagnosis

Crudia curvosa is very similar to *Crudia tenuipes* but differs in having two alternate leaflets (vs. three in *Crudia tenuipes*) and laterally compressed and glabrescent legumes (vs. pubescent and subglobose in *Crudia tenuipes*). The leaflet curvature associated with a stretched and almost subfalcate apex, distinguishes this species from others.

Habit: small tree, 2-10 m high, unknown DBH. Stipules: caducous. Leaves: Two alternate leaflets, petiole and rachis together 1.2-1.9 cm long, glabrous or with sparse short hairs. Leaflet: lanceolate to sub-ovate, with a curved midvein, 8.5-13.2 x 3.4-5.8 cm, upper surface glabrous, lower surface glabrous or sometimes with sparse short hairs, base obtuse to rounded, apex acuminate to subfalcate, 4-6 pairs of lateral veins, petiolule 2.8-5.5 mm long, glabrous or with a few hairs. Inflorescence: 2-4.9 cm long glabrous, basal bracts absent, pedicel, 4-8 mm long, glabrous, pedicel bracts triangular, 0.1 mm long, glabrous, pedicel bracteoles triangular, 0.1 mm long glabrous. Flower: hypanthium, 1.1-1.7 mm long, glabrous; sepals 4; elliptic, 2.3-4.2 x 1.6-2.1 mm, a few hairs on the inner surface, glabrous on outer surface; stamens 10; gynoecium stipe 0.3 mm, glabrous or hairy, ovary hairy, 1.9-2.9 mm long, style glabrous except at the base. Legume: flat, glabrescent. Seeds: unknown.

Specimens studied

Borneo. Sarawak, upper Rejang River, 1929 (st.) *Clemens 21796* (K); Sarawak, Ulu Sg. Kana, Btg. Anap, Tatau, 4th Division, 16 June 1982, (fl., st.), *Abg. Mokhtat & Jugah S41789* (AAU, L, K, KEP, SAN); Sarawak, Bukit Batu Tiban, Ulu Sg. Balleh, 7th Division, 18 Apr. 1986, (fl., st.), *Yii S52109* (holo: K; iso: AAU, L, KEP); Sabah, Tawau, Mt. Wullersdorf forest reserve, July 2008, (fl?, st.) *Suzana, Joel, Jeisin, Tawadong SAN148396* (K, SAN)

Diagnostic features

The curved midvein, in combination with the flattened fruit, distinguishes *Crudia curvosa* from other species of the genus in Asia. The leaves of *Crudia curvosa* have two alternate leaflets.

Related species

Crudia curvosa is probably related to *C. tenuipes*, which also has a curved midvein, but differs in the number of leaflets per leaf as well as in fruit morphology.

Synonyms

No synonym is known for *Crudia curvosa*.

Conservation status

We do not have any precise record location point for *Crudia curvosa*; thus we could not use GeoCAT. However, given that this species is only known to be located in North Borneo we hypothesize that conservation status of *Crudia curvosa* ranges from endangered (EN) to critically endangered (CR), similar to the sympatric Bornean species *Crudia tenuipes* which is endangered (EN), due to environmental threats caused by human activities (Sodhi et al. 2004, Sodhi et al. 2010, Wilcove et al. 2013).

Distribution and habitat

North Borneo (Sarawak). Mixed dipterocarp forest.

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***Crudia cynometroides* Hosok.** Trans. Nat. Hist. Soc. Formosa 28:62 (1938). *Type*: Palau island, *Hosokawa 9028* (holo: L; iso: A)

Description from Hosokawa (1938)

Habits: tree, 5-8 m height, unknown DBH. Stipules: unkown. Leaves: Two opposite (unijugate) leaflets, sometimes one single leaflet, petiole and rachis together 0.5-1 cm long, hairiness unknown. Leaflets: ovate-lanceolate or elliptic-lanceolate, coriaceous, midvein straight, 8-12 x 2.5-4.5 cm, upper and lower surface hairiness unknown, base rounded, apex acuminate, with an obtuse acumen, lateral veins pairs unknown, petiolule 0.5 mm long, hairiness unknown. Inflorescence: a raceme, 3 cm long, hairiness unknown, pedicel 3 mm long, hairiness unknown, basal pedicel bracts deltate, laciniate, 1 mm long, hairiness unknown, pedicel bracteoles ciliate, subdeltate, size unknown, hairiness unknown. Flower: hypanthium 1 mm long, hairiness unknown; sepals 4, orbicular-ovate 3 x 2 mm, glabrous; petals absent; stamens 8; gynoecium stipe 1 mm long, hairy, ovary 1.5 mm long, hairy, style 2.5 mm long, glabrous. Legume: dehiscent, flattened, oblong or ovate, size unknown. Seeds: unknown.

Specimen studied (online)

Palau. Ngchesar Municipality, SE Babeldaob, 7°27'N 134°35'30"E, 28 Jan. 1978, (fl., st.), *Canfield 436* (US) (http://n2t.net/ark:/65665/3d35ff082-0483-4abc-a02e-7066bc34005a) ; Ngerikiil River, Airai, 15 March 1970 (st.) *Fisher 45* (US) (http://n2t.net/ark:/65665/338264dee-60f0-4e76-9b2e-cfbfa2d60ccb)

Diagnostic features

Bifoliolate leaves are characteristic of the species. This species is uniquely endemic to Palau

Related species

Crudia cynometroides has leaves with opposite to (rarely) subopposite leaflets: this morphological feature is also present in *Crudia papuana*. The stamen number per flower for *Crudia cynometroides* is reported to be eight (Hosokawa 1938), which differs from *C. papuana* (10 stamens). The fruit of *Crudia papuana* is slightly pubescent with some prominent veins on the surface whereas the fruit of *C. cynometroides* is smooth without veins. Although the phylogenetic analysis remains inconclusive regarding whether *Crudia papuana* and *C. cynometroides* are the same species (Chap II), we consider the two species as distinct here because of their differing fruit morphologies. However, the two species are probably very closely related, as the bifoliolate leaf character is not common in genus *Crudia*, even if they are not located on the same archipelago.

Hosokawa (1938) suggested *Crudia cynometroides* is "closely allied to *Crudia subsimplicifolia* Merr., differing in its 8 stamens, and much longer pedicells". However the leaflet morphology is quite different between the two species.

Synonyms

No synonym is known for *Crudia cynometroides*

Conservation status

We only have a single record of precise GPS location for *Crudia cynometroides*; the unique occurrence may bias its designation as critically endangered (CR) by GeoCAT. However, Palau Island is a very small territory recorded as one of the most biologically valuable ecoregions in the world (Olson et al. 1998, Kingsford et al. 2009), with a high level of endemicity (Kitalong 2008, Costion et al. 2012) threatened by recent increase in tourism industry (Morrison 2012); we thus maintain the conservation status of *Crudia cynometroides* as critically endangered (CR).

Distribution and habitat

Palau Island. On "riverbank where steep hill drops sharply to water (brackish)" [description on specimen *Fisher 45*].

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***Crudia gracilis* Prain** J. As. Soc. Bengal, 66(2):223 (1897). *Type*: Malay Peninsula, *Kunstler (=King's Coll.) 8468* (iso: K; photo: L)

Crudia brevipes Ridl. J. Str. Br. Roy. As. Soc., 82:183 (1920b). *Type*: Malay Peninsula, *Ridley 12623* (holo: K; photo: L), **syn.**

Crudia teysmannii De Wit. Bull. Bot. Gard. Buitenzorg, 18(3):431 (1950). *Type*: Kalimantan, *Teijsmann 8317* (holo: BO), **syn. nov.**

Crudia evansii Ridl. J. Fed. Mal. States Mus. 10:133 (Ridley 1920a). *Type*: Malay Peninsula, *Evans s.n.* (holo: K; photo: L), **syn. nov.**

Crudia velutina Ridl. Kew Bull. 1929(8):257 (1929). *Type*: Sarawak, *Haviland 3071* (holo: K; iso: BM, L), **syn. nov.**

Crudia katikii Verdc. Kew Bulletin 32(2):470 (1978). *Type*: Papua New Guinea, *Katik NGF 46520* (holo: BRI; iso:, L), **syn. nov.**

Crudia subsimplicifolia Merr. Philipp. J. Sc. Bot. 5(1):39 (1910). *Type*: Luzon, *Klemme FB4287* (holo: K), **syn. nov.**

Crudia sparei Whitmore. Gard. Bull. Sing. 24:4 (1969). *Type*: Malay Peninsula, *Spare SFN 34494* (holo: K; iso: L), **syn. nov.**

Habit: small to large tree, sometimes leaning, 7-20 m high, 3-25 cm DBH. Stipules: caducous. Leaves: one to three alternate leaflets, petiole and rachis together 0.9-3.9 cm long, glabrous or with a few hairs (indumentum density depends on leaf age). Leaflets: obovate, oblanceolate, or lanceolate (distal part often wider than proximal part), midvein straight, 5.1-18.2 x 2.3-7.8 cm, upper surface glabrous or hairy (but only on very young leaflets), lower surface glabrous to hairy, base obtuse, apex acute to obtuse, often laterally widened and distally shortened, 4-7 pairs of lateral veins, petiolules 2.8-6.3 mm long, glabrous or hairy. Inflorescence: 5-13.6 cm long, glabrous or hairy, basal bracts absent, pedicels, 0.9-1.5 mm long glabrous to hairy, flowers almost sessile, pedicel bracts triangular, 0.2-1.1 mm long, glabrous or hairy, pedicel bracteoles linear-triangular, 0.3-0.4 mm long, glabrous or hairy. Flower: hypanthium 0.4-0.8 mm long, glabrous to hairy; sepals 4, oblong, lanceolate, or elliptic, 1.9-2.7 x 0.8-2 mm, glabrous on inner surface, hairy or glabrous on outer surface; stamens 10; gynoecium stipe, 0.4 mm long, glabrous, ovary, 0.7-3.6 mm long, hairy, style 0.6-4 mm, glabrous. Legume: lanceolate to oblanceolate, 4.9-12.7 x 2.5-4.5 cm, pubescent, surface smooth or with slightly prominent reticulate veins. Seeds: two to four.

Specimens studied

Malay Peninsula. Pahang, Gunongsenyum, June 1917, (fl., st.), *Evans s.n.* (K); Kepong, Selangor, Tg. Sedili Kechil East, Johore Coast, 27 Feb. 1968, (fl?, st.), *Cockburn FRI7676* (K); Perak, Feb. 1886, (fl?, st.), *Kunstler 8468* (K); Province Wellesley, Tasek Gelugur, 19 Feb. 1907, (fl., st.), *Ridley 12623* (K)

Borneo. West Kalimantan, Danau Sentarum Wildlife Reserve, between lake Bekuan and Belitung River, 0°45'N 112° E, *Giesen 64* (K); East Kalimantan, Berau, Inhutani I area, Trayek E, 2°05' N 117°17' E, 15 Feb. 1997 (st.) *Kessler 291* (K, L); Kalimantan Timur, Berau, P.T. Inhutani I logging area, near km 20, Trayek D, 1°58'N 117°11'E, 17 Oct. 1998, (fl., st.), *Kessler & Arbainsyah B1405* (K, L); Pulo Malju D. Luar, near the beach, 8 Oct. 1949, (fl?, st.), *Main 1981* (K); East Kalimantan, P.T. ICTI, Gunung Meratus, 26 Nov. 1997, (fl., st.), *Ambriansyah AA2177* (K, L); Central Kalimantan, Danau Tahai, near Pulau Kaja, 1°56'S 113°46'E, (fr., st.), *Sidiyasa 2511* (K, L); Central Kalimantan, Kabupaten Kapuas, Katunjung village, 2°10'S 114°25'E, 16 Oct. 2001, (fr., st.), *Sidiyasa 2640* (K, L); Sarawak, Bintulu, Apr. 1893, (fl., st.), *Haviland 3071* (K); Sarawak, 1888?, (fr., st.), *Beccari 3351* (K, L photo); Central Kalimantan, Bukit Raya and upper Katingan (Mendawai) River area, c. 50-100 km WNW of Tumbang Samba, c. 112°40'E 1°15'S, 23 Dec. 1982, (fl., st.), *Mogea 4393* (K); Brunei, Belait, Melilas, 4°12'N 114°41'E, 26 July 1993, (fl?, st.), *Sands 5978* (K); Brunei, Belait District, Sg. Damit, near Kuala Balai, 4°26'N, 114°19'E, (fl., st.), *Dransfield 6799* (K); Sandakan, Lahad Datu District, Bukit Silam Forest Reserve, 15 Apr. 1992, (fl., st.), *Madani 133921* (K, L, SAR, KEP, SING, BO, PNH, AA, OX)

Philippines. Luzon, Province of Cagayan, June 1906, (fl., st.), *Klemme 4287* (K)

Thailand. Narathiwat, Pas Ye, Su Ngi Pasdee, 14 Apr. 1988, (fl?, st.), *Niyomdham & Ueschirakan 1801* (K); Province of Nakhon Si Thammarat, Tha Samet, Jan. 1928, (fr., st.), *Kerr 14295* (K)

Papua New Guinea. Madang District, Madang Subdistrict, Gogol River, 5°10'S 145°35'E, 12 Oct. 1971, (fr., st.), *Katik NGF 46837* (K, L, BRI, CANB, A)

Diagnostic features

Compared to other species of *Crudia* in Asia, *Crudia gracilis* displays greater morphological variation between individuals and within populations, especially with regard to leaflet shape (obovate, oblanceolate, lanceolate) and leaflet number per leaf (from one to three). Leaflet apex shape is quite characteristic of this species.

Related species:

King (1897) states that *Crudia gracilis* is "extremely closely related to *Touchiroa bantamensis* Hassk. [now *Crudia bantamensis*], which has also 3- (or by abortion 2-) foliolate leaves, but has larger leaflets, puberulous rachis and sepals, and distinct though very short pedicels". As with De Wit (1950), we also disagree with King's conclusions, because leaflets of *Crudia gracilis* have a clear acute apex while *Crudia bantamensis* leaflets have a more rounded apex.

Synonyms

Although we could not directly access the only known herbarium specimen of *Crudia sparei* (i.e. the type), we consider it identical to *Crudia gracilis* based on the original description (Whitmore 1969, Hou et al. 1996) and online specimen consultation. We thus consider that *Crudia sparei* is a synonym of *Crudia gracilis*, based on morphological features.

Based on observations of the leaves and fruits of *Crudia teysmannii*, *C. evansii*, *C. velutina*, *C. katikii*, *C. subsimplicifolia*, we conclude that their morphology also corresponds to the description of *Crudia gracilis*; and we consider these five species also to be synonyms of *Crudia gracilis*. We also consider *Crudia teysmannii*, *C. evansii*, *C. velutina*, *C. katikii*, *C. subsimplicifolia*, as synonyms of *Crudia gracilis*.

Crudia brevipes was considered as a synonym of *Crudia gracilis* by Larsen et al. (1984), Hou et al. (1996) because morphological characters were similar between the two species.

Conservation status

The synonymous name *Crudia brevipes* is listed as Vulnerable D2 on the IUCN red list. However, based on the few location data collected and the use of the GeoCAT tool, the species conservation status is endangered (EN). Once again, it appears that, despite a widespread species range, its natural environment is threatened by human activities (Sodhi et al. 2004, Sodhi et al. 2010), and the conservation status could indeed be considered as endangered.

Distribution and habitat

Borneo, Philippines, Malay Peninsula, New Guinea, Thailand, Java. Growing in wet, dense, swampy low-altitude forests, riverbanks, seasonally to continuously inundated grounds (De Wit 1950, Hou et al. 1996).

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***Crudia ornata* De Wit** Bull. Bot. Gard. Buitenzorg III. 18:427 (1950). *Type*: Sabah, *Elmer 20708* (holo: BM ; iso: K, A, BRI, L, MO)

Crudia venenosa De Wit Bull. Bot. Gard. Buitenzorg III. 18:433 (1950). *Type*: Sabah*, Maidin SAN1692* (BO holo; photo: K, L), **syn. nov.**

Habit: shrub or tree, 4-18 m high, 35-90 cm DBH. Stipules: caducous. Leaves: Four to six alternate leaflets, petiole and rachis together 7.8-12.2 cm long, glabrous or hairy. Leaflets: lanceolate, 6.8-15.5 x 4.4-6.0 cm, upper surface glabrous, lower surface glabrous or with few sparse hairs, leaflet base obtuse to rounded, apex acuminate, 7-8 pairs of lateral veins, petiolule, 3.3-6.8 mm long, glabrous or hairy. Inflorescence: 6.6-12.1 cm long, hairy, pedicel 11.4-16.5 mm long, hairy, basal bracts absent, pedicel bracts lanceolate to oblanceolate, 8.7-10.7 mm long, hairy, pedicel bracteoles, lanceolate, 3.5-6.8 mm long, hairy. Flower: hypanthium 0.7-2.9 mm long, hairy; sepals 4, elliptic lanceolate, 2.9-4.9 x 1.7-2.7 mm, a few sparse hairs on inner surface, hairy on outer surface; stamens 10; gynoecium stipe 0.5 mm long, glabrous, ovary 2.8-4.9 mm long, hairy, style 2-4.1 mm long glabrous. Legume: unknown. Seeds: One.

Specimens studied

Borneo. unknown location, unknown date, (fl?, st.), *Wood 1317* (K); Sabah, Kinabatangan, 20? March? 1932?, (fl., st.), *Maidin SAN1692* (K); Timbun Mata Island Forest Reserve, 31 July 1937, (fl., st.), *Enggoh 7663* (K); Tawau, Sabah, Oct. 1922, (fl., st.), *Elmer 20708* (BM, K); Sandakan, Kinabatangan District, near Sopiloring Hill, 16 Apr. 1963, (fl., st.), *Ampuria 33341* (K); Sandakan, Tawau District, Ulau Balong Mile 31, 24 Nov. 1964, (fl., st.), *Gansau 47821* (K); Sabah, Sandakan, Segaliud Lokan Forest Reserve, 17 Jan. 1975, (fl?, st.), *Gibot 81145* (K, L, SAR, KEP, SING)

Diagnostic features

Leaflets are equally spaced along the rachis and have a characteristic lanceolate shape. Another feature used to recognize this species is the pedicel bracts and pedicel bracteoles that are often well developed compared to other Asian species.

Related species

Crudia ornata and *C. abbreviata* are keyed out together, showing closely related morphology. However, leaflets of *Crudia ornata* are bigger than the ones of *C. abbreviata* and the two species are not located in the same geographical area. Thus, the two species are easily distinguished.

Crudia ornata was described as a distinct species by De Wit (1950), who used a specimen previously described as *Crudia reticulata* (now synonymized under the name of *Crudia bantamensis*, in this study) as a type for *Crudia ornata*. Thus, *Crudia ornata* could have some morphological affinities with *Crudia bantamensis*, particularly concerning leaflet overall shape.

Synonyms

The type specimen *Maidin SAN 1692* is the only available specimen of *Crudia venenosa* (Hou et al. 1996). This specimen shows wide broad leaflets, evenly spaced along the leaf rachis, as seen in *Crudia ornata*. Given the similarity between the two species and the lack of additional collections of *Crudia venenosa* since its description in 1950, we consider this species to be a synonym and morphological variant of *Crudia ornata*. As stated by De Wit (1950), "the species [*Crudia venenosa*] is reported to be poisonous, which is the only case known in the genus".

Conservation status

Given the few location data point available, the correct estimation of the conservation status for *Crudia ornata* using GeoCAT is difficult but is recorded as endangered (EN). Given that this species is mostly located in North Borneo where logging exploitation and oil palm culture occur (Berry et al. 2010, Wilcove et al. 2010), an endangered status for this species is probable.

Distribution and habitat

Borneo (Sabah). Hou et al. (1996) described the habitat of this species as primary forest, from lowland up to 200m altitude, sometimes occurring on sand- and limestone

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***Crudia papuana* Kosterm** Reinwardtia, 6(3):292 (1962). *Type*: Papua New Guinea, *McVeagh NGF 8275* (holo: K; iso: L, BRI, CANB)

Crudia dewitii Kosterm. Reinwardtia, 6(3):291 (1962). *Type*: Papua New Guinea, *Lam 854* (holo: K; iso: L, U), **syn. nov.**

Habit: tree 3-30 m high, unknown diameter. Stipules: caducous. Leaves: Two subopposite to opposite leaflets at the end of the rachis, rachis and petiole together 0.39-1.82 cm long, glabrous, prolonged beyond the two terminal petiolules into a short tip. Leaflets: lanceolate to elliptic, constant in shape, 7.4-18.5 x 2.3-7.9 mm, upper surface glabrous, lower surface glabrous or hairy, base obtuse, apex acute to acuminate, 5-7 pairs of lateral veins, petiolules 4.2-6.9 mm long, glabrous. Inflorescence: 4.3-11.3 cm long, glabrous, pedicels, 0.6-1.5 mm long glabrous, basal bracts absent, pedicel bracts triangular, 0.5mm long, glabrous but hairy on the edge, pedicel bracteoles inconspicuous hairy. Flower: hypanthium 0.3-0.7 mm long, glabrous; sepals 4, elliptic, 2.5-2.8 x 1.8-1.9 mm, glabrous on inner and outer surface; stamens 10; gynoecium stipe, 0.2 mm long, hairy, ovary, 1.4-1.7 mm long, hairy, style 1.1-2.1 mm long, glabrous. Legume: elliptic, lanceolate, 6.5-7.2 x 3.4-4.0 cm, pubescent, surface smooth or with slightly prominent veins. Seeds: One to sometimes two.

Specimens studied

Australia. Queensland, Jardine River, 10°55’S, 142°15’E, 2 Feb. 1980, (fl., st.), *Hyland 10245* (K)

Papua New Guinea. unknown locality, 21 Aug. 1920, (fl., st.), *Lam 854* (K); Gulf District, near Ravikivau, Purari delta, 19 Feb. 1966, (fl., st.), *Craven and Schodde 868* (K, CANB, LAE, L, A, BRI, BO); Thu Vailala River, 9 Feb. 1926 (st.) *Brass 908* (K); Gulf district, one mile east of junction of Vailala and Lohiki rivers, 27 Jan. 1966, (fr., st.), *Schodde and Craven 4338* (K); Western District, Oriomo River, Daru, 8°55’S, 143°15’E, 5 July 1968, (fl., st.), *Womersley NGF37163* (K)

Diagnostic features

Subopposite to opposite leaflets are a striking characteristic of this species, as leaflets are usually alternate in *Crudia*. Kostermans (1962) described two species of *Crudia* in Papua New Guinea (i.e. *Crudia dewitii* and *Crudia papuana*) based on indumentum differences, but after consultation of several specimens, we determined that leaflet indumentum was quite variable within both species. Therefore, species cannot be differentiated based only on indumentum features, which is why we choose to consider them as the same ensemble. The narrow distribution range of this species (confined to Papua New Guinea) also favors retaining only one species instead of two.

Related species

The bifoliolate leaf with two opposite leaflets is not a widespread character in *Crudia*: it is only found in *Crudia papuana* and *Crudia cynometroides*. This suggests that these two species may be closely related. Furthermore, *Crudia cynometroides* grows only on the Palau Island, which is located northward of Papua New Guinea, where *Crudia papuana* is also found. This may be indicative of a past long distance dispersal event, or island hopping, followed by speciation.

Synonyms

We consider *Crudia dewitii* and *Crudia papuana* as synonyms, based on similar diagnostic features.

Conservation status

Based on the few location data we have at our disposal, and using the GeoCAT tool, we consider the conservation status of this species as endangered (EN). Forest cover is threatened by human activities in Papua New Guinea (Filer et al. 2009, Shearman et al. 2009), especially related to mining exploitation during the 20th century, degrading soils and cutting forest to open roads (Laurance et al. 2009), leading us to consider *Crudia papuana* truly endangered. However, more sampling may be needed to increase the confidence in conservation status estimation.

Distribution and habitat

Papua New Guinea, Northern Australia (Queensland). The species grows mostly on river banks (Kostermans 1962), particularly in lowland or alluvial forest subject to freshwater tides (Hou et al. 1996)

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***Crudia penduliflora* Ridl.** J. Straits Br. Roy. As. Soc. 61:3 (1912). *Type*: Malay Peninsula, *Ridley 3304* (holo: K) [erroneously labeled as *Ridley 3004* in the original description]

Crudia lanceolata Ridl. J. As. Soc. Straits 75:29 (1917). *Type*: Langkawi, *Ridley 15539* (holo : K), **syn. nov.**

Crudia beccarii Ridl. Kew Bulletin 8:257 (1929). *Type*: Sarawak, *Beccari 3903* (holo: K), **syn. nov.**

Crudia ripicola De Wit. Bull. Bot. Gard. Buitenzorg III. 18:428 (1950). *Type*: Borneo, *Endert 2024* (holo:BO; iso: K, L), **syn. nov.**

Crudia acuta De Wit Bull. Bot. Gard. Buitenzorg III. 18:415 (1950). *Type*: Sumatra, *Achmad 1646* (holo: BO; iso: L), **syn. nov.**

Crudia mansoni Prain J. As. Soc. Beng 73:199 (1904). *Type*: Tenasserim, *Manson's Coll 172 & 306* (unknown location), **syn. nov.**

Crudia mutabilis De Wit Bull. Bot. Gard. Buitenzorg III. 18:454 (1950). *Type*: Sumatra, *Dorst 1-PT-763* (holo : BO ; iso : L), **syn. nov.**

Habit: tree 15-30m, 25-80 cm DBH. Stipules: caducous. Leaves: Four to six, sometimes seven alternate leaflets, rachis and petiole together 4.1-11.5 cm long, glabrous or with a few sparse hairs. Leaflet: lanceolate to sometimes slightly obovate, 5.2-25.2 x 1.7-6.5 cm, upper surface glabrous, lower surface glabrous or hairy, leaflet base obtuse or cuneate, apex usually acuminate, sometimes acute to attenuate, 7-10 pairs of lateral veins, petiole 2-4.9 mm long, glabrous or with a few sparse hairs. Inflorescence: 10.9-31.3 cm long, hairy, pedicels 1-3.8 mm long, hairy, basal bracts absent, pedicel bracts triangular to orbicular, 0.2-1.1 mm long, glabrous or with hairs on the edge; pedicel bracteoles linear, 0.3-0.7 mm long, hairy. Flower: hypanthium 0.4-1.1 mm long, hairy; sepals 4, elliptic, 1.7-3.9 x 1.6-2.8 mm, glabrous or hairy on outer surface, hairy on external surface; stamens 10; gynoecium stipe unknown, ovary 2.2-3.5 mm long, hairy; style 2.6-5.8 mm long, glabrous. Legume: lanceolate, 5.6-8.1 x 2.9-5.5

cm, base and apex attenuate, valves with slightly prominent veins, pubescent. Seeds: One to two.

Specimens studied

Thailand. Unknown locality, 12 Sept. 1933, (fl., st.), *Collins 2364* (K); Pathalung Province, Ta Mot Wildlife Sanctuary, 27 Apr. 1999 (st.) *Herendeen 27-IV-1999-1* (K); Pathalung Province, Ta Mot Wildlife Sanctuary 27 Apr. 1999, (st.), *Herendeen 27-IV-1999-5* (K)

Java. Culta in Hort. Bogor sub No. I.E.9 [originally from Borneo Island], 30 Dec. 1957, (fl., st.), *Mukri s.n.* (K)

Malay Peninsula. Malacca, foot of Gunong Mering, Mt. Ophir, June 1892, (fl., st.), *Ridley 3304* (K); Langkawi Island, 12 Aug. 1994, (fr., st.), *Zainudin, Salleh & Mohamad AZ5260* (K); Langkawi, Kedah, 20 Sept. 1930, (fl., st.), *Dolman 20758* (K); Narathiwat, Bacho, 6 Nov. 1961, (fr., st.), *Sangkhachand 36952* (K)

Borneo. East Kalimantan, Sungai Pedang, Kota Bangun Ulu, Samarinda, 23 Feb. 1992, (fr., st.)*, Ambri & Arifin AA449* (K); Central East Borneo, 19 June 1925, (fl?, fr., st.), *Endert 1506* (K); Central Kalimantan, Kabupaten Kapuas, Katunjung village, Kampung Mangkutup, 2°11’S 114°23’E, 15 Oct. 2001 (st.) *Sidiyasa 2616* (K); Sarawak, Oct. 1867, (fl., st.), *Beccari 3903* (K)

Diagnostic features

This species is mostly recognizable by its large leaflets possessing an acuminate apex with a prolonged tip, as well as a long and slender inflorescence. Leaflet size is generaly quite variable within this species.

Related species

Some individuals of *Crudia penduliflora* can occasionally be mistaken for *Crudia caudata* based on leaflet shape and size. Also, in *Crudia penduliflora*, few sparse hairs can be present on the leaflet and sometimes on the rachis of the leaf, but the indumentum – when present – is never as dense as in *Crudia caudata*.

Synonyms

In the original description of *Crudia penduliflora* (Ridley 1912), five stamens per flower are reported. In direct contradiction of this, we observed 10 stamens in the flowers of the type specimen *Ridley 3304*, the only collection by which the species is known. Ridley (1912) recognized *Crudia penduliflora*, as a distinct species mostly because of “long simple racemes and small flowers”. However, we did not see a difference in the inflorescence length and shape between *Crudia penduliflora* and *C. lanceolata*, which lead us to consider the two species as synonymous based on this shared morphological feature.

Specimens of *Crudia beccarrii* have leaflets identical to those of *Crudia penduliflora* (regularly spaced along the leaf rachis), as well as a relatively elongate inflorescence. We thus consider *Crudia beccarri* and *Crudia penduliflora* to be synonymous.

Specimens of *Crudia ripicola* have a leaf morphology with the typical elongate and lanceolate leaflets, which leads us to consider this species as synonymous with *Crudia penduliflora*.

We did not have access to specimens of the following species: *Crudia acuta*, *Crudia mansoni*, and *Crudia mutabilis*. However, based on the description by De Wit (1950) and consultation of online specimens (https://plants.jstor.org/), *Crudia acuta* is likely a synonym of *Crudia penduliflora*: it has small flowers with a short pedicel and 4-6-foliolate leaves with oblanceolate leaflets. Similarly, *Crudia mansoni* might be synonymous with *Crudia penduliflora* but we base this assumption only on the description given by Prain (1904) as we did not have access to any other information. *Crudia mutabilis* seems to be the same as *Crudia penduliflora,* showing the same number and shape of leaflets, again based on the description by De Wit (1950).

Conservation status

As described on the IUCN redlist website (IUCN), *Crudia lanceolata* has a vulnerable (VU) status (category B1 & D2). Although expansion of its distribution range suggests the species may not be threatened, further studies of the conservation status of the habitat of *Crudia penduliflora* are necessary before a new evaluation can be given. Like other *Crudia* species in Pacific Asia, its natural environment is threatened by human activities and biodiversity erosion, and will likely remain vulnerable. We thus choose to keep the status as vulnerable. Supplementary data, especially new occurrence data, might allow a better characterization of the conservation status.

Distribution and habitat

North Borneo (Kalimatan), Malay Peninsula, Thailand. Hou et al. (1996) noted that this species occurs “in forest, ridge top and hillside”.

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***Crudia tenuipes* Merr.** Philipp. J. Sc. 11:83 (1916). *Type*: Sarawak, *Native Collector BS1358* (iso: K, A, US)

Habit: tree 6-20 m high, 10-60 cm DBH. Stipules: caducous. Leaves: One to mostly three alternate leaflets, rachis and petiole together 1.9-7.2 cm long, glabrous. Leaflets: lanceolate, 8.7-11.6 x 3.3-5.1 cm, upper and lower surfaces glabrous, leaflet base obtuse to rounded, leaflet apex acuminate, 4-5 pairs of lateral veins, petiolules 2.6-4.4 mm long, glabrous. Inflorescence: 7.0-17.0 cm long, glabrous, basal bracts absent, pedicels 17-23 mm long, glabrous, pedicel bracts inconspicuous, crescent-shaped, glabrous, pedicel bracteoles, inconspicuous, triangular, glabrous. Flower: hypanthium 0.9-1.2 mm long, glabrous; sepals 4, elliptic, 4-4.6 x 3.3 mm, a few sparse hairs on the inner surface, glabrous on the outer surface; stamens 9-10; gynoecium stipe 0.5 mm long, hairy, ovary, 3.3-3.8 mm long, hairy, style 5-8.7 mm long, glabrous but with few hairs at the base. Legume: inflated, almost ovoid to lanceolate, 4.2-6.9 x 2.2-3.5 cm, apex elongate-acuminate, pubescent, the surface smooth without any noticeable venation. Seeds: One or two.

Specimens studied

Borneo. Kalimantan Timur, PT. Inhutani area, Plot 6, Sq. 3 RKL 1, 1°55’N 117°13’ E, 7 may 1998, (fl., st.), *Sidiyasa 1205* (K); Kalimantan Timur, PT. Inhutani area, Plot 6, Sq. 3 RKL 1, 7 may 1998, (fr., st.), *Sidiyasa 1208* (K); Kalimantan Timur, Berau, P.T. Inhutani I logging area, near km35, camp BFMP, 1°53’N 117°11’E, oct 1998, (fr., st.), *Kessler & Arbainsyah B1363* (K, L); Kalimantan Timur, Berau, P.T. Inhutani I logging area, km31, along logging road near plot 5, RKL1, 1°55’N 117°11’E, oct 1998, (fl., st.), *Kessler & Arbainsyah B1412* (K); Sarawak, Mount Dulit, 25 may 1932, (fl., st.), *Richards 1453* (K); Central Kutei, Belajan R., G. Kelopol near Tabang, 19 Apr 1955, (fr., st.), *Kostermans 10535* (K); Sandakan, Lahad Datu

District, Takun Kennedy Bay section 33, 7 sep 1961, (fr., st.), *Chai SAN26092* (K); Sandakan, Beaufort District, 15 may 1965, (fr., st.), *Sadau 49540* (K)

Diagnostic features

This species is highly distinctive due to its curved leaflet midvein which differentiates it from nearly all other *Crudia* species. Consequently, the leaflet blade is highly asymmetric.

Related species

Both *Crudia tenuipes* and *Crudia curvosa* have a curved midvein, and might be mistaken for each other. However, the leaflet apex is not strongly acuminate in *Crudia tenuipes* in contrast to *Crudia curvosa* in which the apex is much more elongated. *Crudia tenuipes* also displays usually more leaflets per leaf compared to *Crudia curvosa*.

Synonyms

No synonym is known for *Crudia tenuipes*.

Conservation status

Based on occurrence data and using the GeoCAT tools, we determine the conservation status as endangered (EN). In light of the human exploitation of natural resources in North Borneo including the natural habitat of *Crudia* species, we are confident with this estimation.

Distribution and habitat

Borneo (Kalimatan). Widespread in forests, often on limestone (Hou et al. 1996)

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***Crudia zeylanica* (Thw.) Benth.** Trans. Linn. Soc. London 25:314-315 (1865) - *Detarium zeylanicum*, Thw. Enum. Pl. Zeyl. 414-415 (1864). *Type*: Ceylon [Sri Lanka], *Thwaites CP3714* (holo: P; iso: K, BM) [identified as *Detarium zeylanicum* Thw. on the specimen]

Crudia chrysantha (Pierre) K. Schum. Fl. Thailand 4(1):90 (1984) - *Apalatoa chrysantha* Pierre, Fl. for. Cochinch. 5:384 (1898). *Type*: Cochinchine [Vietnam], *Pierre 419* (holo : K), **syn. nov.**

Crudia speciosa Prain. J. As. Soc. Bengal 66(2):222 (1897). *Type*: Thailand, *Curtis 2955* (holo: K), **syn. nov.**

Habit: tree, 8-30 m, unknown DBH. Stipules: caducous. Leaves: Sometimes three, mostly four to five alternate leaflets, petiole and rachis together 2.9-7.1 cm long, glabrous or with a few small hairs. Leaflets: ovate, sometimes subcordate, 2.0-9.3 x 1.9-5.7 cm, upper surface glabrous, lower surface glabrous or hairy, leaflet base rounded, sometimes obtuse, leaflet apex acute, or obtuse with a short rounded terminal protrusion, 5-8 pairs of lateral veins, petiolules 1.2-4 mm long, glabrous or hairy. Inflorescence: 7.8-23.6 cm long, hairy, pedicels 2.1-6.2 mm long, glabrous or hairy, basal bracts absent, pedicel bracts, linear, 0.2-0.4 mm long, hairy, pedicel bracteoles, triangular, 0.3-0.5 mm long hairy. Flower: hypanthium, 0.4-0.9 mm long, glabrous to hairy; sepals 4, elliptic to orbicular, 2.3-4.6 x 1.3-2.5 mm, with a few hairs to glabrous on the inner surface, glabrous on outer surface; stamens 10; gynoecium stipe 0.5-0.8 mm long, glabrous, ovary, 2.3-10.1 mm long, hairy, style, 0.5-3.8 mm long, glabrous. Legume: elliptic, flat, 2.5-4.5 x 2.4-3.1 cm, surface smooth or bearing slightly prominent veins, apex sub-mucronate. Seeds: One or two.

Specimens studied

Sri Lanka. Galpaata, near Caltura [Kalutara], Sept. 1863, (fl., st.), *Thwaites CP3714* (holo: PDA; iso: K, BM).

Malay Peninsula. Pungah, Rajah's garden [as written on the herbarium sheet], Feb. 1893, (fl., st.), *Curtis 2955* (K).

Vietnam. ad Caybe in proefectum My tho [as written on the herbarium sheet], Feb. 1869, (fl., st.), *Pierre 419* (K).

Thailand. Surin Province, 28 Feb. 1927, (fl., st.), *Put 665* (K); Bangkok, 25 Dec. 1927, (fl., st.), *Marcan 2306* (K); Bangkok, 11 Sept. 1920 (st.) *Kerr 4460* (K); Phra Nakhon Si Ayutthya, Sena, along the road in Sena Distric, 6 Apr. 2010, (fr., st.), *Pooma & Pattharahirantricin 7457* (K); Bangkok, 18 Apr. 1926, (fr., st.), *Kerr 10675* (K); N. Sukhothai, Sukhothai, 24 July 1973, (fr., st.), *Murata, Fukuoka & Phengklai 17003* (K); Aran Pralet, 9 Aug. 1930, (fr., st.), *Kerr 19607* (K)

Cambodia. Stoeung Treng Province, Thala Barevath District, Feb. 2006, (fr., st.)*, Monyrak 185* (K); unknown locality, 10 Feb. 1924, (fl., st.), *Marcan 1637* (K)

Diagnostic features

The numerous rounded, to almost cordate leaflets are very characteristic of *Crudia zeylanica*, and allow easy recognition of the species. This species also has a characteristic obtuse leaflet apex with a short rounded terminal tip.

Related species

Some specimens of *Crudia blancoi* could be mistaken with *Crudia zeylanica*, particularly in leaflets size and number. Also, *Crudia blancoi* and *Crudia zeylanica* are evolutionary closely related based on molecular features (Chap. II), but have distinct distribution ranges.

Synonyms

Specimens of *Crudia chrysantha* are widespread in continental Southeastern Asia (Thailand, Vietnam, and Cambodia) and characterized by numerous rounded leaflets and flat pubescent fruits with indistinct veins on the surface. The overall morphology of the leaflets is identical to that observed in specimens of *Crudia zeylanica*, as well as the very typical short spike-like inflorescences with densely clustered flowers. Pedicels of mature flowers are elongated compared to pedicels of young buds, which are extremely short to almost absent. We therefore consider *Crudia chrysantha* and *Crudia zeylanica* to be synonymous. Due to priority name rules, we keep the name *Crudia zeylanica* for the species.

Crudia speciosa is only known from two specimens (Larsen et al. 1984) including the type *Curtis 2955*. The original description of the leaflets (King 1897) is identical to those observed in *Crudia chrysantha* and *Crudia zeylanica*; therefore we also consider *Crudia speciosa* to be synonymous with *Crudia zeylanica*.

Conservation status

Crudia zeylanica specimens were previously known only from Sri Lanka, but the species is now considered to be extinct (IUCN red list). However, because we consider *Crudia speciosa* and *C. chrysantha* as synonyms of *C. zeylanica,* we do not consider this species extinct and delimit a more widespread distribution. Specimens first considered in the initial description of *Crudia zeylanica* represent the western edge of the present distribution of *C. zeylanica* as delimited here. We do not have enough specimen occurrence data to estimate accurately the conservation status of the species, but knowing biodiversity in the Thai-Malay Peninsula is globally threatened (e.g. Olson et al. (1998)), the status conservation could range from vulnerable (VU) to critically endangered (CR).

Distribution and habitat

As newly circumscribed, *Crudia zeylanica* displays a wide distribution, from Sri Lanka to Cambodia and Thailand. The species is the most widely distributed Asian *Crudia* taxon. It grows along streams and in inundated forests (Larsen et al. 1984).

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I.6 – Doubtful species

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Crudia orientalis **Hassk.** Cat. Hort. Bot. Bogor. 288 (1844). *Type: unknown*, **nomen nudum**

Hasskarl (1844) only mentioned this species but never described it. Both De Wit (1950) and Hou et al. (1996) also considered this species as doubtful.

******

Crudia splendens **De Wit** Bull. Bot. Gard. Buitenzorg III. 18:429 (1950). *Type*: Kalimantan, *Teysmann s.n.* (holo: BO)

We had the opportunity to access a non-type specimen, identified as *Crudia splendens* De Wit from the Singapore Herbarium (*Valera 9442*). Based on this single specimen and on the literature descriptions (De Wit 1950), the species seems likely to be closely related to *Crudia ornata* based on leaflet shape and number per leaf. However, in the original description, *Crudia splendens* has free showy stipules, and we did not observe stipules in *Crudia ornata*.

The validity of *Crudia splendens* is questionable: there is no description of the flowers in the protologue and it is known from only a few collections. It may be a morphological variant of another widespread *Crudia* species, but given the difficulty in accessing herbarium material and the incomplete description, we consider *Crudia splendens* as a doubtful species.

******

Crudia viridiflora **Whitmore** Gard. Bull. Sing. 26:285 (1973). *Type*: Malay Peninsula, *FRI 15949* (holo: K)

We consider *Crudia viridiflora* to be closely related to *Crudia bantamensis*, based on the descriptions of Whitmore et al. (1973), Hou et al. (1996). The two species have similar leaflet shape and number per leaf. However, the inflorescences of *Crudia viridiflora* are short-spikelets with densely clustered flowers, differing from *Crudia bantamensis* inflorescences which are much longer. No fruit is available to compare with the typical fruit of *Crudia bantamensis*. *Crudia viridiflora* is known only from very few specimens, including the type, and is perhaps a distinct species based on inflorescence characters. At present we do not have enough data to conclude if this is a distinct species or a variant of another widespread *Crudia* species.

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Crudia wrayi **Prain** J. As. Soc. Beng., 66(2):222 (King 1897). *Type*: Malay Peninsula, *Wray 2874* (holo: K; iso:, L)

Crudia havilandii Prain, J. As. Soc. Beng. 73(2):199 (Prain 1904). *Lectotype*: Sarawak, *Haviland 3070* (holo: K). *Syntype*: Sarawak, *Haviland & Hose 3703* (syn: K) **syn.**

We examined several specimens attributed to *Crudia wrayi* (see list below) and concluded that the specimens often differ from each other and do not display consistent morphological features (for example the shape of the leaflet lamina is highly variable). Many specimens have been wrongly attributed to *Crudia wrayi* (some specimens can clearly be attributed to *Crudia ornata,* whereas other might be mistaken for *C. curtisii*). Misidentifications put aside, *Crudia* *wrayi* is a doubtful species, representing an amalgamation of different species. Further molecular studies (Chap II) may help to resolve the status of this name.

Specimens studied (identified as *Crudia wrayi*)

Borneo. Sarawak, Kuching District, Arboretum Semengoh Forest reserva, 22 Jan. 1960, (fl., st.), *Anderson S11019* (K); Sarawak, Kuching District, Arboretum Semengoh Forest reserva, 2 Jan. 1962, (fr., st.), *Anderson S15253* (K); Sarawak, Kuching District, Arboretum Semengoh Forest reserva, 16 March 1962, (fr., st.), *Anderson*, *S15610* (K); Sarawak, Semengoh forest reserva, 13 March 1973, (fr., st.), *Ismawi S32099* (K); Sarawak, Semengoh Arboretum, 14 Oct. 1978, (fl., st.), *bin Latip S38503* (K)

Synonyms

The specimens of *Crudia wrayi* are also often identified under the synonym *Crudia havilandii.*

Figure I.1: Leaflet curvature

Blue and green lines are positioned tangentially to the midvein, respectively at the apex and at the base. The resulting angle can be measured with a protractor. Degree of curvature is shown by the red angle.

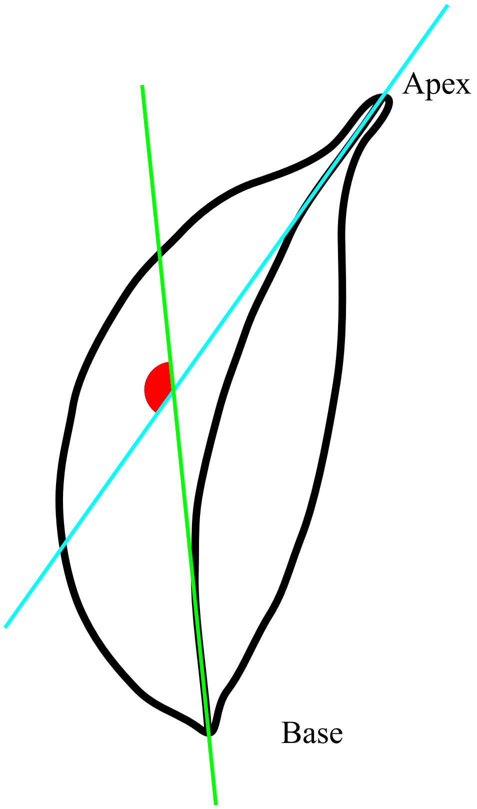
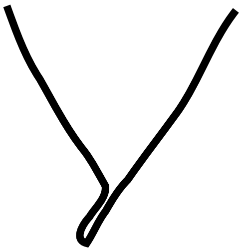
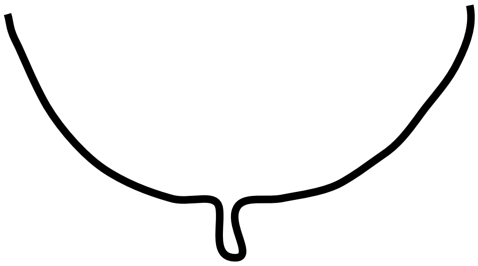


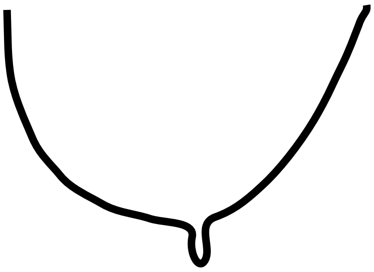
Figure I.2: Leaflets base and apex



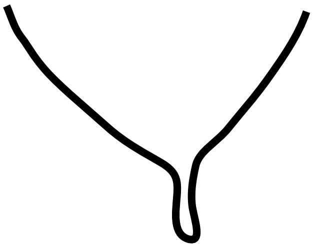
Cuneate
Crudia penduliflora
(specimen Collins 2364)



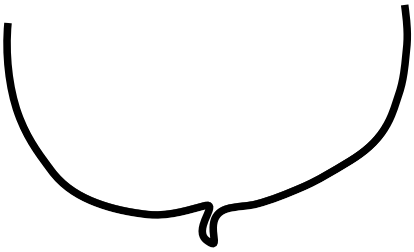
Rounded
Crudia ornata
(specimen Ampuria 33341)



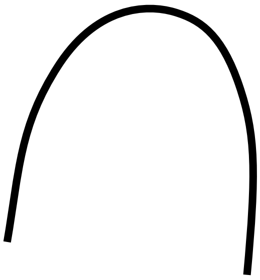
Asymetrical
Crudia blancoi
(specimen Merrill 882)



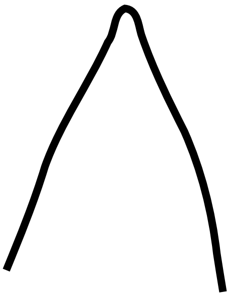
Obtuse
Crudia gracilis
(specimen Kunstler 8468)



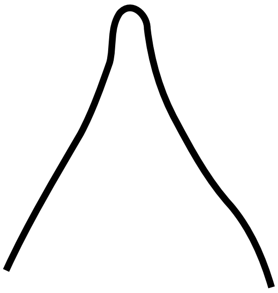
Subcordate
Crudia zeylanica
(specimen Pierre 419)



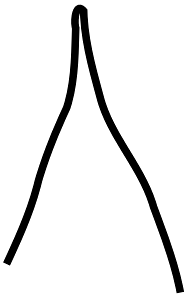
Rounded
Crudia bantamensis
(specimen unknown 629)



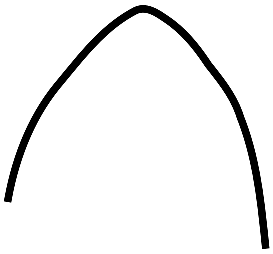
Attenuate
Crudia abbreviata
(specimen Hyland 3079)



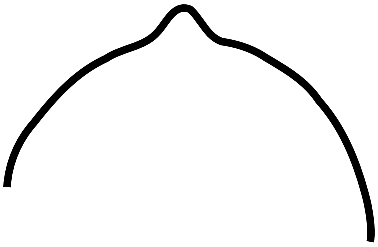
Acute
Crudia blancoi
(specimen Merrill 882)



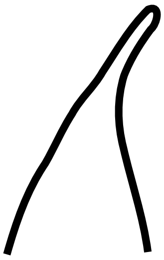
Acuminata
Crudia caudata
(specimen Corner SFN28606)



Obtuse
Crudia bantamensis
(specimen Hasskarl sn.)

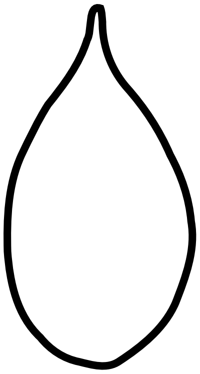


Mucronate
Crudia zeylanica
(specimen Marcan 2306)

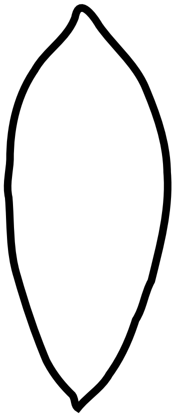


Falcate
Crudia curvosa
(specimen Clemens 21796)

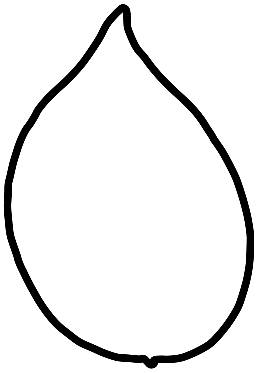
Figure I.3: Leaflet outer shape



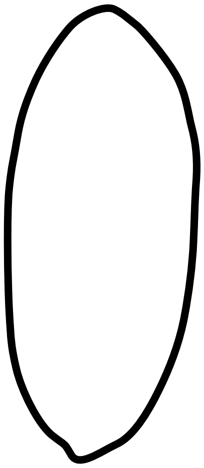
Ovate
Crudia caudata
(specimen Becarri 1763)



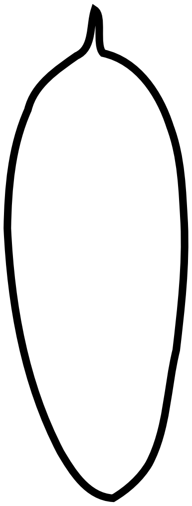
Oblanceolate
Crudia gracilis
(specimen Niyomdham &
Ueschirakan 1801)



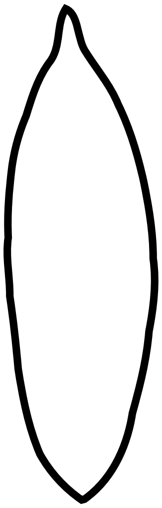
Subcordate
Crudia zeylanica
(specimen Thwaites CP3714)



Elliptic
Crudia papuana
(specimen Hyland 10245)

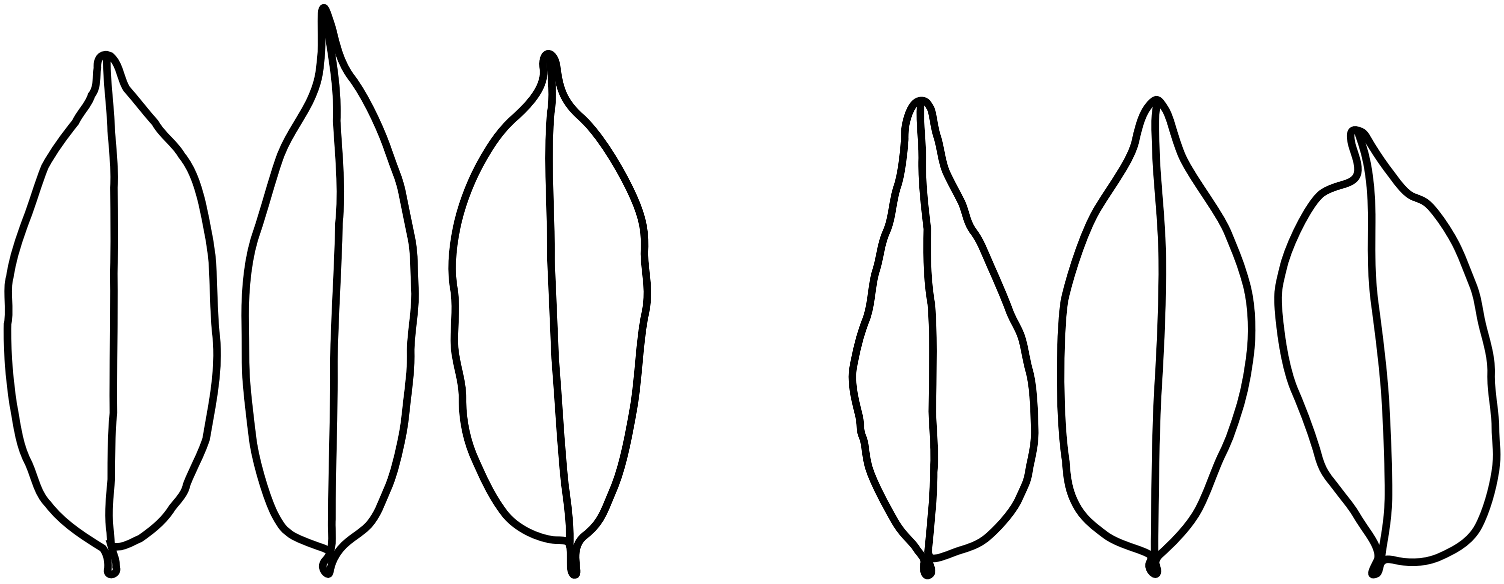


Obovate
Crudia bantamensis
(specimen Ambriansyah &
Hamdi AA 2056)



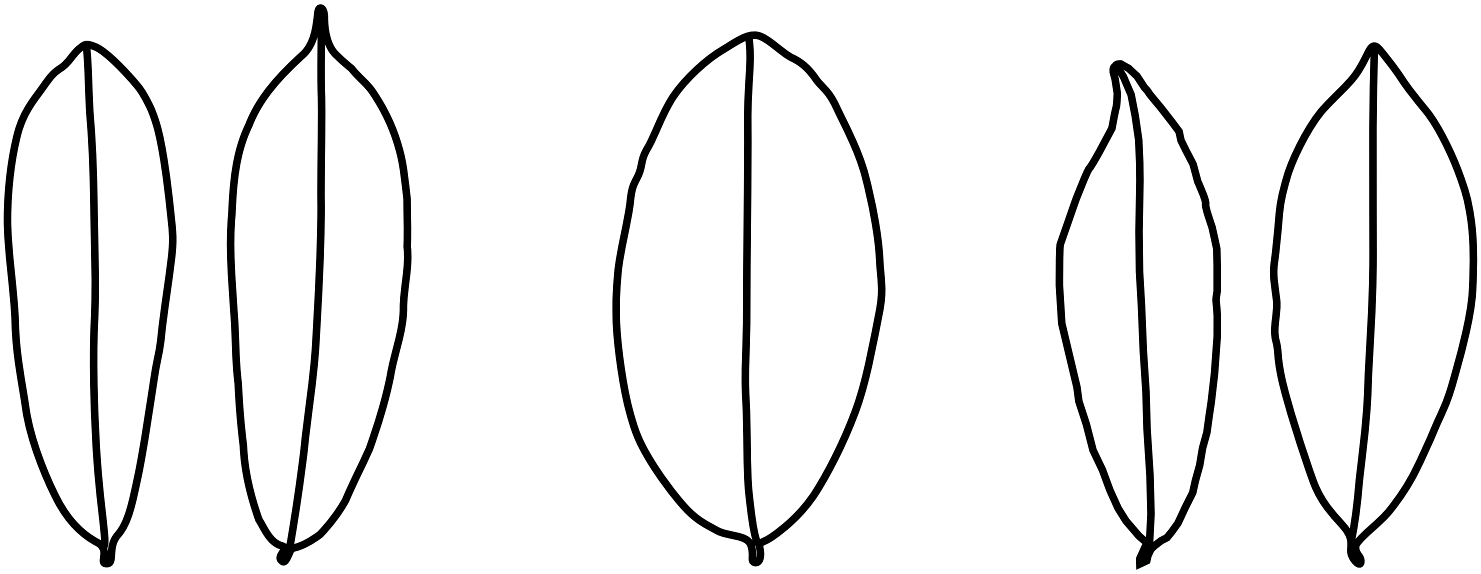
Lanceolate
Crudia penduliflora
(specimen Ridley 15539)

Figure I.4: Leaflets morphology



Crudia curtisii

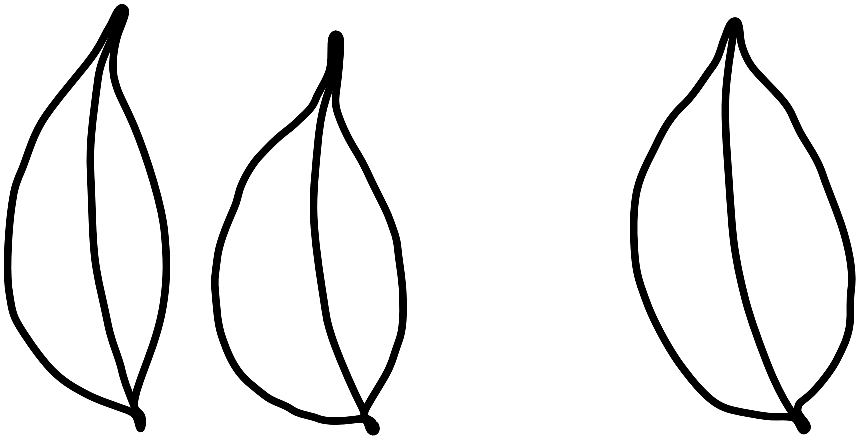
Crudia blancoi



Crudia bantamensis

Crudia papuana

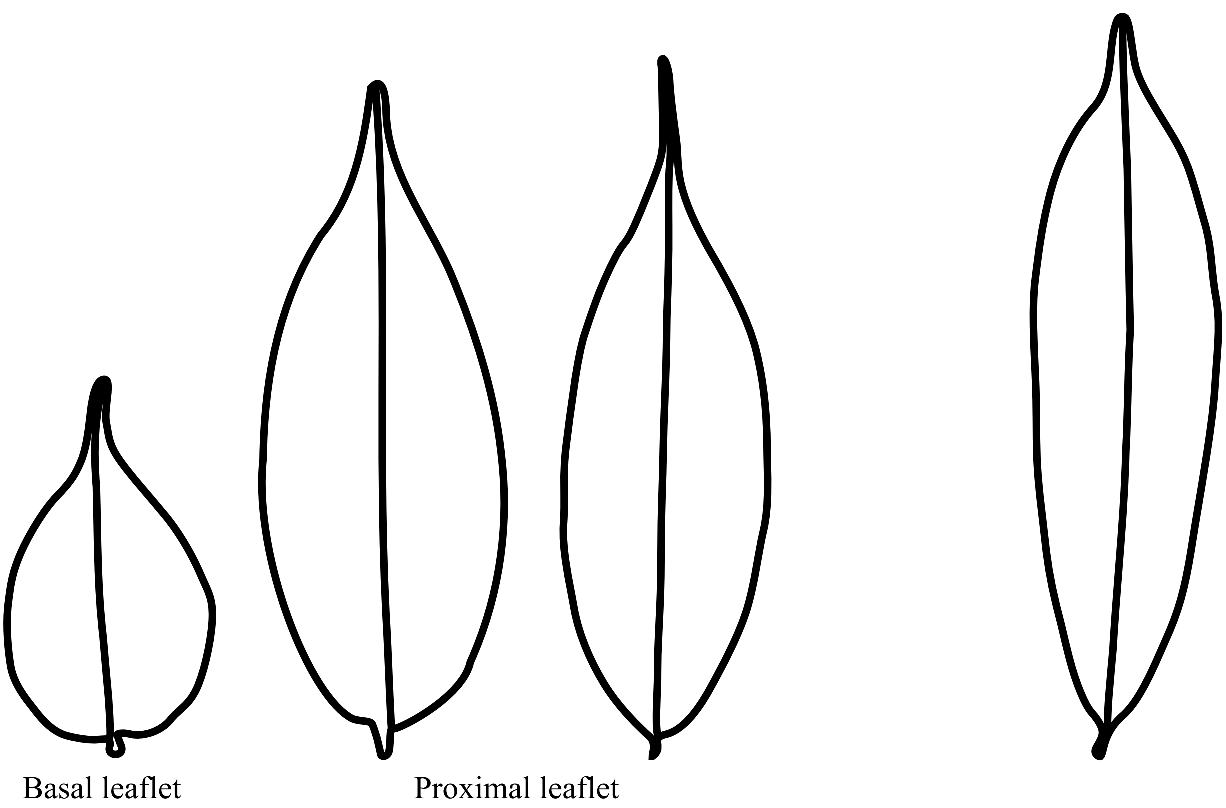
Crudia gracilis



Crudia curvosa

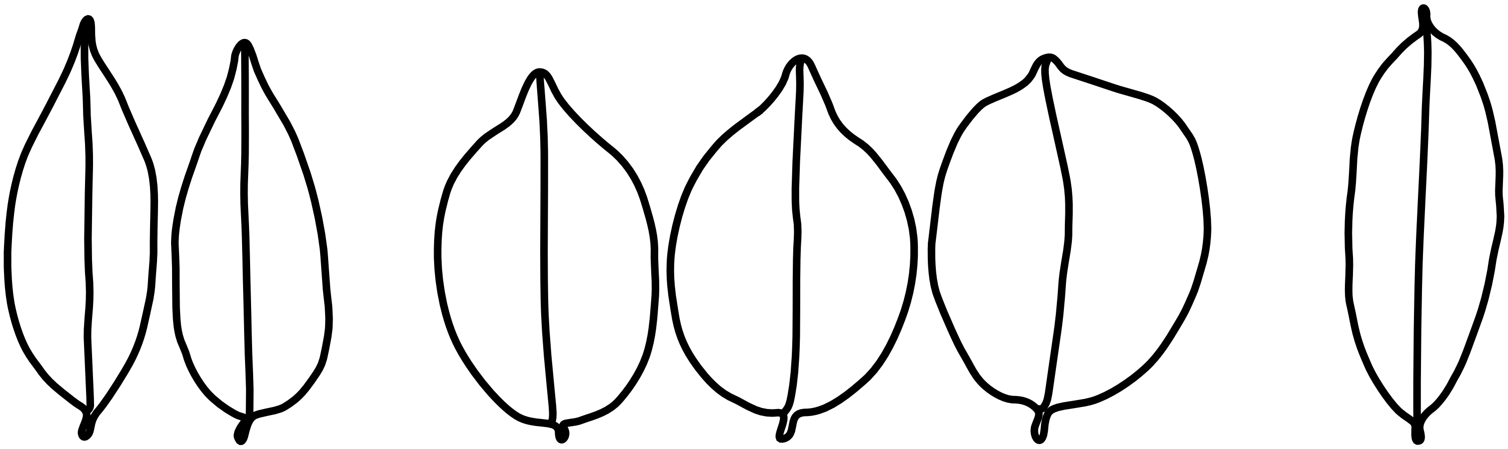
Crudia tenuipes

Figure I.4 (continued)



Crudia caudata

Crudia penduliflora



Crudia abbreviata

Crudia zeylanica

Crudia ornata

Table I.1: Species of the genus *Crudia* Schreb. by chronologic order of publication, with newly circumscribed names.

Names in blue indicate the previous name is identical to the new one; names in black show a change from one study to the next one.

chronologic reference	**described species**	**old nomenclature (valid name)**	**new nomenclature (our study)**	**type locality & species distribution**
(Aublet 1775a)	*Apalatoa spicata* Aublet	*Crudia spicata* (Aublet) Willdenow	*Crudia spicata* (Aublet) Willdenow	America – French Guiana, forest
	Touchiroa aromatica Aublet	*Crudia aromatica* (Aublet) Willdenow	*Crudia aromatica* (Aublet) Willdenow	America – French Guiana, swampy forests
(Aublet 1775b)	*Parivoa tomentosa* Aublet	*Crudia tomentosa* (Aublet) Macbride	*Crudia tomentosa* (Aublet) Macbride	America – French Guiana, large river banks, in humid savanas, down to mountains
(Linné et al. 1799)	*Crudia spicata* (Aublet) Willdenow	*Crudia spicata* (Aublet) Willdenow	*Crudia spicata* (Aublet) Willdenow	America – French Guiana
	Crudia aromatica (Aublet) Willdenow	*Crudia aromatica* (Aublet) Willdenow	*Crudia aromatica* (Aublet) Willdenow	America – French Guiana
(de Candolle 1825)	*Crudia parivoa* DC.	*Crudia tomentosa* (Aublet) Willdenow	*Crudia tomentosa* (Aublet) Willdenow	America – French Guiana
(Bentham 1840)	*Crudia bracteata* Bentham	*Crudia bracteata* Bentham	*Crudia bracteata* Bentham	America – French Guiana
(Steudel 1843)	*Hirtella glaberrima* Steudel	*Crudia glaberrima* (Steudel) Macbride	*Crudia glaberrima* (Steudel) Macbride	America
(Bentham 1844)	*Crudia acuminata* Bentham	*Crudia acuminata* Bentham	*Crudia acuminata* Bentham	America – Central America
	Crudia oblonga Bentham	*Crudia oblonga* Bentham	*Crudia oblonga* Bentham	America – Cayenne
(Hasskarl 1844)	*Crudia orientalis* Hasskarl*	*doubtful species*	*doubtful species*	Asia
(Blanco 1845)	*Crudia spicata* Willdenow *sensu* Blanco	*Crudia blancoi* Rolfe	*Crudia blancoi* Rolfe	Asia – Philippines, Manilla, Parañaque
(Hasskarl 1855)	*Touchiroa bantamensis*	*Crudia bantamensis*	*Crudia bantamensis*	Asia

	Hasskarl	(Hasskarl) Bentham	(Hasskarl) Bentham	
(Miquel 1855)	*Pryona bantamensis* Miquel	*Crudia bantamensis* (Hasskarl) Bentham	*Crudia bantamensis* (Hasskarl) Bentham	Asia – Sumatra
(Grisebach 1864)	*Crudia obliqua* Grisebach	*Crudia glaberrima* (Steudel) Macbride	*Crudia glaberrima* (Steudel) Macbride	America – Trinidad, swamps
(Bentham 1865)	*Crudia bantamensis* (Hasskal) Bentham	*Crudia bantamensis* (Hasskal) Bentham	*Crudia bantamensis* (Hasskal) Bentham	Asia – Java
	Crudia senegalensis Planchon	*Crudia senegalensis* Planchon ex Bentham	*Crudia senegalensis* Planchon ex Bentham	Africa – Senegambia (Senegal + Gambia), rivers
	Crudia zeylanica Bentham	*Crudia zeylanica* (Thwaites) Bentham	*Crudia zeylanica* (Thwaites) Bentham	Asia – Ceylon (Sri Lanka)
(Baillon 1870)	*Apalatoa bantamensis* (Hasskarl) Baillon	*Crudia bantamensis* (Hasskarl) Bentham	*Crudia bantamensis* (Hasskarl) Bentham	Asia
(Martius 1870)	*Crudia obliqua* Grisebach	*Crudia glaberrima* (Steudel) Macbride	*Crudia glaberrima* (Steudel) Macbride	America – Cayenne, Suriname, Guyana
	Crudia amazonica Spruce Mss	*Crudia amazonica* Spruce ex Bentham	*Crudia amazonica* Spruce ex Bentham	America – Manaus, Santarem
	Crudia pubescens Spruce Mss	*Crudia oblonga* Bentham	*Crudia oblonga* Bentham	America – Amazon, Santarem, Manaus
(Rolfe 1884)	*Crudia blancoi* Rolfe	*Crudia blancoi* Rolfe	*Crudia blancoi* Rolfe	Asia – Philippines
(Taubert 1891)	*Apalatoa amazonica* (Spruce ex Bentham) Taubert	*Crudia amazonica* Spruce ex Bentham	*Crudia amazonica* Spruce ex Bentham	America
	Apalatoa pubescens (Bentham) Taubert	*Crudia oblonga* Bentham	*Crudia oblonga* Bentham	America
(King 1897)	*Crudia speciosa* Prain	*Crudia speciosa* Prain	*Crudia zeylanica* (Thwaites) Bentham	Asia – Thailand
	Crudia scortechinii Prain	*Crudia scortechinii* Prain	*Crudia curtisii* Prain	Asia – Malay Peninsula
	Crudia caudata Prain	*Crudia caudata* Prain	*Crudia caudata* Prain	Asia – Borneo
	Crudia curtisii Prain	*Crudia curtisii* Prain	*Crudia curtisii* Prain	Asia – Malay Peninsula
	Crudia wrayi Prain	*Crudia wrayi* Prain	doubtful species	Asia – Malay Peninsula

	Crudia gracilis Prain	*Crudia gracilis* Prain	*Crudia gracilis* Prain	Asia – Malay Peninsula
	Crudia glauca Prain	*Crudia curtisii* Prain	*Crudia curtisii* Prain	Asia – Malay Peninsula
(Pierre 1898)	*Apalatoa chrysantha* Pierre	*Crudia chrysantha* (Pierre) K.Schum.	*Crudia zeylanica* (Thwaites) Bentham	Asia – Vietnam
(Schumann 1900)	*Crudia chrysantha* (Pierre) K.Schum.	*Crudia chrysantha (Pierre) K.Schum.*	*Crudia zeylanica* (Thwaites) Bentham	Asia
(Prain 1904)	*Crudia havilandii* Prain	*Crudia wrayi* Prain	*doubtful species*	Asia – Malay Peninsula
	Crudia mansonii Prain	*Crudia mansonii* Prain	*Crudia penduliflora* Ridley	Asia – Thailand
(Merrill 1905)	*Apalatoa blancoi* (Rolfe) Merrill	*Crudia blancoi* Rolfe	*Crudia blancoi* Rofle	Asia – Philippines
(de Wildeman et al. 1905)	*Crudia gabonensis* Harms*	*Crudia gabonensis* Pierre ex De Wild.	*Crudia gabonensis* Pierre ex De Wild.	Africa
	Crudia zenkeri Harms	*Crudia zenkeri* Harms ex De Wild	*Crudia zenkeri* Harms ex De Wild	Africa
	Crudia senegalensis Planch.	*Crudia senegalensis* Planch. ex Benth.	*Crudia senegalensis* Planch. ex Benth.	Africa
(Urban 1909)	*Crudia antillana* Urban	*Crudia spicata (Aublet) Willdenow*	*Crudia spicata (Aublet) Willdenow*	America – Jamaica
(Merrill 1910)	*Crudia subsimplicifolia* Merrill	*Crudia subsimplicifolia* Merrill	*Crudia gracilis* Prain	Asia – Philippines, Luzon
(Harms 1910)	*Crudia ledermannii* Harms	*Crudia ledermannii* Harms	*Crudia ledermannii* Harms	Africa – West Africa
(Harms 1911)	*Crudia gabonensis* Pierre	*Crudia gabonensis* Pierre ex De Wild.	*Crudia gabonensis* Pierre ex De Wild.	Africa – Gabon
	Crudia zenkeri Harms	*Crudia zenkeri* Harms ex De Wild	*Crudia zenkeri* Harms ex De Wild	Africa – Cameroon
	Crudia senegalensis Planch.	*Crudia senegalensis* Planch. ex Benth.	*Crudia senegalensis* Planch. ex Benth.	Africa
(Ridley 1912)	*Crudia penduliflora* Ridley	*Crudia penduliflora* Ridley	*Crudia penduliflora* Ridley	Asia – Malay Peninsula
(Lecomte et al.	*Crudia chrysantha* var	*Crudia chrysantha*	*Crudia zeylanica*	Asia – Vietnam

1913)	*harmandii* (Pierre) Gagnepain	(Pierre) K.Schum.	(Thwaites) Bentham	
(de Wildeman 1914)	*Crudia harmsiana* De Wildeman	*Crudia harmsiana* De Wildeman	*Crudia harmsiana* De Wildeman	Africa – Congo Belge
(Merrill 1916)	*Crudia tenuipes* Merrill	*Crudia tenuipes* Merrill	*Crudia tenuipes* Merrill	Asia – Borneo
(Ridley 1917)	*Crudia lanceolata* Ridley	*Crudia lanceolata* Ridley	*Crudia penduliflora* Ridley	Asia – Malay Peninsula
(Merrill 1918)	*Crudia reticulata* Merrill	*Crudia reticulata* Merrill	*Crudia bantamensis* (Hasskarl) Bentham	Asia – Borneo
(Macbride 1919)	*Crudia glaberrima* (Steudel) Macbride	*Crudia glaberrima* (Steudel) Macbride	*Crudia glaberrima* (Steudel) Macbride	Asia
	Crudia tomentosa (Aublet) Macbride	*Crudia tomentosa* (Aublet) Macbride	*Crudia tomentosa* (Aublet) Macbride	Asia
(De Wildeman 1920)	*Crudia gabonensis* Pierre ex De Wildeman	*Crudia gabonensis* Pierre ex De Wildeman	*Crudia gabonensis* Pierre ex De Wildeman	Africa – Gabon
	Crudia zenkeri Harms	*Crudia zenkeri* Harms ex De Wildeman	*Crudia zenkeri* Harms ex De Wildeman	Africa – West Africa
	Crudia laurentii De Wildeman	*Crudia laurentii* De Wildeman	*Crudia laurentii* De Wildeman	Africa – West Africa
	Crudia klainei Pierre ex De Wildeman	*Crudia klainei* Pierre ex De Wildeman	*Crudia klainei* Pierre ex De Wildeman	Africa – Gabon
(Ridley 1920b)	*Crudia brevipes* Ridley	*Crudia gracilis* Prain	*Crudia gracilis* Prain	Asia – Malay Peninsula
(Ridley 1920a)	*Crudia evansii* Ridley	*Crudia evansii* Ridley	*Crudia gracilis* Prain	Asia – Thailand, Malay peninsula
(Ducke 1922)	*Crudia aequalis* Ducke	*Crudia aequalis* Ducke	*Crudia aequalis* Ducke	America – Amazon
(Standley 1923)	*Apalatoa choussyana* Standley	*Crudia choussyana* Standley	*Crudia acuminata* Bentham	America – Salvador
(Standley 1929)	*Crudia choussyana* Standley	*Crudia choussyana* Standley	*Crudia acuminata* Bentham	America – Salvador

(Ridley 1929)	*Crudia velutina* Ridley	*Crudia velutina* Ridley	*Crudia gracilis* Prain	Asia – Borneo
	Crudia becarrii Ridley	*Crudia becarrii Ridley*	*Crudia penduliflora* Ridley	Asia – Java
(Kleinhoonte 1933)	*Crudia unifoliata* Kleinhoonte	*Crudia aromatica* (Aublet) Willdenow	*Crudia aromatica* (Aublet) Willdenow	Asia
(Hosokawa 1938)	*Crudia cynometroides* Hosokawa	*Crudia cynometroides* Hosokawa	*Crudia cynometroides* Hosokawa	Asia – Palau
(Standley et al. 1940)	*Crudia lacus* Standley & Steyermark	*Crudia lacus* Standley & Steyermark	*Crudia acuminata* Bentham	America – Central America
(De Wit 1950)	*Crudia ripicola* De Wit	*Crudia ripicola* De Wit	*Crudia penduliflora* De Wit	Asia – Borneo
	Crudia teysmannii De Wit	*Crudia teysmannii* De Wit	*Crudia gracilis* Prain	Asia – Sumatra, Borneo
	Crudia acuta De Wit	*Crudia acuta* De Wit	*Crudia acuta* De Wit	Asia - Sumatra
	Crudia venenosa De Wit	*Crudia venenosa* De Wit	*Crudia ornata* De Wit	Asia – Borneo
	Crudia splendens De Wit	*Crudia splendens* De Wit	doubtful species	Asia - Borneo
	Crudia mutabilis De Wit	*Crudia mutabilis* De Wit	*Crudia penduliflora* Ridley	Asia – Sumatra, Java
	Crudia ornata De Wit	*Crudia ornata* De Wit	*Crudia ornata* De Wit	Asia – Borneo
	Crudia bracteolosa De Wit	*Crudia caudata* Prain	*Crudia caudata* Prain	Asia – Borneo
(Léonard 1950b)	*Crudia michelsonii* J.Léonard	*Crudia michelsonii* J.Léonard	*Crudia michelsonii* J.Léonard	Africa – Congo
(Merrill 1954)	*Crudia cauliflora* Merrill	*Crudia cauliflora* Merrill	*Crudia cauliflora* Merrill	Asia – Philippine islands
(Kostermans 1962)	*Crudia papuana* Kostermans	*Crudia papuana* Kostermans	*Crudia papuana* Kostermans	Asia – New Guinea
	Crudia dewitii Kostermans	*Crudia dewitii* Kostermans	*Crudia papuana* Kostermans	Asia – New Guinea
(Whitmore	*Crudia sparei* Whitmore	*Crudia sparei*	*Crudia gracilis* Prain	Asia – Malay peninsula

1969)		Whitmore		
(Whitmore et al. 1973)	*Crudia viridiflora* Whitmore	*Crudia viridiflora* Whitmore	doubtful species	Asia – Malay Peninsula
(Verdcourt 1978)	*Crudia katikii* Verdcourt	*Crudia katikii* Verdcourt	*Crudia gracilis* Prain	Asia – Papua New Guinea
(Lock 1989)	*Crudia bibundina* Harms	*Crudia ledermannii* Harms	*Crudia ledermannii* Harms	Africa – West Africa
(Sanjappa 1994)	*Crudia balachandrae* Sanjappa	*Crudia balachandrae* Sanjappa	*Crudia balachandrae* Sanjappa	Asia – great Nicobar Island
(Breteler et al. 2008)	*Crudia liberica* Breteler & Nguema	*Crudia liberica* Breteler & Nguema	*Crudia liberica* Breteler & Nguema	Africa – West Africa
	Crudia letouzeyi Breteler & Nguema	*Crudia letouzeyi* Breteler & Nguema	*Crudia letouzeyi* Breteler & Nguema	Africa – West Africa
(Bean 2010)	*Crudia abbreviata* A.R.Bean	*Crudia abbreviata* A.R.Bean	*Crudia abbreviata* A.R.Bean	Asia – Australia, Queensland, Cape York Peninsula

*in observation only, without description

Table I.2 : Geographic location and voucher specimens for Asian species of Crudia

Species	Longitude	Latitude	Voucher ID*	Herbarium
Crudia abbreviata A.R.Bean	141.11666666666667	-8,6333333	Ridsdale NGF33512	K
	142.16666666666666	-13.4166667	Hyland 3079	K
	142.64083333333332	-12.4552778	Gray 08932	K
Crudia bantamensis (Hassk.) Benth.	112.75	-0.683333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982026	L
	112.833333	-0.716667	http://data.biodiversitydata.nl/naturalis/specimen/L.1982010	L
	116.31944444444444	0.2497222	Lee SL403	K
	116.819556	-1.099389	http://data.biodiversitydata.nl/naturalis/specimen/L.3894794	L
	116.833333	-1.133333	http://data.biodiversitydata.nl/naturalis/specimen/L.3814807	L
	116.939731	-0.989192	http://data.biodiversitydata.nl/naturalis/specimen/L.3895583	L
	117.0	-1.0	http://data.biodiversitydata.nl/naturalis/specimen/L.1982132	L
	117.495833	4.933333	http://medialib.naturalis.nl/file/id/L.1982028/format/large	L
	117.7875	4.6375	http://data.biodiversitydata.nl/naturalis/specimen/L.1982425	L
	117.808333	5.470833	http://data.biodiversitydata.nl/naturalis/specimen/L.1982029	L
	117.916667	5.833333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982021	L
	117.983333	5.866667	http://data.biodiversitydata.nl/naturalis/specimen/L.1981978	L
	118.341667	4.341667	http://data.biodiversitydata.nl/naturalis/specimen/L.1982423	L
	118.466667	4.633333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982422	L
Crudia caudata Prain	101.75	6.5	http://data.biodiversitydata.nl/naturalis/specimen/L.1982149	L

	109.95	-1.25	http://data.biodiversitydata.nl/naturalis/specimen/L.1982153	L
	114.416667	4.283333	http://data.biodiversitydata.nl/naturalis/specimen/L.3884887	L
Crudia gracilis Prain	112.05	0.833333	http://data.biodiversitydata.nl/naturalis/specimen/L.3894125	L
	118.333333	4.966667	http://medialib.naturalis.nl/file/id/L.1982030/format/large	L
	112.666667	-1.250000	http://medialib.naturalis.nl/file/id/L.1982368/format/large	L
	113.766667	-1.933333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982366	L
	114.31666666666666	4.4333333	Dransfield 6799	K
	114.683333	4.2	http://data.biodiversitydata.nl/naturalis/specimen/L.1982139	L
	114.68333333333334	4.2	Sands 5978	K
	117.283333	2.083333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982416	L
	145.416667	-5.166667	http://medialib.naturalis.nl/file/id/L0018867_MLN/format/large	L
	145.58333333333334	-5.1666667	Katik NGF46837	K
Crudia penduliflora Ridley	114.383333	-2.183333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982137	L
	114.38333333333334	-2.1833333	Sidiyasa 2616	K
Crudia ornata De Wit	117.533333	5.483333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982060	L
	117.716667	4.416667	http://data.biodiversitydata.nl/naturalis/specimen/L.1982053	L
	117.945833	4.4625	http://data.biodiversitydata.nl/naturalis/specimen/L.1982054	L
Crudia papuana Kosterm.	142.25	-10.9166667	Hyland 10245	K
	142.25	-10.916667	http://data.biodiversitydata.nl/naturalis/specimen/L.3892357	L
	143.000000	-9.000000	http://medialib.naturalis.nl/file/id/L0018870_MLN/format/large	L
	143.25	-8,9166667	Womersley NGF37163	K
	143.25	-8.916667	http://data.biodiversitydata.nl/naturalis/specime	L

			n/L.1982032	
Crudia tenuipes Merrill	112.36	-0.61	http://data.biodiversitydata.nl/naturalis/specimen/L.3885612	L
	115.75	5.35	http://data.biodiversitydata.nl/naturalis/specimen/L.1982391	L
	117.183333	1.916667	http://medialib.naturalis.nl/file/id/L.1982395/format/large	L
	117.183333	1.883333	http://medialib.naturalis.nl/file/id/L.1982396/format/large	L
	117.216667	1.916667	http://data.biodiversitydata.nl/naturalis/specimen/L.1982345	L
	117.408333	4.616667	http://medialib.naturalis.nl/file/id/L.1982385/format/large	L
	117.425	5.825	http://data.biodiversitydata.nl/naturalis/specimen/L.1982379	L
	117.483333	4.408333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982387	L
	117.533333	0.783333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982346	L
	117.55	0.816667	http://data.biodiversitydata.nl/naturalis/specimen/L.1982347	L
	117.7875	4.6375	http://data.biodiversitydata.nl/naturalis/specimen/L.1982404	L
	117.950000	4.416667	http://medialib.naturalis.nl/file/id/L.1982407/format/large	L
	118.004167	4.275	http://data.biodiversitydata.nl/naturalis/specimen/L.1982380	L
	118.333333	4.966667	http://medialib.naturalis.nl/file/id/L.1982409/format/large	L
Crudia zeylanica (Thw.) Benth.	105.707889	17.499444	http://data.biodiversitydata.nl/naturalis/specimen/L.1982100	L
	106.49594329439844	13.772700090043717	voucher unknown	?

Chapitre II : Systematics and biogeography of the pantropical genus *Crudia* (Leguminosae, Detarioideae)

Boris Domenech[1], Manuel de la Estrella[2,6], Luciano Paganucci de Queiroz[3], Rafael Barbosa Pinto[4], Cristiane Snak[3], Royce Steeves[5], Anne Bruneau[1]

[1]Institut de Recherche en Biologie Végétale and Département de sciences biologiques, Université de Montréal, 4101 Sherbrooke Est, Montréal, Québec, H1X2B2, Canada
[2]Comparative Plant and Fungal Biology Department, Royal Botanic Gardens, Kew, Richmond, TW9 3DS, United Kingdom
[3]Universidade Estadual de Feira de Santana, Departamento de Ciências Biológicas, Av. Transnordestina, s/n, Novo Horizonte, 44036-900 Feira de Santana, Bahia, Brazil
[4]Instituto de Ciências Biológicas I, Universidade Federal de Goiás Campus II - Samambaia, saída para Nerópolis – Km 13, Chácaras Califórnia, 74001-970, Goiânia – Goiás, Brazil
[5]Department of Fisheries and Oceans Canada, Gulf Fisheries Center, 343 Université Avenue, P.O. Box 5030, Moncton, NB, E1C 9B6
[6]Departamento de Botánica, Ecología y Fisiología Vegetal, Facultad de Ciencias, Campus de Rabanales, Universidad de Córdoba, 14071, Córdoba, Spain

Résumé

Connaitre les modalités de l’évolution de lignées possédant une distribution étendue, reliée à des évènements géologiques et climatiques passés, nous permet de mieux comprendre l’histoire de la vie sur Terre. La présente étude apporte de nouvelles connaissances à propos de la systématique et de la biogéographie du genre pantropical *Crudia* (Leguminosae, Detarioideae) à l’aide de cinq marqueurs nucléaires (ETS, ITS, *AGT1, AIGP, CALTL*) et d’un échantillonnage presque complet des espèces. Des méthodes d’inférence bayésienne ont été utilisées pour reconstruire les relations phylogénétiques entre les espèces. Nos analyses phylogénétiques montrent que *Crudia* est monophylétique, avec une structure interne révélant un clade regroupant les espèces asiatiques et un autre regroupant les espèces africaines et américaines. Si la délimitation des espèces via des méthodes de phylogénie moléculaire et de taxonomie traditionnelle engendre des résultats congruents, il est en revanche difficile de résoudre les relations entre les espèces au sein de chaque clade, particulièrement dans le cas du clade asiatique. Les espèces américaines sont plus facilement différenciables entre elles grâce à plusieurs caractères morphologiques et moléculaires. Les analyses biogéographiques indiquent que le genre *Crudia* provient initialement d'Afrique, comme la majorité des Detarioideae. Les analyses de datation montrent une apparition lors de l'Éocène puis un établissement indépendant en Amérique du Sud et en Asie du Sud Est, via des voies terrestres en empruntant des routes migratoires passant par les boréotropiques, ou via dispersion océanique sur de longues distances.

Mots clés : Boréotropiques, datation, dispersion longue distance, distribution pantropicale, ITS, ETS, *AGT1*, *AIGP*, *CALTL*, Leguminosae, taxonomie, phylogénie

Abstract

Studying the evolution of widely distributed lineages in conjunction with past geological events and climatic features leads to a better understanding of life's history on Earth. Here, we investigate the systematic and biogeography of the pantropical genus *Crudia* (Leguminosae, Detarioideae) using five nuclear markers (ETS, ITS, *AGT1, AIGP, CALTL*) and an exhaustive, nearly complete species sampling. We used Bayesian inference to reconstruct phylogenetic relationships between species. Our phylogenetic analysis strongly supports *Crudia* as monophyletic, with an internal structure resolving one clade of Asian species and another of African and American ones. While species assignments using both molecular phylogeny and traditional taxonomy are congruent, relationships among species within each clade remain mostly unresolved, particularly for Asian species. American species are more easily discriminated based on molecular features and morphological characters. Biogeographical analyses indicate the genus *Crudia* originated in Africa, like most Detarioideae. Divergence time analyses show the genus *Crudia* appeared during the Eocene, then arrived independently in South America and Southeastern Asia, either through terrestrial boreotropical migration or oceanic long distance dispersal.

Key words: Boreotropics, divergence time analysis, long distance dispersal, pantropical distribution, ITS, ETS, *AGT1*, *AIGP*, *CALTL*, Leguminosae, Taxonomy, Phylogeny

II.1 – Introduction

The study of biogeography aims to reconstruct the history of life on Earth, leading to an understanding of how life and Earth evolved together through time (Wen et al. 2013). Species are not distributed randomly across the Earth, but rather occur in recurrent patterns, found repeatedly in several taxonomic groups (Anderson 1994). Species areas range from narrow, insular, and endemic (Beheregaray et al. 2004, Givnish et al. 2009, Nie et al. 2013, Armstrong et al. 2014, Smedmark et al. 2014, Andriananjamanantsoa et al. 2016) to broad, world-wide distributions (Dick et al. 2007, Razafimandimbison et al. 2010, Takayama et al. 2013, Smedmark et al. 2014). Some angiosperms are restricted to tropical latitudes, but are present on more than one continent. This pattern referred to as a pantropical distribution and can be observed at various taxonomic levels (Thorne 1972, Baker et al. 2013a, Couvreur et al. 2013, Takayama et al. 2013). Angiosperm families such as Malpighiaceae, Annonaceae, Myristicaceae, Arecaceae (Davis et al. 2002, Davis et al. 2004, Doyle et al. 2004, Couvreur et al. 2011b), genera like *Diospyros* L., *Canavalia* Adans. (Good 1927, 1974, Duangjai et al. 2009, Snak et al. 2016) and even some species like *Ceiba pentandra* L., *Cocos nucifera* L. (Dick et al. 2007, Harries et al. 2014) can display pantropical distribution patterns. Due to the distances between continents, pantropical distributions are necessarily disjunct: oceans and seas interrupt terrestrial communication between landmasses. Attempts to explain disjunct pantropical distributions must take several processes into account, accounting for the age, ecology and evolutionary history of the taxon.

The break-up of Gondwana (Raven et al. 1974), starting in the early Cretaceous and ending at the Palaeogene/Neogene boundary (Jokat et al. 2003), is hypothesized to be responsible for some disjunct pantropical distributions, especially in old clades like ferns (Korall et al. 2014). Particularly, Gondwanian vicariance is one phenomenon used to explain the currently disjunct distribution of Mesozoic-originating animal taxa such as crocodiles, lungfishes, and plant taxa such as Cupressaceae, found on distant continents (e.g. Turner (2004), Upchurch (2008), Mao et al. (2012)). However, other phenomena responsible for pantropical disjunct distributions also exist, such as long distance dispersal through the boreotropics. This hypothesis proposes that pantropical distribution patterns can be explained by dispersal of individuals between distant places through terrestrial migration (Givnish et al. 2004). Dispersal of this type likely took place as a result of northern terrestrial connections such as the Bering land bridge which linked Asia and Western North America until the Pliocene, and via the Trans-Atlantic land Bridge (also called the Thulean Route), which connected Europe and North America from the late Paleocene to early Eocene (Sanmartin et al. 2001, Morley 2003, Brikiatis 2014, Wen et al. 2016). Stepping stone processes using islands are also probably responsible for dispersal from Africa to Europe through the Tethys Sea (Morley 2003) during the Eocene. Although the Tethys seaway was already closing at that time, ephemeral islands rose and sank between Africa and Europe (Scotese 2014), likely providing dispersal paths for angiosperms. Tropical fossils (Wolfe 1975) belonging to high-latitude rainforests (Wolfe 1971, Davis et al. 2004, Erkens et al. 2009) testify to the existence of those northern paths. These migration processes are thought to have played a major role in the development of a number of distinct tropical plant families such as Symplocaceae (Fritsch et al. 2015), Malpighiaceae (Davis et al. 2004), and Annonaceae (Couvreur et al. 2011b).

Many recent taxa that likely appeared during the Miocene (e.g. long after continents drifted away from each other), such as *Paederia* Puff (Rubiaceae), *Thespesia* Sol. ex Corrêa (Malvaceae, Gossypieae), *Trichosanthes* L (Cucurbitaceae). (Nie et al. 2013, de Boer et al. 2015, Areces-Berazain et al. 2016), have disjunct tropical distributions attributed not to boreotropical dispersal but instead to oceanic long distance dispersal (Renner 2004, de Queiroz 2005a, Nathan 2006, Nathan et al. 2008, de Queiroz 2014). Because these genera are too young to have undergone boreotropical migration, long distance dispersal through oceans is a more likely explanation to the observed distribution pattern. Furthermore, several studies have demonstrated that, unlike previously thought, long distance oceanic dispersals are a rare but non-random process (Higgins et al. 2003, Nathan et al. 2011, Gillespie et al. 2012) and might be considered as one explanation for disjunct distributions of recently diverged clades.

Reconstructing biogeographic history can be a hampered by many factors, including the presence of lineages with incomplete taxon sampling (Clark et al. 2008) or with a weak fossil record (Sauquet et al. 2012, Wen et al. 2013). These issues can be particularly problematic at the family-level (Davis et al. 2002, Davis et al. 2004, Couvreur et al. 2011a, Couvreur et al. 2011b, Baker et al. 2013a, Couvreur et al. 2013). Rather than studying widespread families with potentially low taxonomic sampling coverage, we suggest that studies of disjunct distributed pantropical genera can be used to understand biogeographic history. Indeed, exhaustive taxonomic sampling is more likely to be achieved even in broadly distributed genera – except perhaps for very large genera, such as *Astragalus* L. (Scherson et al. 2005, Scherson et al. 2008). Similar biogeographical questions can be addressed at the generic level as at the family level, and generic level studies can provide a good framework to understand the dynamics and evolution of plant taxa in space and time.

Crudia Schreb. is one of the ten most species-rich genera in subfamily Detarioideae of the Leguminosae (Lewis et al. 2005, Bruneau et al. 2008, de la Estrella et al. 2017). The genus historically included about 55 species (De Wit 1950, Hou et al. 1996, Mackinder 2005, Breteler et al. 2008), however our recent taxonomic revision of Asian species brought the total number of species to 34 (Chap I) with ten species in Africa (Breteler et al. 2008), nine in South America (Amshoff 1953, Vieira 1990) and fifteen species in Southeastern Asia and the West Pacific Islands (Chap I; Fig. II.1). The number of species of *Crudia* is unusual among Detarioideae genera, since more than half of the 81 genera are monotypic or have fewer than 10 species (Mackinder 2005). In addition to this, the genus *Crudia* presents a pantropical distribution, whereas the majority of Detarioideae genera are restricted to Africa (around 58% of the genera, with 329 species (Mackinder 2005, de la Estrella et al. 2017)).

In Southeastern Asia, species are found westward of the Wallace Line, with the highest diversity in Borneo (see De Wit (1950)); species are also located eastward of the Wallace Line, in northern Australia and Papua New Guinea. De Wit (1950) noted that Asian *Crudia* species grow either in marshy, swampy, alluvial, periodically-to-near-periodically inundated areas, often close to riverbanks or seashores, or on never-inundated slopes with nutrient-poor soils. In Africa, Breteler et al. (2008) found most species in tropical lowland rainforests and gallery forests, at low altitudes, sometimes in swamp forests, bordering lagoons, rivers and seashores. African species are found all along the African west coast, from Guinée-Bissau to the Democratic Republic of Congo (Breteler et al. 2008), with the highest species diversity recorded for Cameroon, Equatorial Guinea and Gabon. In South America, Vieira (1990) described the habitats of *Crudia* as never-inundated forests on solid ground ("*mata de terra firme*") and seasonal lowland forests ("*mata de várzeas estacional*"), riverbanks, wetlands, seasonally flooded lands ("*igapó*"), estuaries, all at low altitudes. In South America, species are mostly located in the Brazilian Amazon basin, though species are also present in

Colombia, Venezuela, French Guiana, Guyana and Suriname (Amshoff 1939, 1953, Vieira 1990) and extending northward in Central America (Bentham 1844, Tucker 2001).

Previous studies of *Crudia* have focused on descriptive morphology and floristic accounts (Bentham 1840, 1844, 1865, Merrill 1905, 1910, Ridley 1911, 1912, Merrill 1916, Ridley 1917, Merrill 1918, Ridley 1920a, b, 1929, De Wit 1950, Merrill 1954, Sanjappa 1994, Hou et al. 1996, Bean 2010). Little is known about species relationships and global evolution of the genus. As only a few species have been included in previous phylogenetic broad scale analyses (Bruneau et al. 2008, de la Estrella et al. 2017) it is difficult to interpret interspecific relationships. Although Mackinder (2005) expressed doubts about its monophyly, the genus is currently considered monophyletic based on limited species sampling (de la Estrella et al. 2017, LPWG 2017).

Morphology based taxonomic treatments of *Crudia* were conducted independently in Africa (Breteler et al. 2008), South America (Amshoff 1953, Vieira 1990, Stergios 2002) and Southeastern Asia (De Wit 1950, Sanjappa 1994, Hou et al. 1996, Bean 2010)(also see Chap. I). However, no comprehensive molecular phylogenetic analysis currently exists for the whole genus, with only partial analysis in previous studies (Bruneau et al. 2001, Bruneau et al. 2008, de la Estrella et al. 2017, LPWG 2017). The pantropical distribution of *Crudia* raises questions about the processes underlying this distribution; a robust, generic level phylogenetic analysis is required to unravel the timing of disjunctions between species. Here, we assemble the largest dataset of DNA sequences of *Crudia* to date, with the intention of solving many issues related to the systematics and biogeography of the genus. First, we present a phylogenetic analysis of *Crudia* derived from nuclear DNA sequences to reveal new insights into species monophyly and intrageneric patterns. Second, we use this species level phylogeny as a framework to evaluate the biogeographic history of the genus and test whether the ancestral area of genus *Crudia* is Africa, as it is for subfamily Detarioideae (de la Estrella et al. 2017) and for numerous other genera in the subfamily, e.g. *Zenkerella* Taub., *Gilbertiodendron* J.Léonard, *Berlinia* Sol. ex. Hook.f, *Didelotia* Baill. (Mackinder 2005, Mackinder et al. 2006, Wieringa et al. 2013, de la Estrella et al. 2014). Third, we evaluate the possibility that biogeographic processes, such as boreotropical terrestrial dispersal (Wolfe 1975, Lavin et al. 1993, Davis et al. 2002, Erkens et al. 2009, Couvreur et al. 2011b, Thomas et al. 2015), and oceanic long distance dispersal (Renner 2004, de Queiroz 2005a, Nathan 2006, Nathan et al.

2008), together or separately, in relationship to past worldwide climatic phenomena, can explain distribution patterns in *Crudia*.

II.2 – Material and Methods

II.2.1 – Taxon sampling and outgroup selection

One hundred and twenty five specimens of *Crudia* were included in our analysis, representing seven of ten African species, 11 of 15 species from Asia and Oceania (Chap I), and all nine species from Central and South America. Globally, our sampling covers about 79% of *Crudia* species. Using Bruneau et al. (2008) as a guide to target closely related genera, we selected *Neochevalierodendron* J.Léonard*,* *Gilbertiodendron*, *Brownea* Jacq., *Leonardendron* Aubrév., *Hymenostegia* Harms., *Zenkerella* Taub. and *Leonardoxa* Aubrév. from subfamily Detarioideae as outgroup taxa to root our trees and to later identify the sister genus to *Crudia* (suppl. mat 1). Both silica gel-dried leaflets and herbarium specimens were used for DNA extraction.

II.2.2 – DNA extraction, PCR and sequencing

Whole genomic DNA was extracted following a modified CTAB method from Doyle (1991) in which DNA was precipitated onto paramagnetic beads using PEG 8000 rather than with isopropyl alcohol and centrifugation. For some specimens, we used the commercial Macherey Nagel NucleoSpin® Plant II (ref. 740770.50) extraction kit (Toronto, ON). We confirmed that both methods produced an equal amount of DNA, suitable for PCR amplification, by independently preparing some specimen extractions (e.g. specimen Kerr 19607) with both methods and comparing the PCR amplification signal. The amplification products obtained with the two extraction methods also resulted in the same signal quality after sequencing.

Three low copy nuclear loci were selected, *AGT1* coding for an enzyme responsible for catalyzing the alanine-glyoxylate aminotransferase reaction in peroxisomes (Li et al. 2008, Naumann et al. 2011), *AIGP* involved in Auxin-independent growth (Choi et al. 2004, Babineau et al. 2013), *CALTL* a putative calreticulin gene (Choi et al. 2006, Choi et al. 2013), the nuclear ribosomal internal transcribed spacer (ITS) and external transcribed spacer (ETS) regions. We initially used primers from Choi et al. (2006) for *AIGP* and *CALTL* and from Li et al. (2008) for *AGT1*. However, to increase primer specificity, we designed additional internal and specific primers for *Crudia* as follows: *AGT1*-Cru-R 5'-CCCAGAAGGCTCTTTCNCTC, *AGT1*-Cru-F 5'-CTGCCAGCCTGTATTTATCA, *AIGP*-Cru-R 5'-CCTTTAACTCCAGAAGAAGTTGGTC, *AIGP*-Cru-F 5'-GTGCCCGAAGTATCTCCTACAGGG, *CALTL*-Cru-R 5'-CCATTGATTGACAACCCAGGTT, *CALTL*-Cru-F 5'-GCAAGCAGCTTAGCATATTCCGG. For the ITS region, we used the AB101 and AB102 primers from Douzery et al. (1999). However, some specimens were not successfully amplified and required that we designed new internal primers as follows: ITS-B 5'-CACACCAAGTATCGCATTTCGC associated with AB101 for amplifying ITS1 only and ITS-C 5'-CTCTCGGCAACGGATATCTCG associated with AB102 for amplifying ITS2 only. For the ETS region, we used a primer from Baldwin et al. (1998), 18-IGS, located in the conserved IGS region, and another primer that we designed specifically for our study, ETS-Cru2 5'-TTCGTTTGCCCCTTCCCATCC. All the new primers were designed using the website tool Custom Primers - OligoPerfect™ Designer (Thermo Fisher Scientific 2017) and synthesized by Alpha DNA (Montréal, QC). For more exhaustive details, see Table II.1.

The following PCR protocols were used to amplify DNA, with some adjustments slightly different from industrial protocols. The PCR reactions for *AGT1*, *AIGP* and *CALTL* were carried out in 25µL reactions, each containing 1-2 µL template DNA, 7.2 µL Phire reaction buffer 5X (ref. F-524) (Fisher Scientific, Whitby, ON), 0.5 µL dNTPs (10mM) (Fisher Scientific), 1 µL Tween solution 10% (Fischer Scientific), 0.5 µL BSA (10mg/mL) (New England Biolab, Whitby, ON), 0.8 µL forward primer (10mM) (Alpha DNA, Montréal, QC), 0.8 µL reverse primer (10mM) (Alpha DNA), 1.5 µL 100% DMSO (Fisher Scientific), 0.2 µL Phire Hot Start II DNA Polymerase 1 X (Fisher Scientific), topped with ultrapure water (q.s.p. 25 µL). The PCR program included an initial denaturation step at 98°C for 30 sec; followed by 50 cycles of 10 sec denaturation at 98°C, 20 sec annealing at 54°C (*AGT1*), 56°C (*AIGP*), 58°C (*CALTL*), and 20 sec extension at 72°C. The cycle was terminated with an extension at 72°C for 1 min.

We used a slightly different PCR protocol for ITS and ETS. For ITS, PCR reactions were carried out in 25µL reactions, containing 1-2 µL template DNA, 7.2 µL Phire reaction buffer 5X (ref. F-524), 0.5 µL of dNTPs (10mM), 1.5 µL 100% DMSO (Fisher Scientific, Whitby, ON), 0.5 µL BSA (10mg/mL), 0.8 µL forward primer (10mM), 0.8 µL reverse primer (10mM), 0.2 µL Phire Hot Start II DNA Polymerase 1 X, topped with ultrapure water (q.s.p. 25 µL). For ETS, PCR reactions were carried out in 25µL reactions, containing 1-2 µL template DNA, 7.2 µL Phire reaction buffer 5X (ref. F-524), 0.5 µL dNTPs (10mM), 1.5 µL Tween solution 10%, 0.5 µL BSA (10mg/mL), 0.8 µL forward primer (10mM), 0.8 µL reverse primer (10mM), 0.2 µL Phire Hot Start II DNA Polymerase 1 X, topped with ultrapure water (q.s.p. 25 µL). The PCR program for ITS, ITS1 and ITS2 was an initial denaturation at 98°C for 3 min, followed by 30 cycles of 10 sec denaturation at 98°C, 15 sec annealing at 60°C, and 20 sec extension at 72°C. The cycle was terminated with an extension at 72°C for 1 min. The PCR program for ETS was an initial denaturation at 98°C for 3 min, followed by 35 cycles of 20 sec denaturation at 98°C, 20 sec annealing at 56°C, and 30 sec extension at 72°C. The cycle was terminated with an extension at 72°C for 2 min.

II.2.3 – Phylogenetic analyses

Contigs were assembled, using raw forward and reverse sequences, with the software Geneious version 7.1.7 (http://www.geneious.com, Kearse et al. (2012)). All sequences were subjected to a BLAST search in GenBank (Altschul et al. 1990) to ensure that they were indeed Leguminosae sequences.

Sequences were aligned with the MAFFT (v7.130b) software (Katoh et al. 2014) and checked visually with BioEdit (v7.2.5) (Hall 1999). In order to maximize species sampling and minimize the amount of missing data in our matrix, we kept only specimens for which we had sequences for at least three of five nuclear markers. All loci were analyzed separately to check for congruent phylogenetic signal and none of them produced phylogenetic conflict. ITS and ETS gave the highest resolved trees compared to *AIGP, AGT1* and *CALTL*, which produced less resolved phylogenies. A concatenated matrix was then built with sequences retrieved from the five markers giving congruent phylogenetic signal. Bayesian analyses were carried out using Markov Chain Monte Carlo (MCMC) methods implemented in MrBayes v.3.2 (Ronquist et al. 2012). Nucleotide substitution models for Bayesian analyses were evaluated separately for each marker using the Akaike information criterion (AIC) in MrModeltest v.2.3 (Nylander 2004). Different models were considered as best-fitting for each of the five markers: the GTR+G model for *AGT1*; the HKY+I model for *AIGP*; the HKY+G model for *CALTL*; the HKY+I+G model for ETS and the GTR+I+G model for ITS. Two parallel independent analyses were run for 10 million generations each. The Markov chains were sampled every 100 generations, resulting in 100,000 sampled trees from each chain. The trace files were inspected in Tracer v.1.6 (Rambaut et al. 2014), with a burn-in of 25%. We checked for chain convergence by retaining only analyses where ESS (effective sampling size) were higher than 200 after burn-in. The remaining trees were summarized into a majority-rule consensus tree including the posterior probabilities (PP) as branch support estimates. Computations were conducted on the supercomputer Briaree from Université de Montréal, managed by Calcul Québec and Compute Canada.

II.2.4 – Divergence time analysis

We conducted a divergence time analysis using the software BEAST v. 1.8.1 using the concatenated dataset containing 138 terminal taxa (125 *Crudia* specimens and 13 closely related outgroups) with an independent evolutionary model for each marker (Drummond et al. 2007). We used the graphic interface BEAUti v. 1.8.1 to create the .xml BEAST input file. An uncorrelated relaxed clock was applied for each marker and we chose a Birth-Death speciation model with Incomplete Sampling. Different priors were used for each calibration point. The first calibration point was placed at the root of the tree, and represents the age of the Legume family as reconstructed by Bruneau et al. (2008). We used a normal prior with an initial value set at 70 Ma, mean 65.5, standard deviation 1.0. The second calibration point was placed at the stem node of the American clade and represents two macrofossils of *Crudia* described in Herendeen et al. (1990): a fruit of *Crudia grahamiana* Herendeen & Dilcher, and a leaflet of *Crudia brevifolia* Herendeen & Dilcher. Both fossils were found in the same geological layer with an age of 45 Ma (Herendeen et al. 1990) and are thought to be related to American species based on their location (i.e. North America) and morphology (i.e. twisted petiolule, which is more pronounced in American species of *Crudia* than in Asian or African ones; microstructures of the leaf epidermis are also similar between fossils and living species; similarities in size and shape to fruits of current South American species like *Crudia glaberrima* and *C. acuminata*). We discarded other potential *Crudia* fossils found in the literature due to taxonomic uncertainty or inconclusive dating. For example, we considered including the pollen *Striatricolpites catatumbus* Gonzalez from Colombia (Gonzalez-Guzman 1967), and from the Paleocene of Nigeria (Adegoke et al. 1978) but diverging morphological features suggest that this pollen cannot be attributed to the genus *Crudia* (Banks, pers. comm.). There is also a potential microfossil from Panama (Eocene) belonging to *Crudia*, but without accurate taxonomic placement (Graham 1985) it could not be used in our analysis. Other fossils associated with the genus *Crudia* were found in Thailand during the Miocene (Songtham et al. 2003) and in Colombia during the Pliocene (Pons 1980), but were too young to be used as calibration points in our analysis. Using the fossils retrieved from the study of Herendeen et al. (1990), we used a normal prior with an initial value of 50 Ma, mean of 45, and standard deviation of 1.0 to restrain the age of the fossils. We used a normal prior as suggested by Ho et al. (2009): this reflects the flexible placement of *Crudia* fossils within the genus, as the fossils are known to be closer to American species but their exact phylogenetic placement is uncertain. We used a third calibration point, placed at the crown-node age of the [*Neochevalierodendron* + *Crudia*] clade. This calibration was determined by a divergence time analysis of Detarioideae (described further). We used a normal prior, with an initial value of 50 Ma, mean of 49.7, and standard deviation of 1.0. We set the analysis at 100 million generations, sampling every 10,000 generations. We used the phylogenetic tree obtained through the MrBayes analysis as a starting tree, previously transformed to be ultrametric with predefined branch lengths using the functions *chronos* and *multi2di* in the APE package for R (Paradis et al. 2004) to avoid negative likelihoods. Time-series plots of all parameters were analyzed in Tracer v.1.6 to check for adequate ESS (> 200), with 10% burn-in. We then used TreeAnnotator to summarize the information from a sample of trees produced by BEAST onto a single tree and retrieved a maximum clade credibility (MCC) consensus tree from our analysis.

II.2.5 – Ancestral area reconstruction

We assigned species to five geographical areas based on present day distributions (Fig. II.1) and natural biogeographic units (Morrone 2015): Central America with the Caribbean and South America were considered as two separate biogeographic areas based on historical features, particularly with the oceanic gap between the two areas prior to the closing of the Panama Isthmus (Iturralde-Vinent 2006, Montes et al. 2012, Bacon et al. 2013), although plants were still able to disperse even in the absence of a physical terrestrial link (Gentry 1982). We initially considered splitting Africa into two areas: the Congolian region and the Guinean region because they correspond to two areas of endemism (Linder et al. 2012) separated by the Dahomey Gap (Salzmann et al. 2005). However, since the Dahomey Gap is a very young barrier (de la Estrella et al. 2014, Demenou et al. 2016, Demenou et al. 2017) it did not seem appropriate to split Africa into two distinct areas. In Asia, we initially considered following the classification system of Turner et al. (2001) and Ung et al. (2016) but those studies highlighted endemism areas rather than biogeographic realms. We instead choose to follow the biogeographic units of Michaux (2010) and used the Wallace Line as a barrier between Southeastern Asia and Australasia, resulting in only two biogeographic areas in Asia.

We used the package BioGeoBEARS (Matzke 2016) for R (2014), to reconstruct the ancestral areas on the MCC tree obtained with BEAST. We tested the six reconstruction default models available in this package, and used the Akaike Information Criterion (AIC) to retain only the best-fitting model for our dataset. The maximum number of reconstructed ancestral areas at each node was set to two to avoid over-aggregating areas at deeper nodes, and to keep the reconstruction meaningful (Lawing et al. 2014, Bauret et al. 2017). We set four connectivity matrices in our analysis (Fig. II.2). Our oceanic dispersal model was set using past oceanic surface currents as a prior for areas connectivity and assigned various dispersal costs between areas depending on the reconstruction of the paleocurrents (Haq 1981). Additionally, our terrestrial dispersal model was set using past terrestrial physical bridges as a prior for area connectivity and assigned various dispersal costs between areas depending on the relative position of landmasses through time. Matrices were separated by two time slices, ranging from the Cretaceous to Late Eocene (70 to 30 Ma, shortened to "Eocene" in Fig. II.2) and from Late Eocene to present (30 Ma to present, shortened to "Miocene" in Fig. II.2).

II.2.6 – Divergence time analyses and ancestral area reconstruction at the subfamily level

External secondary calibration points were required to improve estimates of divergence times within *Crudia* at the species level. This was done by conducting a divergence time analysis with a broader outgroup sampling. In order to arrive at a calibration for the root of our phylogenetic divergence time analyses, we first used a reduced version of a dataset retrieved from de la Estrella et al. (2017). In particular, we wanted to determine the age of the divergence between *Crudia* and its sister group. We kept the alignment of ITS, *matK-trnK, rpl16, trnG-trnG2G* published by de la Estrella et al. (2017) but only retained 105 terminal taxa belonging to subfamily Detarioideae (reduced matrix in suppl. mat. 2), with at least one species per genus. This reduced dataset was used to conduct a divergence time analysis using BEAST version 1.8.1 (Drummond et al. 2012). First we carried out a Bayesian analysis to obtain a phylogenetic tree to be used as the starting tree in the BEAST analysis. The Bayesian analysis was carried out using Markov Chain Monte Carlo (MCMC) methods implemented in MrBayes v.3.2. We used the same parameters (i.e. nucleotide substitution models) as de la Estrella et al. (2017). Two parallel independent analyses were run for 20 million generations each. The Markov chains were sampled every 1,000 generation, resulting in 20,000 sampled trees from each chain. The trace files were analyzed in Tracer v.1.6 with a burn-in of 25%. The remaining trees were summarized into a majority rule consensus tree, then transformed to be ultrametric with predefined branch lengths using the *chronos* function in the APE package for R (Paradis et al. 2004) to avoid negative likelihood. We used the graphic interface BEAUti v.1.8.1 to create the BEAST file. An uncorrelated relaxed clock was applied for each marker under a Birth-Death speciation model with Incomplete Sampling. Eight calibration points were used. Seven of the calibration points were obtained from de la Estrella et al. (2017) and were used to constrain the BEAST analysis. All fossil calibration points were applied using a lognormal distribution with a mean of zero, a standard deviation of 1.0 and an offset value equivalent to the age of the fossil (Table II.2). The eighth calibration point was applied to the root of the tree using a normal distribution with a mean of 65.0 (age of the Legume family as estimated by Bruneau et al. (2008)), a standard deviation of 10.0, with an upper truncation of 71.0 to avoid overestimating the age of the tree. We set the analysis at 100 million generations, sampling every 10,000 generation. Time-series plots of all parameters were analyzed in Tracer v.1.6 to assess convergence of the runs by checking for adequate effective sample sizes (ESS > 200) with 10 % burn-in. We then used TreeAnnotator to summarize the information from a sample of trees produced by BEAST onto a single tree and retrieve a maximum clade credibility (MCC) consensus tree from our analysis (available in suppl. mat. 3).

To broaden the outgroup sampling for the ancestral area reconstruction and cross-check the estimation of the ancestral area of genus *Crudia*, we used the same subsampling of the subfamily Detarioideae, retrieved from de la Estrella et al. (2017) as in the divergence time analysis. We hypothesized that using a broader outgroup sampling may lead to a more accurate reconstruction of ancestral areas especially for the crown-node of the genus of interest. In addition, this analysis allowed us to discard the noise generated when using many areas (Matzke 2016). Only three geographical areas based on the present-day distribution of Detarioideae species (Mackinder 2005, GBIF 2017) were used: Africa, South and Central America, and Tropical Southeastern Asia. As in the generic level analysis presented above, we used the package BioGeoBEARS (Matzke 2016) for R (2014), to reconstruct the ancestral areas on the MCC tree for Detarioideae obtained with BEAST.

II.3 – Results

II.3.1 – Sequence characteristics

The aligned length of *AGT1*, *AIGP*, *CALTL*, ETS and ITS (including the 5.8 S region) are respectively 243 bp for the ingroup (409 bp for the ingroup and outgroup together, with 304 constant characters), 319 bp (420 bp with the outgroup, with 343 constant characters), 249 bp (390 bp with the outgroup, with 252 constant characters), 315 bp (328 bp with the outgroup, with 165 constant characters) and 691 (821 bp with the outgroup, with 468 constant characters). Among all the markers, ETS is the most variable, followed by ITS, then *CALTL*, *AGT1*, and *AIGP*. The total alignment after concatenation measured 2,368 bp. All sequences were produced *de novo*.

II.3.2 – Phylogenetic analysis

The topologies obtained with MrBayes and BEAST are congruent, both showing three major groups within *Crudia* (Figs. II.3, II.4, II.5). The genus *Crudia* is clearly monophyletic, and is strongly supported by a posterior probability (PP) of 1.0 (Fig. II.3). *Crudia* is resolved as sister to the monospecific *Neochevalierodendron*, also with a PP of 1.0. A strongly supported clade including all Asian species (PP=1.0) occurs as sister to a moderately supported clade that groups the [American+African] species (PP=0.87). A strongly supported clade of all American species (PP=1.0) is found within the [American+African] clade. The pronounced dichotomy between one Asian clade and one [African+American] clade was also found in previous studies (e.g. Bruneau et al. (2008)), even with reduced sampling.

Within the Asian clade, some species group into well-identified clades (i.e. *C. tenuipes* Merr., *C. zeylanica* (Thw.) Benth., *C. curtisii* Prain, *C. blancoi* Rolfe, *C. abbreviata* A.R.Bean, each with PP=1.0) whereas others are located in a well-supported but poorly resolved and poorly structured clade. Within the African group, the first diverging clade comprised of *Crudia ledermannii* Harms and *C. zenkeri* Harms ex De Wild. is weakly supported with a PP=0.66. The African clade that is sister to the American clade includes specimens of *Crudia harmsiana* De Wild., *C. klainei* Pierre ex De Wild. and *C. senegalensis* Planch. ex. Benth. and is also poorly supported (PP=0.53). *Crudia gabonensis* Pierre ex. De Wild. and *C. ledermannii* are the two African species that are not recovered as monophyletic. The American clade is strongly supported and American species are clearly distinct phylogenetically, but relationships among species within the clade are mostly poorly resolved and form a polytomy. However, some American species do group in the same clade with moderate support: *Crudia aromatica* (Aubl.) Willd. and *C. spicata*. (Aubl.) Willd. are sister species with PP=0.66, and *C. glaberrima* (Steud.) J.F.Macbr is sister to [*C. spicata* + *C. aromatica*] with PP=0.62. *Crudia acuminata* Benth. and *C. tomentosa* (Aubl.) J.F.Macbr. are reconstructed as sister species with strong support (PP=1). All species are monophyletic except for *Crudia aequalis* Ducke with specimens occurring in two different clades.

II.3.3 – Divergence time analysis

The split between the genera *Crudia* and *Neochevalierodendron* occurred during the early Eocene, around 50 Ma (49.16 to 52.71 Ma; 95% highest probability density HPD). The genus *Crudia* has a crown node at approximately 46 Ma (43.9 to 48.69 Ma; 95% HPD) (Figs. II.4, II.5, suppl. mat. 4). Within *Crudia*, the Asian clade diversified at the Oligocene/Miocene boundary at 24 Ma (16.22 to 31.94 Ma; 95% HPD). The [African + American] clade has a crown node at around 45 Ma (42.64 to 47.04 Ma; 95% HPD), and the American clade diversified during the Miocene around 19 Ma (11.94 to 27.26 Ma; 95% HPD). The African clades have crown nodes respectively at 24 Ma (12.12 to 38.73 Ma; 95% HPD) and 20 Ma (9.45 to 31.8 Ma; 95% HPD).

II.3.4 – Ancestral area reconstruction

For both reconstructions of ancestral areas (i.e. with oceanic or terrestrial dispersal models), the unconstrained DEC+J model had the lowest AIC value compared to other models (Table II.3) and was selected as the most appropriate model for our data in the BioGeoBears analysis. Africa is the estimated ancestral area for the genus, either with oceanic or terrestrial dispersal. In the case of terrestrial dispersal, the ancestral area of genus *Crudia* can alternatively be formed by Africa and Southeastern Asia, but this scenario has a very low probability (around 15%). Likewise, with the inclusion of denser outgroup sampling retrieved from the data of de la Estrella et al. (2017), we reconstruct Africa as the most probable ancestral area with 85% probability for the genus *Crudia*, with the other 15% for America and Asia (suppl. mat. 5). Africa is reconstructed as the ancestral area for the [American+African] clade for both terrestrial and oceanic dispersal methods. South America is reconstructed as the ancestral area for American species, with two independent events of migration from South America to Central America and Caribbean. In the Asian clade, the ancestral area is reconstructed to be Continental Southeastern Asia, with two independent migration events from mainland to Australasia.

II.4 – Discussion

II.4.1 – Systematics, phylogeny and taxonomy of Crudia

II.4.1.1 – Genus *Crudia* shows a clear subgeneric phylogenetic structure supported by molecular characters

In the current study, we have clearly demonstrated that *Crudia* is monophyletic based on molecular sequence data analysis. Despite this, we could not find a single morphological synapomorphy: *Crudia* is characterized by the combination of many characters. *Crudia* is distinct from other Detarioideae genera by the complete absence of the corolla whorl (De Wit 1950, Vieira 1990, Tucker 2001, Bruneau et al. 2014) due to aborted primordia development and their incorporation "as parts of adjacent stamen filaments or the receptacle during enlargement" (Tucker 2001), in combination with the compound leaves with alternate leaflets and a generally twisted petiolule (Breteler et al. 2008). However, the absence of petals is also characteristic of other Detarioideae genera like *Guibourtia* Benn. (Léonard 1950a). Compound leaves with alternate leaflets and twisted petiolule are not unique to the genus, occurring in other Detarioideae genera such as *Afzelia* Sm. and *Lebruniodendron* J.Léonard which both have twisted petiolules (Polhill et al. 1981), and *Copaifera* L., *Kingiodendron* Harms, *Brandzeia* Baill., or *Gossweilerodendron* Harms (Mackinder 2005) which display clear alternate leaflets. Fruits of *Crudia* are laterally compressed, sometimes with prominent veins, sometimes smooth and containing one to three seeds (pers. obs.). Throughout the genus, seeds have a relatively conserved morphology displaying a hollow between the two cotyledons, which might allow buoyancy (De Wit 1950, Kubitzki et al. 1994)(pers. obs. on *Crudia amazonica*, specimen Luize 43, INPA; *Crudia bantamensis*, specimen Wirawan 112, K).

The internal phylogenetic structure of *Crudia* mirrors its geographical distribution, with an ancestral split between a strongly supported Asian clade and a moderately supported [American+African] clade. Such a geographically-related structure is not unusual among plant lineages (e.g. Adhikari et al. (2015), Snak et al. (2016), Tosso et al. (2018)). However, no morphological character is known to clearly distinguish the Asian and [Africa+America] clades, or that otherwise would support the phylogenetic relationships as reconstructed here. Numerous characters, such as bifoliolate or unifoliolate leaves, glabrous or densely pubescent fruits, or midvein curvature, are useful for species diagnosis, but they are spread across the phylogeny without evident structure and do not appear to be synapomorphies for particular clades. The flower size and morphology are globally similar between species throughout the whole genus. However, small differences in the length and twisting of the petiolule do occur between the two clades: twisting seems less pronounced and less frequent in the Asian clade, than in the [America+Africa] one, and petiolules appear shorter in the American species compared to Asian species. Additionally, while evaluating possible relationships between *Crudia* fossils and current living species based on fruit morphology, Herendeen et al. (1990) found that fruits of Asian species generally appear smaller than those of African and American ones.

Finally, the lack of internal resolution in the tree, mainly in the American clade as well as in the Asian clade, might be due to high levels of variation in the nuclear markers. In the future, adding relevant chloroplast markers in the dataset could help to discriminate species based on molecular characters and help to resolve internal relationship because plastid genomes evolve more slowly than nuclear genome (Wolfe et al. 1987).

II.4.1.2 – Not all Asian species are well-circumscribed based on the phylogeny

Within the strongly supported clade of all Asian *Crudia* species, five early diverging species are clearly supported as monophyletic with all their respective specimens grouping together. *Crudia tenuipes* Merr. is differentiated by a conserved number of three leaflets, with a pronounced curved central nerve and a subglobose, densely pubescent fruit; it is found in Borneo. *Crudia abbreviata* A.R.Bean has around four to seven small, asymmetrical leaflets and a laterally compressed fruit, as well as persistent bracts and bracteoles along the pedicels; it is strictly found in Queensland, Australia. *Crudia zeylanica* (Thw.) Benth. is one of the Asian species exclusively distributed in the western, mostly continental, part of the genus's Asian area: it is recognizable by its very characteristic rounded leaflets with an obtuse apex. *Crudia curtisii* Prain, located in the narrow Malay Peninsula, displays a characteristic flat and pubescent fruit. The fifth species, *Crudia blancoi* Rolfe, is located among the early diverging Asian species. This species is represented in our phylogeny with a single specimen, and therefore no conclusion can be drawn about its monophyly. However this species bears a high number (above seven) of small, asymmetrical leaflets and has an ovoid, non-flattened fruit; it is found in Northern Philippines and could be considered as a well identified species. *Crudia tenuipes*, *C. blancoi*, *C. abbreviata*, *C. zeylanica* and *C. curtisii* successively diverge early in the Asian clade; although no clear geographic signal can be drawn from this branching pattern (i.e. *C. tenuipes* is located in Borneo*, C. blancoi* in Northern Philippines, *C. abbreviata* in Australia and Papua New Guinea, *C. zeylanica* in Asian mainland, *C. curtisii* in Malay Peninsula), it is noted that leaflet number is typically greater than three, and leaflets are never opposite or subopposite among these five species, as opposed to other members of the Asian clade (i.e. the unresolved clade grouping most of the Asian specimens) whose leaves have single or opposite to subopposite leaflets. Furthermore, leaflets of the five early diverging species are usually smaller than 10 cm, whereas species located in the polytomy can bear leaflets around 20 cm long. Among the five early diverging species, only two show densely flowered inflorescences with more than 50 flowers (*C. blancoi* and *C. abbreviata*) whereas other species (*C. tenuipes*, *C. curtisii* and *C. zeylanica*) have around 20 flowers. However, densely flowered inflorescences are not exclusive to early diverging species, as *Crudia penduliflora* Ridl. (located in the unresolved clade) has a very visible and densely flowered inflorescence.

The polytomy groups seven species (without including specimens of *Crudia wrayi*, as we consider it to be a doubtful species, see Chap. I), with specimens scattered across the clade. Our sampling of Asian species is nearly exhaustive, based on our revised species taxonomy (Chap. I), but lacks specimens for *Crudia curvosa* Domenech spec. nov., *Crudia balachandrae* Sanjappa, and *Crudia cauliflora* Merr. All other species, re-identified following our new classification system, have specimens that are scattered across this large polytomy and do not form clades that match the morphology-based species boundaries. The lack of resolution in this clade might be related to local hybridization processes between species (i.e. gene introgression), caused by the insular nature of their environment in Asia compared to a mainland environment in Africa and America. This may explain why specimens of a same species do not group together. Also, some studies show that rate of molecular evolution slows down especially for insular species compared to continental ones (Wright et al. 2003), which might explain why most Asian species group in an unresolved but well supported clade. Indeed, while early diverging Asian species span across large islands or mainland, some species in the polytomy are located on smaller islands (e.g. *Crudia cynometroides* on Palau Island, or *Crudia papuana* in Papua New Guinea) or scattered across several distant areas (e.g. *Crudia gracilis*). Lastly, a polyphyletic pattern can be found even for species with highly conserved morphology (e.g. *Crudia bantamensis*). This might be attributed to a lack of resolution, rather than biological causes. Polyphyletic species in our tree might become paraphyletic or monophyletic if other informative molecular markers were included in the analysis.

II.4.1.3 – Morpho-species delimitation and molecular phylogeny are often but not always congruent among African species

The African specimens form at least three well supported and well-characterized species clades, corresponding to three morpho-species: *Crudia zenkeri*, *C. klainei*, and *C. senegalensis*. In addition to forming well-supported clades, these species are morphologically distinctive (Breteler et al. 2008): *Crudia zenkeri* presents three to five rounded leaflets, almost symmetrical, with an elongated apex; *Crudia klainei* has distinctive enlarged, membranous stipules, not seen in other African species; and *Crudia senegalensis* presents elongated, persistent, but not enlarged stipules. Other species such as *C. letouzeyi* Breteler & Nguema and *C. harmsiana* were only represented by a single specimen in our phylogeny, thus no conclusion about species monophyly can be drawn. However, one moderately supported clade groups *C. ledermannii* and *C. zenkeri* together, with the former paraphyletic to the latter. Such a pattern of nested, non-monophyletic species as observed in *C. ledermannii* may be typical of some rainforest tree species (Naciri et al. 2015, Pennington et al. 2015), because of the very nature of the tree habit of the species; tropical trees in rainforest environments will potentially have a tendency to keep ancestral genetic polymorphism, leading to a longer coalescence process than for species in drier and more open environments. Therefore, a monophyletic concept of species criterion might be inappropriate. Species non-monophyly can also be the manifestation of many biological processes: boundaries between two species can be difficult to detect based on molecular characters if the amount of time since species split is not very long, i.e. if speciation event is recent (Knowles et al. 2007); non-monophyly can also account for a past founder effect, where an initial ancestral species on the mainland gives rise to a new island species after a dispersal event, with survival of both species (De Queiroz et al. 1988, Hudson et al. 2002), although this scenario is unlikely in our case, as *Crudia* species in Africa are not located on islands. In our case, studying the phylogenetic relationships between *Crudia ledermannii* and *C. zenkeri* would benefit from a more exhaustive sampling of individuals to conduct a population study of genetic diversity, as well as phylogeographic studies using more specific molecular markers (e.g. Emerson et al. (2010), Cavers et al. (2013)). This could lead to a better understanding of the evolutionary patterns between those two species.

In our phylogeny, three specimens that are clearly identified to *Crudia gabonensis* based on morphology do not group in a single clade, with two specimens (Wieringa 3946, Wieringa 8313) located in the Congolian Region of Africa (sensu Linder et al. (2012)) and one specimen located in the Guinean Region of Africa (sensu Linder et al. (2012)). Geographic distribution seems to match the branching pattern, with specimens from either sides of the Dahomey Gap belonging to two different lineages. *Crudia gabonensis* is the most widespread *Crudia* species in Africa, and is morphologically the most variable among African species (Breteler et al. 2008). This disjunct pattern between the two African regions is also found in another Detarioideae genus, *Gilbertiodendron*, and clearly matches the separation of African rainforest by the Dahomey Gap biogeographic discontinuity (but see de la Estrella et al. (2014)). This piece of land is unfavorable to tropical rain forest growth and was recently formed during the Holocene (Demenou et al. 2016). However, in the case of *Gilbertiodendron diphyllum* and *G. preussii* (de la Estrella et al. 2014), the Dahomey Gap does not seem to represent a barrier to genetic flow within widespread species. In our case, more molecular data and greater sampling of specimens from across the range of *Crudia gabonensis* on each side of the Dahomey Gap will be necessary to better understand the evolutionary history and observable diversity of this particular species. Based on our molecular phylogeny, we suspect that *Crudia gabonensis* might hide a more complex evolutionary pattern. Other African species show genetic divergence between populations east and west of the Dahomey Gap: this is correlated with geographic distance (Fontaine et al. 2004) and was probably caused by reduced gene flow while the Dahomey Gap was established during the Holocene, splitting the tropical forest in two parts (Hardy et al. 2013). But whereas species located on both sides of the Dahomey Gap display some genetic divergence, they show a well-conserved morphology and are not necessarily considered as two distinct cryptic species, but rather as two more genetically variable populations (de la Estrella et al. 2014). On the other hand, Dainou et al. (2014) demonstrated that long-living tree species with conserved morphological features can undergo speciation events resulting in cryptic species emergence. Thus, it will require more data to confirm the existence of one species with genetic variation among populations, or several cryptic species for *Crudia gabonensis*.

II.4.1.4 – Molecular phylogeny and morphology give congruent patterns and clear species delimitation for most of the American species

Although relationships among the species in the strongly supported American clade are poorly resolved, species are generally well delimited, with clades corresponding to recognized morphological entities. Six species, *Crudia acuminata, C. tomentosa, C. amazonica, C. oblonga, C. glaberrima,* and *C. aromatica,* are supported as monophyletic. In addition to being resolved in well-supported clades in the molecular phylogeny, these species are characterized by well-defined morphological autapomorphies. *Crudia acuminata* displays fruits with pronounced-veined surface, slightly pubescent, enclosing one or two seeds only (Bentham 1844)(pers. obs. on *Crudia acuminata*, specimen Maxon 7187, US); this species has the most northern distribution among American species. *Crudia tomentosa* presents a conserved leaf morphology with four asymmetrical and curved leaflets; fruits enclose a single seed and are almost spherical with a veined and pubescent surface (Vieira 1990)(pers. obs. on living specimen at the Botanical Garden of Rio de Janeiro, RB). *Crudia amazonica* has up to 13 very narrow leaflets (Vieira 1990), which is the highest leaflets number among the American species, and displays large, flattened, pubescent fruits (pers. obs. on *Crudia amazonica*, specimen Pinto 535, INPA). *Crudia oblonga* displays ovoid to rounded leaflets (the apex is often merged with the leaflet outline) and rounded, pubescent fruits (pers. obs. on *Crudia oblonga*, specimen Pinto 538, INPA). *Crudia glaberrima* has obovate, slightly curved leaflets, and flattened, pubescent fruits with thick, prominent veins (Amshoff 1953, Vieira 1990). *Crudia aromatica* is the only American species with unifoliolate leaves (Amshoff 1953) and glabrous fruits. Specimens Loubry 1779, Loubry 844, Prevost 1388, Forest & Prevost 131 were initially attributed to *Crudia bracteata* (suppl. mat. 2), but regarding several characters (hereafter discussed), we suspect that *C. bracteata* is synonym with *C. spicata*. First, specimens previously attributed to *Crudia bracteata*, now identified as *Crudia spicata*, are grouping in a single clade with other specimens of *C. spicata*. Among American species, only *Crudia bracteata* and *C. spicata* have persistent bracts on every pedicel that often enclose the flower. In addition, their leaflet morphology is similar, even if the leaflets of specimens attributed previously to *C. bracteata* are slightly smaller and rounder than those of *C. spicata* specimens. In their monographic descriptions, Amshoff (1939, 1953) and Vieira (1990) noted that the two species are nearly identical, except for the pubescence of the rachis and leaflets. It is not unusual for every *Crudia* species to have both pubescent and glabrous individuals within the same species, or even glabrous and pubescent leaves on the same specimen, depending on factors such as the age of the leaf as well as the position of the leaf on the tree. For all these reasons, we suggest that the two entities should be recognized as a single species under *Crudia spicata*. Priority should be given to *Crudia spicata* (Aubl.) Willd., the type of the genus, described by Aublet (1775a) under *Apalatoa spicata* Aublet, over *Crudia bracteata*, described by Bentham (1840). Nevertheless, further taxonomic studies based on morphological analysis of numerous specimens from throughout the distribution range would be required to strengthen this species combination. Lastly, although *Crudia aequalis* specimens are resolved in two distinct clusters, this species is morphologically homogeneous, characterized by its elongated, smooth, flattened and glabrous fruits. We hypothesize that the recovered branching pattern of the phylogeny is related to the different localities of specimens. Specimens Redden 3561, Redden 3409, McDaniel 29892 are respectively located in Venezuela and Peru, while specimens Ducke 35196, Neves 2028, Neves 1979 are located in the Amazon Basin and specimen Proctor 27912 is located in the Caribbean. Although the specimens are morphologically similar, this branching pattern could reflect the existence of cryptic species, with species defined by geographical features and potentially by environment.

Two American species were not included in our analysis: *Crudia humboldtiana* Stergios only known from one non-flowering specimen (Stergios 2002), and *C. lacus* Standl. & Steyerm. only known from the type collection (Standley et al. 1946). After studying online specimens and descriptions of *Crudia humboldtiana*, we believe that this species might be synonymous with *C. amazonica*. Similarly, *C. lacus* is likely a synonym of *C. acuminata* based on highly similar morphological characters (Standley et al. 1940, 1946). Another species from Central America, *Crudia choussyana* Standl. (with one specimen included in our analysis, Hughes 1249) was described by Standley (1923) but is likely a synonym of *C. acuminata* based on the leaflet morphology and on its phylogenetic position, where the two specimens *C. acuminata* (Maxon 7187, US) and *C. choussyana* (Hughes 1249, US) group together (Fig. II.3). Further morphological and molecular analyses are required to better assess the taxonomic status of these species.

II.4.2 – Divergence time analysis and ancestral area patterns: links between lineages arising and past geological events

II.4.2.1 – When and where did the *Crudia* lineages arise?

The genus *Crudia* is estimated to have originated in Africa (Figs. II.4, II.5, suppl. mat. 5) during the Eocene (Zachos et al. 2001). This result is not surprising, as previous studies suggest that the subfamily Detarioideae originated in Africa, with 58% of extant Detarioideae genera located in Africa (Doyle et al. 2003, Mackinder 2005, de la Estrella et al. 2017). Several environmental features might have favored the origination, establishment and sustained presence of *Crudia* in its African cradle. Optimal environmental parameters, like constant heat and high rainfall rates, usually have positive impact on lineage diversity (Brown 2014). At the beginning of the Eocene, tropical rain forests were the dominant habitat in Africa, South America and what would become Asia (Bush et al. 2007) with a global climate warmer than at any other time during the Cenozoic. During the early Eocene, mean temperatures were 5 to 8 °C warmer than at present (Zachos et al. 2001, Rohl et al. 2007, Zachos et al. 2008, McInerney et al. 2011). Warmer temperatures have been shown to be correlated with diversification bursts in some higher level taxonomic lineages during the Paleocene-Eocene Thermal Maximum (PETM) (Jaramillo et al. 2010) (e.g. Arecaceae, Bombacoideae, Leguminosae, Araceae, Convolvulaceae), as well as with the appearance of new families (e.g. Myrtaceae, Sapotaceae, and Passifloraceae), including Leguminosae (Koenen et al. 2013). These warmer climates may have facilitated, or maybe even triggered, the appearance of new generic lineages including *Crudia*.

Deep lineages within *Crudia* split early during the Eocene (between 46 and 42 Ma, Figs. II.4, II.5) and our reconstruction shows no new lineage appeared in the following 20 Ma. Fossil occurrence of the genus is recorded in North America during the Middle Eocene (Herendeen et al. 1990) and in Central America during the Late Eocene (Graham 1985), suggesting a more northerly distribution of genus *Crudia* compared to its current distribution in Central and South America. Due to the warmer climate in the Eocene (Zachos et al. 2001, Zachos et al. 2008), the northward presence of *Crudia* is not surprising. Likewise fossil occurrences of other strictly tropical plants taxa also show they had a much more northern distribution (e.g. Daghlian (1981), Couvreur et al. (2011a)). After 24 Ma, more recent lineages diverged and diversified, exemplified by Asian and American crown-nodes that arose during the Oligocene/Miocene transition (Figs. II.4, II.5). Both our biogeographic reconstruction and fossil occurrence data (Songtham et al. 2003) indicate the genus was already present in continental Asia by the Miocene, and colonized Australasia independently twice. In the meantime, our analyses reveal American species diversified in South America and later independently colonized the Caribbean area twice.

II.4.2.2 – Rejection of the Gondwanian vicariance hypothesis

Pantropical distributions of plant lineages have been attributed to Gondwanian vicariance in some taxa (Swenson et al. 2001, Korall et al. 2014), but necessarily imply the study group must be older than the Gondwana break-up which began during the Mesozoic (Scotese 2001, Jokat et al. 2003, Scotese 2004). However, the appearance of Leguminosae is dated to the Late Cretaceous (Bruneau et al. 2008), long after landmasses were separated by oceans following continental drift. Our analysis also suggests *Crudia* arose during the Middle Eocene, when Africa, America, and Asia where already separated by oceans (see Scotese (2014) for more detailed coasts outline during the Cenozoic). Consequently, the pantropical distribution of genus *Crudia* cannot be attributed to Gondwanian vicariance but rather must be explained by other more recent processes.

II.4.2.3 - Terrestrial dispersal across the boreotropics during the Eocene period

Normal dispersal is defined as the movement of organisms within or at the edge of their natural distribution range (de Queiroz 2014). During the Eocene, increasing global temperatures allowed the existence of widespread warm environments, favorable to tropical species (Kurschner et al. 2009). Boreotropical forests extended from equatorial latitudes to higher latitudes northward and southward (Morley 2003, Boucot et al. 2013). Boreotropics were present from the Late Cretaceous until the Oligocene when global climate drastically changed (Wolfe 1975). During the Eocene, tropical floras were typically reaching boreal and austral latitude, around 60° N and 60° S (Bush et al. 2007). For many pantropical taxa (younger than the Gondwanian breakup), one explanation for the observed disjunct pattern is the boreotropical hypothesis (Couvreur et al. 2011b, Fritsch et al. 2015, Thomas et al. 2015), which might account for how taxa of African origin reached Asia and South America. Many non-related flowering plant taxa migrated throughout this warm and stable terrestrial environment and colonized distant locations (e.g. Malpighiaceae (Davis et al. 2002, Davis et al. 2004), genus *Guatteria* Ruiz & Pav. (Erkens et al. 2009)), mostly through the North Atlantic Land Bridge (Tiffney 1985). Paths from Africa through Europe and Greenland to North America were made easier by presence of smaller distances between mainlands (e.g. Weeks et al. (2005)), as well as the emergence of ephemeral straits (Brikiatis 2014). At this time, plants could migrate from North to South America, even though the Panama isthmus had not emerged during the Eocene, by island hopping using insular volcanic arcs (Iturralde-Vinent et al. 1999, Iturralde-Vinent 2006). Plants could have also followed the Tethys coast during the Eocene, from Africa to Asia (e.g. Weeks et al. (2005), Lang et al. (2007).

The occurrence of many tropical legume fossils at northern latitudes is an additional element that supports a terrestrial boreotropical dispersal hypothesis. *Crudia* fossils, reconstructed as closely related to current American *Crudia* species, have been found in deposits from Tennessee in North America dating to the Lower Eocene (Herendeen et al. 1990). These fossils illustrate the extent of the past distribution of this genus, and how terrestrial migration routes could have been shaped. Another Detarioideae fossil, *Aulacoxylon sparnacense* Combes, considered closely related to *Daniellia* Benn., was found in the Paris Basin in Europe, dated from the lower Eocene (de Franceschi et al. 2003). This is not an isolated case among Detarioideae, as many fossils show wet tropical characteristics and that are associated with extant tropical rain forest taxa can be found in areas where the climate is now dry or arid (e.g. *Aphanocalyx* Oliv. and *Cynometra* L. from Tanzania (Herendeen et al. 2000, Jacobs et al. 2004) and Ethiopia (Pan et al. 2010)). In genus *Crudia*, the stem node of the American species clade is dated to 42 Ma (40 to 44 Ma, 95% highest probability density HPD), immediately following the end of the PETM (Zachos et al. 2001), suggesting the potential terrestrial dispersal from Africa into America through North America and the remaining boreotropics. Similarly, the stem node of the Asian clade is dated to 46 Ma (43 to 48 Ma, 95% highest probability density HPD), which again coincides with the presence of a potential passage from Africa to Southeastern Asia right after the PETM or following the Tethys coast.

II.4.2.4 – Alternative scenario: oceanic long distance dispersal during the Eocene period

Long distance dispersal describes the movement of organisms across a natural barrier, that usually prevents dispersal events (de Queiroz 2014). In addition to the boreotropical hypothesis, long distance dispersal across oceans (Givnish et al. 2004, Renner 2004, de Queiroz 2005a, Tosso et al. 2018) may also explain the present-day distribution of *Crudia*. Long distance dispersal is a constant (Gunn et al. 1976, Takayama et al. 2013, Wee et al. 2014) but rare and stochastic process (de Queiroz 2014). It can be facilitated by morphological characters related to water dispersal, such as buoyancy or salt water resistance of diaspores carried in ocean currents (Nathan et al. 2008). As described by De Wit (1950) in his taxonomic revision, in *Crudia* seeds "the cotyledons are concave with a large inner cavity […], which may cause buoyancy and promote dispersal". Experiments on *Crudia amazonica* seeds showed they were able to germinate successfully after 30 days in fresh water (Kubitzki et al. 1994), although germination rate fell to 30% after seven weeks (Parolin et al. 2003). As seeds are buoyant, dispersal of *Crudia* trees at more local scales is also likely to occur through freshwater transportation. The effects of salt water on *Crudia* seeds, however, are unknown. Although it has not been tested, sea water may reduce the germination rate after long exposure in open ocean. Other legume genera with pantropical distributions, like *Dalbergia* L.f. (Vatanparast et al. 2013), *Canavalia* DC. (Snak et al. 2016), or *Mucuna* Adans. (Moura et al. 2016), have seed characteristics related to buoyancy (Gunn et al. 1976). Certain species of *Intsia* Thouars also have a widespread range, facilitated by water-dispersed diaspores (Gunn et al. 1976) in water-related environments, such as river valleys and alluvial lowlands (Lee et al. 2002). In other angiosperm families, seed buoyancy is well-known to be related to extreme long distance dispersal, with individuals of some species growing in open habitats associated with the sea shore or streams (e.g., *Ceiba* Mill. (Dick et al. 2007), *Rhizophora* L. (Takayama et al. 2013, Wee et al. 2014), *Cocos* L. (Harries et al. 2014)). Houle (1998) calculated a maximum average of two weeks for propagules to cross the Atlantic Ocean westward, from Africa to South America. This would allow sufficient time for salt-tolerant seeds to establish and grow on remote river shores after crossing the Atlantic Ocean. During the early Cenozoic, *Crudia* seeds might have dispersed through this transatlantic current, allowing tropical diaspores to be easily carried away (Berggren et al. 1977). *Crudia* seeds might also have take advantage of the Tethys sea way, linking the Atlantic Ocean and what would become the Indian Ocean (Haq 1981, Hsü 1986), during their route from Africa to Asia. Lastly, Houle (1998) refers to the potential role of floating islands on the oceanic dispersal of seeds or seedlings in the past. Although *Crudia* trees mostly grow along fresh water river banks (Hou et al. 1996, Breteler et al. 2008)(pers. obs.) and do not seem to be adapted to salt water survival, it is possible that their long distance dispersal could be facilitated by short-duration extreme meteorological phenomena, such as abundant rainfall (McInerney et al. 2011). These types of rare but plausible events could provide slicks of fresh water floating on top of colder sea water in sufficient quantities to explain seed survival across oceans.

II.4.2.5 – Dispersal during the Miocene

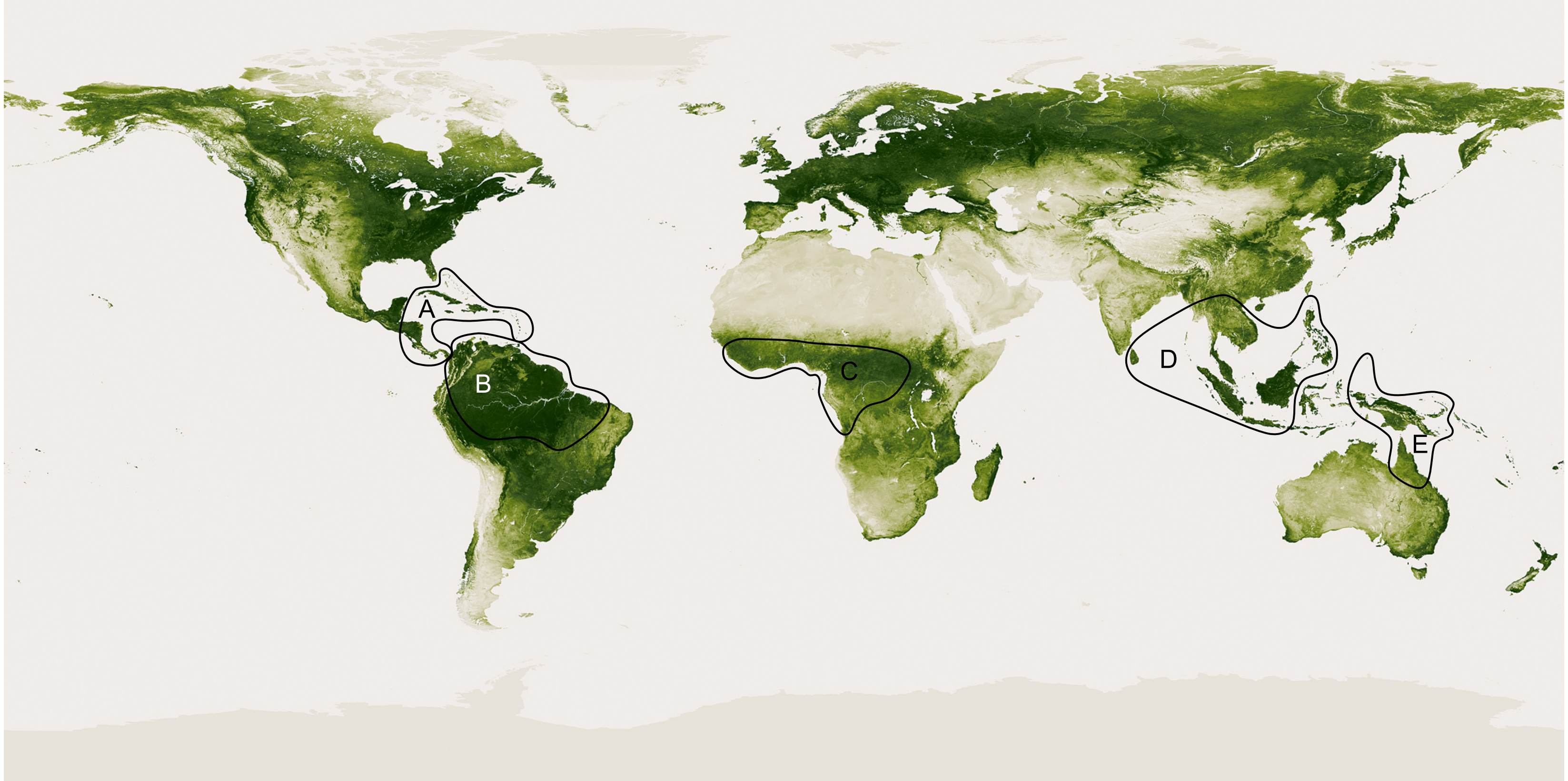
After tropical lineages expanded northward through the boreotropical rainforests, colonizing a northern wet tropical belt (Davis et al. 2002, Huang et al. 2016, Viruel et al. 2016), they withdrew against global climate cooling. This climate change started in the mid-Eocene and became more prominent during the Miocene. As northern latitudes became inhospitable for megathermal floras (Bush et al. 2007), lineages retreated to more southern and equatorial locations, becoming confined to their current distribution on distant continents separated by wide oceans (Buerki et al. 2013, Fritsch et al. 2015, Li et al. 2016).

In Southeastern Asia, plant lineages diversified as the rainforest expanded due to the collision between the Indian and Asian tectonic plates, leading to a mixing of floras (Morley 2000). Continuous continental connections also allowed dispersal of remnant boreotropical elements from tropical Asia (Morley 2000) to Australia, by taking advantage of the uplift of Papua New Guinea during the Miocene (Morley 2003) and of the now-submerged remaining Gondwanian continent Zealandia (de Queiroz 2014). Newly formed volcanic chains of islands (Hall 1996), as well as subsequently bigger islands (e.g. Borneo), likely played a role in step by step island-hopping dispersion (Hall 2009). The increasing probability of migrations during the Miocene was reflected by the use of dispersal cost matrices. As recovered in our analysis (Figs. II.4, II.5), there were two independent dispersal events from Asian mainland to Australasia, crossing the Wallace line, during the Miocene. *Crudia* species were presumably able to disperse and establish throughout Southeastern Asia in the constant warm tropical environment, taking advantage of land connections and using successive island hopping and shallow epicontinental seas to reach remote locations.

In Africa, climatic conditions led to a much more widespread rainforest environment by the end of the Late Miocene than at present (Morley 2000, Hardy et al. 2013) which linked the east and west coasts of that continent (Plana 2004). Globally, African rainforests were refugia during the Oligocene/Miocene transition in which tropical plants were able to diversify without being exposed to the cooling events happening northward and southward on the planet. Because *Crudia* species are strictly associated with tropical biota (Breteler et al. 2008), a constant warm tropical environment during this era could explain why *Crudia* species are widespread in tropical Africa. Based on the divergence time analysis, African *Crudia* lineages were pre-established on both sides of the Dahomey Gap, prior to its formation during the Holocene (Demenou et al. 2016). *Crudia*'s current disjunct distribution pattern from east to west (Breteler et al. 2008) is probably linked to unsuitable environmental conditions in this area during the Holocene, but is not necessarily related with any evolutionary process, as some species did occur on both sides of the Dahomey Gap (i.e. species *Crudia gabonensis*).

In America, the geomorphology of the region changed during the Cenozoic, with the formation of the Panama isthmus beginning in the Miocene (Bacon et al. 2015) being a major event allowing for terrestrial exchanges between South America and Central America. As well, Caribbean volcanic islands were being formed during the Miocene (Iturralde-Vinent et al. 1999) and could have been used by organisms as stepping stones to cross the proto-Caribbean sea and reach both American mainland. According to our estimation of the biogeographic history of *Crudia* (Figs. II.4, II.5), two independent dispersal events are reconstructed from South America to Central America and the Caribbean. Both of these dispersals occurred during the Miocene, which correspond to the period of both heightened volcanic activity and the closure of the Panama isthmus.

Figure I.1 : Distribution of *Crudia* worldwide, with areas used in the biogeography analysis



A : Central America and Carribean
B : South America
C : Africa
D : Continental Asia, Sri Lanka, Sunda Shelf
E : Oceania and Sahul Shelf

Figure II.2 : Dispersal cost matrices

A: Central America and Caribbean; B: South America; C: Africa; D: Continental Asia, Sri Lanka, Sunda Shelf; E: Oceania and Sahul Shelf

Terrestrial long distance dispersal

Eocene

	A	B	C	D	E
A	1	0.5	1	0.01	0.01
B	0.5	1	0.5	0.01	0.01
C	1	0.5	1	1	0.01
D	0.01	0.01	1	1	0.5
E	0.01	0.01	0.01	0.5	1

Miocene

	A	B	C	D	E
A	1	1	0.5	0.01	0.01
B	1	1	0.5	0.01	0.01
C	0.5	0.5	1	0.5	0.5
D	0.01	0.01	0.5	1	1
E	0.01	0.01	0.5	1	1

Oceanic long distance dispersal

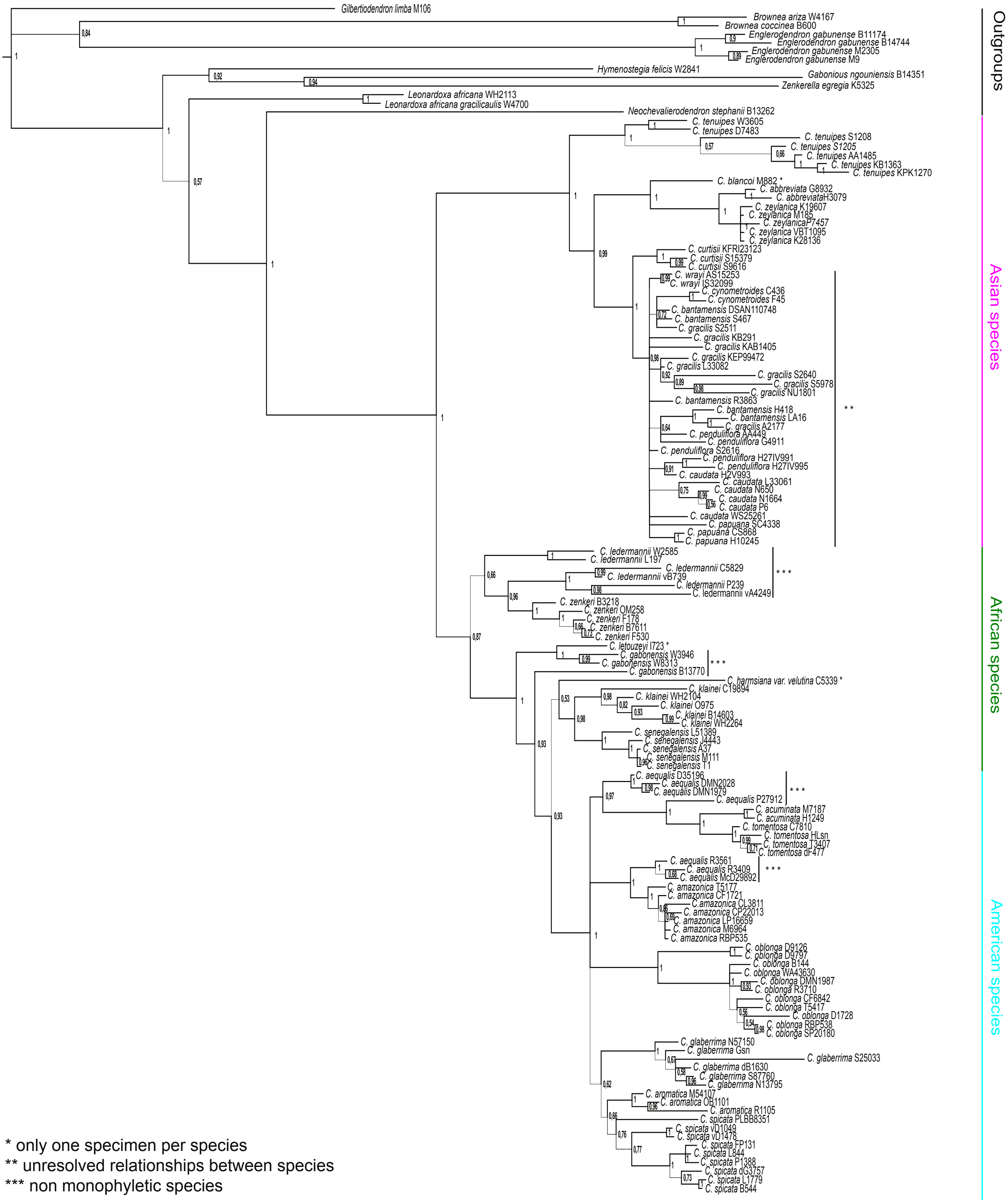
Eocene

	A	B	C	D	E
A	1	0.5	0.5	0.5	0.01
B	1	1	0.5	0.01	0.01
C	0.5	1	1	0.01	0.01
D	0.5	0.5	0.5	1	0.5
E	0.01	0.01	0.01	0.5	1

Miocene

	A	B	C	D	E
A	1	1	0.5	0.5	0.01
B	1	1	0.01	0.01	0.01
C	0.5	1	1	0.01	0.01
D	0.01	0.01	0.01	1	1
E	0.01	0.01	0.01	1	1

Figure : II.3 : Bayesian phylogeny of *Crudia*
Phylogeny based on a combined matrix of ITS, ETS, *AGT1*, *AIGP*, *CALTL*.
Posterior probabilities are indicated at each node. Tip names with "*C.*" stand for *Crudia*



* only one specimen per species
** unresolved relationships between species
*** non monophyletic species

Figure II.4 : Biogeographical scenario (terrestrial dispersal only) for *Crudia* inferred by BioGeoBEARS plotted on the divergence time tree retrieved from BEAST analysis and displaying ancestral ranges estimation. Relevant ages are represented above corresponding nodes.

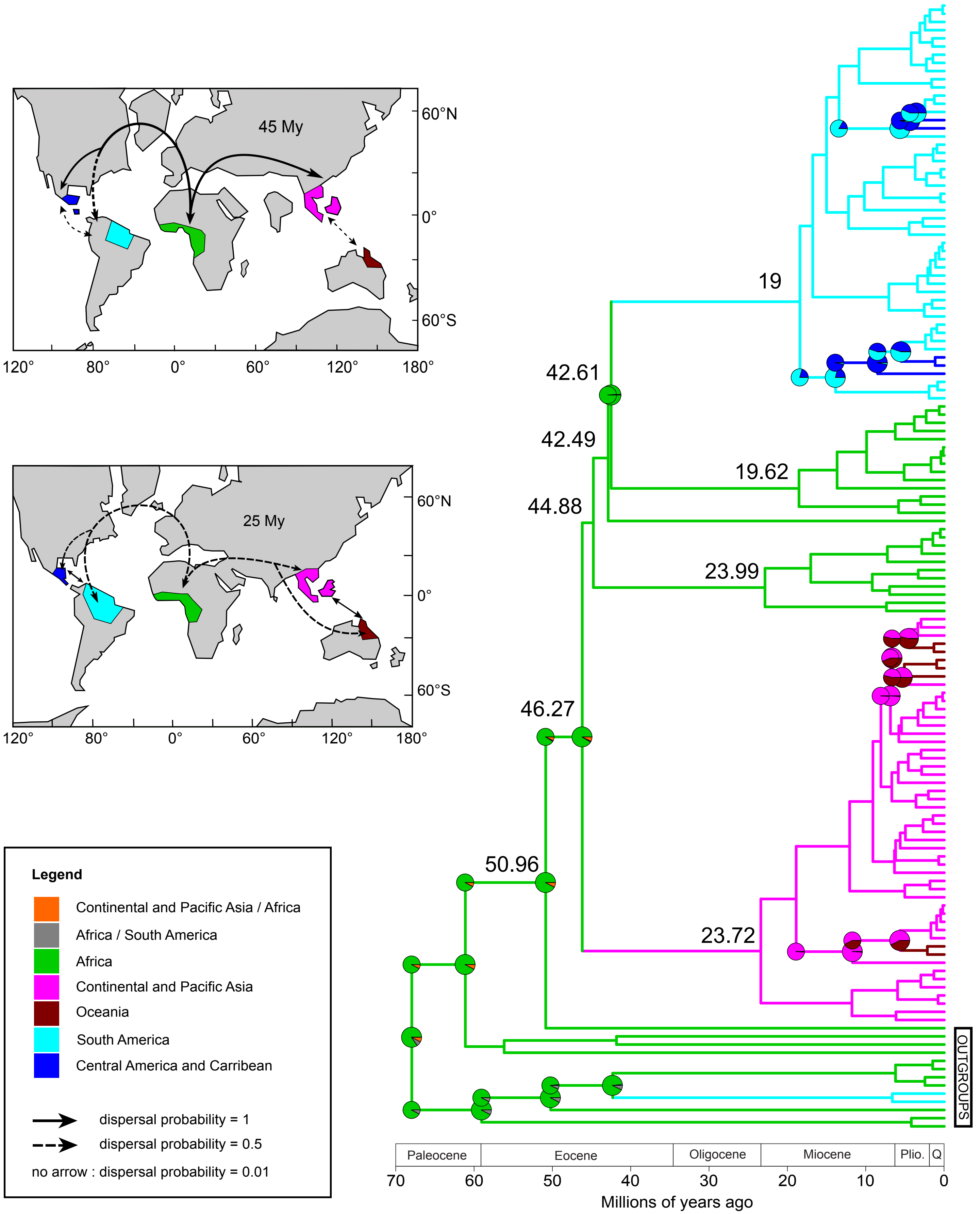


Figure II.5 : Biogeographical scenario (oceanic dispersal only) for *Crudia* inferred by BioGeoBEARS plotted on the divergence time tree retrieved from BEAST analysis and displaying ancestral ranges estimation. Relevant ages are represented above corresponding nodes.

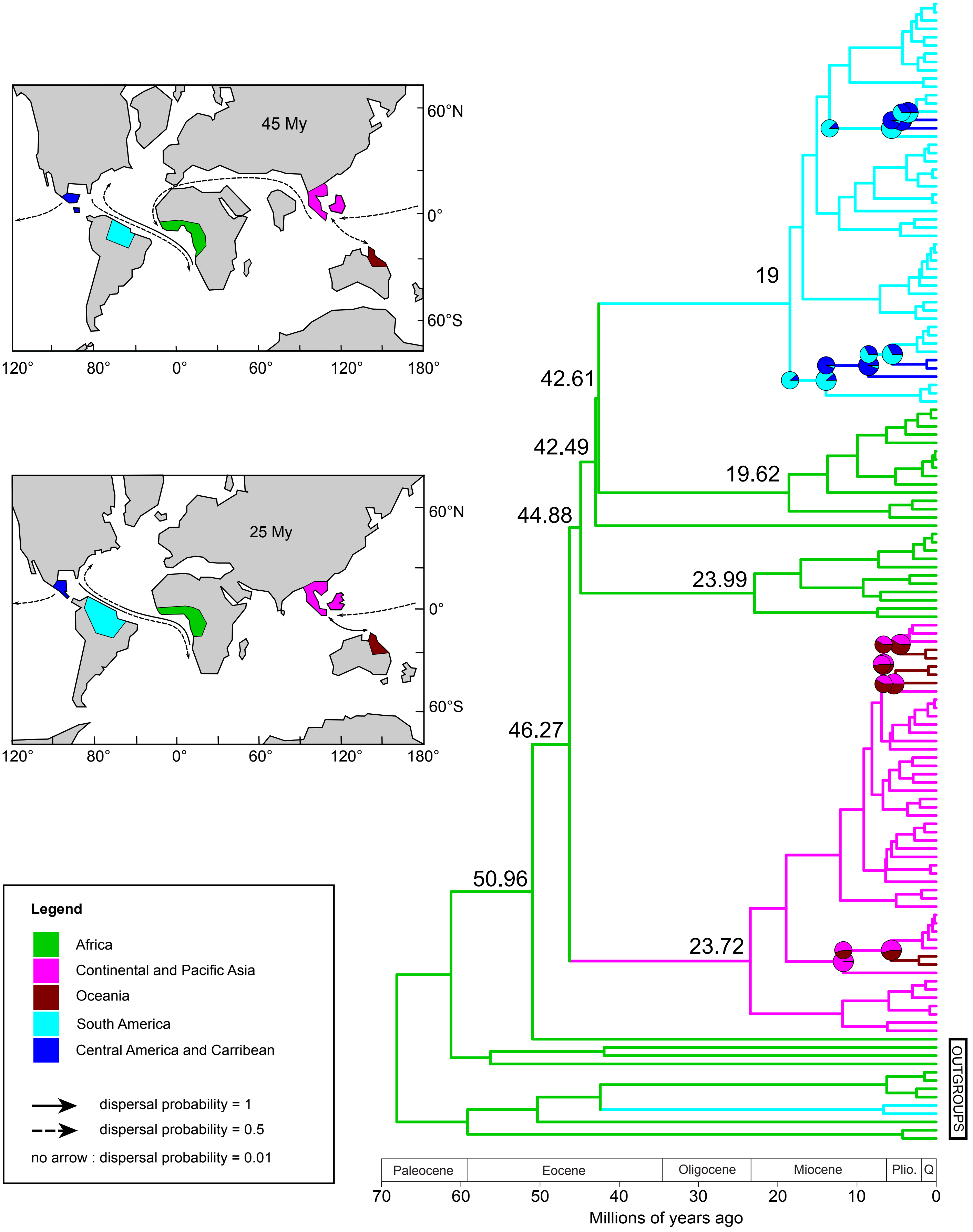


Table II.1 : Primer sequences used for PCR amplification and PCR conditions

DNA region	**primer name**	**primer sequence 5’3’**	**references**	**PCR conditions**					
				pre-melting	denaturation (I)	primer annealing (II)	primer extension (III)	cycles (I+II+III)	Final extension
AGT1	*AGT1*-Cru-R	CCCAGAAGGCTCTTTCNCTC	this study	98°C (30 sec)	98°C (10 sec)	54°C (20 sec)	72°C (20 sec)	50	72°C (1 min)
	AGT1-Cru-F	CTGCCAGCCTGTATTTATCA	this study						
AIGP	*AIGP*-Cru-R	CCTTTAACTCCAGAAGAAGTTGGTC	this study	98°C (30 sec)	98°C (10 sec)	56°C (20 sec)	72°C (20 sec)	50	72°C (1 min)
	AIGP-Cru-F	GTGCCCGAAGTATCTCCTACAGGG	this study						
CALTL	*CALTL*-Cru-R	CCATTGATTGACAACCCAGGTT	this study	98°C (30 sec)	98°C (10 sec)	58°C (20 sec)	72°C (20 sec)	50	72°C (1 min)
	CALTL-Cru-F	GCAAGCAGCTTAGCATATTCCGG	this study						
ITS	AB101	ACGAATTCATGGTCCGGTGAAGTGTTCG	Douzery et al. (1999)	98°C (3 min)	98°C (10 sec)	60°C (15 sec)	72°C (20 sec)	30	72°C (1 min)
	AB102	TAGAATTCCCCGGTTCGCTCGCCGTTAC	Douzery et al. (1999)						
ITS1	AB101	ACGAATTCATGGTCCGGTGAAGTGTTCG	Douzery et al. (1999)	98°C (3 min)	98°C (10 sec)	60°C (15 sec)	72°C (20 sec)	30	72°C (1 min)
	ITS-B	CACACCAAGTATCGCATTTCGC	this study						
ITS2	AB102	TAGAATTCCCCGGTTCGCTCGCCGTTAC	Douzery et al. (1999)	98°C (3 min)	98°C (10 sec)	60°C (15 sec)	72°C (20 sec)	30	72°C (1 min)
	ITS-C	CTCTCGGCAACGGATATCTCG	this study						
ETS	18-IGS	GAGACAAGCATATGACTACTGGCAGGATCAACCAG	Baldwin et al. (1998)	98°C (3 min)	98°C (20 sec)	56°C (20 sec)	72°C (30 sec)	35	72°C (2 min)
	ETS-Cru-2	TTCGTTTGCCCCTTCCCATCC	this study						

Table II.2 : Fossils used as calibration points in the divergence time analysis (from de la Estrella et al 2017)

Fossil	**Age (Ma)**	**Origin**	**Reference**
Copaifera	23	Tunisia	Fessler-Vrolant (1977)
Hymenaea	24	Dominican Republic	Hueber et al. (1986)
Prioria	24	Dominican Republic	Poinar et al. (1999)
Afzelia	27	Ethiopia	Pan et al. (2010)
Crudia	45	USA	Herendeen et al. (1990)
Aphanocalyx	46	Tanzania	Herendeen et al. (2000)
Daniellia – *Brandzeia* clade	53	France	de Franceschi et al. (2003)

Table II.3 : AIC values for oceanic and terrestrial long distance dispersal

Oceanic long distance dispersal

	LnL	numparams	d	e	j	AICc	AICc_wt
DEC	-63.14	2	0.0036	0.0009	0	130.4	2.0e-05
DEC+J	-51.86	3	1.0e-12	1.0e-12	0.022	109.9	0.57
DIVALIKE	-53.51	3	1.0e-12	1.0e-12	0.024	113.2	0.11
DIVALIKE+J	-53.51	3	2.0e-10	1.0e-12	0.024	113.2	0.11
BAYAREALIKE	-53.51	3	1.0e-12	1.0e-12	0.024	113.2	0.11
BAYAREALIKE+J	-53.51	3	1.0e-13	1.0e-13	0.024	113.2	0.11

Terrestrial long distance dispersal

	LnL	numparams	d	e	j	AIC	AIC_wt
DEC	-65.53	2	0.0033	0.0011	0	135.1	1.5e-06
DEC+J	-52.38	3	1.0e-12	1.0e-12	0.025	110.8	0.28
DIVALIKE	-52.55	3	1.0e-12	1.0e-12	0.026	111.1	0.24
DIVALIKE+J	-52.55	3	1.0e-12	1.0e-12	0.026	111.1	0.24
BAYAREALIKE	-52.55	3	1.0e-12	1.0e-12	0.025	111.1	0.24
BAYAREALIKE+J	-56.23	3	1.0e-13	1.0e-13	0.0092	118.5	0.0060

Chapitre III: Is species richness in the genus *Crudia* (Leguminosae) associated with ecological niche shifts or diversification rate shifts?

Domenech Boris[1], Bruneau Anne[1]

[1]Institut de Recherche en Biologie Végétale and Département de sciences biologiques, Université de Montréal, 4101 Sherbrooke Est, Montréal, Québec, H1X2B2, Canada

Résumé

La diversité des espèces n'est pas distribuée de manière homogène dans l'arbre du vivant. Certains groupes taxonomiques présentent une richesse spécifique plus élevée que d'autres. Cette disparité en termes de nombre d'espèces peut être associée à un changement des taux de diversification ou à un changement de niche dans un clade spécifique. Dans cette étude, nous examinons les patrons de diversité spécifique en prenant le genre pantropical *Crudia* (Leguminosae, Detarioideae) comme groupe modèle car celui-ci possède une richesse spécifique élevée comparativement à d'autres genres évolutivement proches. Les variations des taux de diversification au sein des Detarioideae et particulièrement pour le genre *Crudia* ont été caractérisées en utilisant des méthodes bayésiennes (BAMM). Les niches écologiques des espèces de *Crudia* ont été caractérisées à l'aide de 19 variables bioclimatiques. Les résultats montrent que la richesse spécifique du genre *Crudia* n'est pas associée à un changement de taux de diversification, mais qu'il existe en revanche des disparités entre les niches écologiques des espèces en fonction du continent où elles se situent. Les analyses montrent que les variations des taux de diversification chez les Detarioideae ne sont pas uniquement liées à la richesse spécifique des genres, mais que l'âge relatif des différents clades joue un rôle dans les changements des taux de diversification.

Mots clés : Detarioideae, *Crudia*, diversification, BAMM, niches écologiques, richesse spécifique, BioClim

Abstract

Species diversity is not homogeneously spread across the tree of life. Some taxa have higher species richness than others. This disparity can be associated with diversification rate changes or ecological niche shifts in specific clades. In this study, we examined patterns of species diversity using the pantropical genus *Crudia* (Leguminosae, Detarioideae) as a model group, because it displays high species richness compared to other closely related genera. Changes in diversification rates within Detarioideae and the genus *Crudia* were characterized using Bayesian methods (BAMM). Ecological niches of *Crudia* species were characterized using 19 BioClim variables. Results for *Crudia* show species richness is not associated with a change in diversification rate in this genus, and ecological species niches differ depending on the continent where species are encountered. Finally, changes in diversification rates within Detarioideae are not necessarily associated with the species richness of genera, but instead depend on the relative age of the clades.

Key words: Detarioideae, *Crudia*, diversification, BAMM, ecological niches, species richness, BioClim

III.1 – Introduction

In evolutionary biology, species richness is defined as the relative number of species in a given clade (Rabosky et al. 2012, Scholl et al. 2016). It can be studied at various taxonomic levels, from across the entire tree of life (Scholl et al. 2016), down to the level of family (Fiz-Palacios et al. 2011) or genera (Baker et al. 2013b). Species richness is known to vary considerably among clades (Richardson et al. 2001, Scherson et al. 2008, Escudero et al. 2012), with species-rich and species-poor clades often being closely related. Rabosky (2009) formalized this issue by asking the following question: "why do some groups have so many species and why do others have so few?"

Diversification can be thought as the balance between speciation (i.e. formation of new species in a given time frame) and extinction (i.e. disappearance of species in a given time frame) (Morlon 2014). Consequently, variations in diversification rates reflect increases or decreases in speciation and extinction rates. High species richness is often associated with temporal changes in diversification rates, particularly high turnover of both speciation and extinction rates (Alfaro et al. 2009). Speciation rates are directly influenced by the pace of molecular evolution related to mutation rates, intrinsic characteristics of species (i.e. generation time, life span, behavioral reproductive strategy) (Bromham 2009), or on environmental energy features (i.e. amount of light, temperature) (Davies et al. 2004). Speciation rates can also be influenced by the expression of positively selected physiological characters (Baker et al. 2014, Silvestro et al. 2014). Concomitantly, other factors like key morphological innovations (Cubas 2004, Kay et al. 2006) or ecological niche shifts (Velasco et al. 2016) are considered to be part of the evolutionary processes that lead to increased species richness. In species-rich clades, studies have shown correlations between increasing diversification rates and the appearance of key innovation characters, such as spurs in *Aquilegia* L. (Hodges 1997, Hodges 2000) or dental features in Mammals (Hunter et al. 1995). On the other hand, high species richness can also happen in clades without changes in diversification rate: some studies (Magallon et al. 2001, McPeek et al. 2007) suggest that high species richness also results from species and lineages accumulation through time, particularly related with an older clade age. Finally, high species richness is found repeatedly in many independent tropical clades: this pattern is thought to be related with tropics as museum, where lineages can accumulate species through time (Chown et al. 2000, Arita et al. 2008).

While some studies have considered species niches to be conserved through space and time (e.g. Darwin (1859), Losos (2008), Crisp et al. (2012)), others have shown that ecological niches can shift (e.g. Gallagher et al. (2010), Donoghue et al. (2014), Gamisch et al. (2016)). Niche shifts are associated with environmental changes and have been detected in many plant lineages with high species richness, such as Alliaceae (Jara-Arancio et al. 2014), Brassicaceae (Salariato et al. 2017), Leguminosae (Schrire et al. 2009), and Ranunculaceae (Horandl et al. 2011). Many features can be used to describe and characterize ecological species niches: abiotic features, such as temperature, precipitation, sun exposure, or altitude (Evans et al. 2009, Meynard et al. 2012, Salariato et al. 2017), as well as biotic features, such as competition, predation and mutualism (Litsios et al. 2012, Alexandre et al. 2017). In many lineages, climatic variables are the main explanatory factors of species distributions (Donoghue et al. 2014). In particular, past climate change has had a large impact on diversification in relation to niche shifts, especially in species-rich clades by adaptation of species either to dryer and warmer conditions (e.g. Rosaceae, Topel et al. (2012)) or to colder environments (e.g. Hypericaeae, Nurk et al. (2015), genus *Carex* L. Escudero et al. (2012)). Conversely, other factors, such as edaphic features can occasionally have strong effects on the distribution of diversity at smaller scales (Dumetz 1999).

Crudia Schreb. is comprised of trees growing in riverine or wet lowland habitats associated with freshwater streams. This genus, considered of African origin (Chap. II), shows a pantropical distribution, with approximately 34 species (Chap. I, II) spread across the tropical belt in South America, Tropical West Africa and Southeastern Asia. While African species are mostly found in gallery forests (Breteler et al. 2008), American species are primarily located in seasonally flooded lowlands, particularly in the Amazon basin (Amshoff 1939, 1953, Vieira 1990), and Asian species are found in inundated forests and infrequently inundated hill slopes (De Wit 1950, Hou et al. 1996). Overall, these habitats are similar and located near freshwater streams, essential for the dispersion of *Crudia*'s buoyant seeds. Here, our hypothesis is that, based on their habitats similarities, *Crudia* species did not experience ecological niche shifts during successive migrations. Although niche shifts are often described in groups of closely related species located in the same geographic area (Losos et al. 2003, Joly et al. 2014), niche shifts can also occur in clades where species have disjunct distribution (Smith et al. 2010, Liu et al. 2013, Areces-Berazain et al. 2016, Li et al. 2016, Li et al. 2017). Here, we ask whether there is evidence of ecological niche shifts in the pantropical genus *Crudia*. We will test for habitat similarity across continents, using multivariate analyses and abiotic environmental data and compare ecological niche occupation by species.

Species-rich genera have also been associated with shifts in diversification rates particularly relating to a high turnover in speciation or extinction rates (Alfaro et al. 2009). In the subfamily Detarioideae, de la Estrella et al. (2017) highlighted three potential diversification rate shifts during the evolution of the subfamily (respectively during the Eocene, Neogene and Quaternary) but did not demonstrate an association between these shifts and particular genera. Among the Detarioideae, *Crudia* is one of the most species-rich genera (Chap. II) (Lewis et al. 2005, de la Estrella et al. 2017, LPWG 2017), along with genera such as *Cynometra* L. (though now resolved as non monophyletic, see Radosavljevic et al. (2017)), *Copaifera* L. (Veiga et al. 2002), and *Gilbertiodendron* J. Leonard (de la Estrella et al. 2014). To date, no study has focused on determining whether species-rich clades within Detarioideae are specifically associated with shifts in diversification rate. We hypothesize that species richness in the genus *Crudia* is related to increasing diversification rates through time. We will evaluate the occurrence and rate of diversification shifts within genus *Crudia* using Bayesian methods. We will also test whether other genera in subfamily Detarioideae experienced independent changes in diversification rate by including data on species diversity.

III.2 – Materials and methods

III.2.1 – Study area and species occurrence records

We selected occurrence data from GBIF (2017) (data downloaded in October 2017), retaining only data associated with herbarium specimens (suppl. mat. 6). This was necessary to verify species identifications, to update specimen information based on our recent taxonomic treatment (Chap. I, II), and to remove incorrectly identified records. We also added data from our own collections database (especially images of herbarium specimens that are unavailable online from collections awaiting digitization, e.g. at Kew Herbarium), as well as from the New York Botanical Garden (NY) http://sweetgum.nybg.org/science/vh/, Paris (P) https://science.mnhn.fr/ and Naturalis herbaria (L, WAG, U) http://bioportal.naturalis.nl/. Duplicate occurrences were removed. In total, the dataset contained 233 occurrences, for 26 species of *Crudia* (suppl. mat. 6).

The geographic range of *Crudia* in Asia spans from Sri Lanka to Northern Australia, including the Malay-Thai Peninsula, Borneo Island and Northern Philippines. Geographic sampling in Asia is incomplete, as reliable occurrences have only been gathered from continental Asia, Malay Peninsula, Borneo Island, Palau, Papua New Guinea and Northern Australia. A recent taxonomic revision of the African species resulted in a relatively well-distributed sampling of *Crudia* species (Breteler et al. 2008) though sampling effort appears to be concentrated in Gabon and Cameroun, likely due to increased collection campaigns in those regions. Finally, most of the American occurrences come from the Amazon basin, with one occurrence in Central America and one occurrence in the Caribbean.

III.2.2 – Environmental variables

Ecological niches can be described using abiotic environmental variables, such as precipitation and temperature. We extracted 19 environmental BioClim variables developed by Hijmans et al. (2005) (available on the WorldClim website www.worldclim.org, version 2), describing temperature and precipitation at 30 arc-seconds resolution (about 1 km² at the equator). Given that *Crudia* is pantropical, we also used the occurrence data to partition *Crudia* species according to continent (i.e. Africa, America or Asia), and continents were thereafter considered as explanatory variables in multivariate analyses. All analyses were conducted in R (R development Core Team 2014).

III.2.3 – Diversification rate shifts

First, we used phylogenetic data from the study of de la Estrella et al. (2017). We used the original sequence matrix of de la Estrella et al. (2017) to produce a fully resolved and dated phylogenetic tree with BEAST 1.8.1 (Drummond et al. 2007). Seven calibration points were used to constrain the BEAST analysis on 292 terminal taxa (6 outgroups and 286 Detarioideae species). All seven fossil calibration points were applied using a lognormal distribution with a mean of zero, a standard deviation of 1.0 and an offset value equivalent to the age of the fossil. An eighth calibration point was applied to the root of the tree using a normal distribution with a mean of 65.0 Ma (equivalent to the age of the Legume family, as estimated by Bruneau et al. (2008)), a standard deviation of 10.0, with an upper truncation of 71.0 to avoid overestimating the age of the tree. Second, we conducted a BAMM analysis on the divergence time tree of the Detarioideae and of genus *Crudia* (Chap. II) to reconstruct diversification rate shifts. To reconstruct diversification rate shifts in the Detarioideae subfamily we added a new element to the analysis, compared to what was done in de la Estrella et al. (2017): as a prior, we included the number of species per genus (Lewis et al. 2005). This allows BAMM to assess the species diversity within each genus more accurately. BAMM was run for 5,000,000 generations and parameters were sampled every 5,000 generations for both trees (Detarioideae divergence time tree and *Crudia* divergence time tree). MCMC convergence was assessed for both analyses by verifying ESS were over 200 with a 10% burn-in. All analyses were conducted using the BAMMTools package in R (R development Core Team 2014, Rabosky et al. 2014).

III.2.4 – Ecological niche characterization

All multivariate analyses were conducted in R (R development Core Team 2014). In order to determine which BioClim variables had the greatest contribution to variance, we used the *dudi.pca* function in the *ade4* package (Dray et al. 2007) to perform a principal component analysis (PCA) on 233 species occurrences and 19 environmental variables. We extracted eigenvalues, describing the most important BioClim variable for each principal component (PC) (Table III.1). We scaled our data and used Euclidean distances in our data matrix. We constructed a distance matrix using the *betadisper* function and used the *permutest* function on this matrix to test for homogeneity of species occurrence dispersion. To test whether there were significant environmental differences between continents, we conducted a permutational multivariate analysis of variance using distance matrices (PERMANOVA) with continents as an explanatory variable over 10,000 permutations. This was performed using the *adonis* function in the *vegan* package (Dixon 2003, Oksanen et al. 2018). We used the function *pairwise.perm.manova* available in the package *RVAideMemoire* (Hervé 2018) to test for pairwise differences continents.

III.3 – Results

III.3.1 – Diversification rate shifts

At least three shifts in diversification rates can be observed on the summary configuration shift tree for the Detarioideae, including supplementary species sampling in BAMM (Fig. III.1): one shift occurs in the clade including *Isomacrolobium*, *Englerodendron*, *Anthonotha*, *Berlinia* and *Isoberlinia* (crown node dated of 13 Ma, with 95% HPD 9 to 18 Ma), with a marginal clade specific rates of diversification of 9.95 (clade 1 on Fig. III.1); a second shift occurs with *Macrolobium*, *Heterostemon*, *Elizabetha*, and *Paloue* (crown node dated of 23 Ma, with 95% HPD 17 to 28 Ma), with a marginal clade specific rates of diversification of 8.95 (clade 2 on Fig. III.1); and a third shift can be observed with *Cynometra* s.s. (including *Maniltoa*, see Radosavljevic et al. (2017)) and *Zenkerella* (crown node dated of 30.5 Ma, with 95% HPD 23 to 39 Ma) with a marginal clade specific rates of diversification of 7.60 (clade 3 on Fig. III.1). Within clade 2, the genus *Macrolobium* has the highest marginal clade rates of diversification among the Detarioideae with a value of 10.98. No variation in diversification rate shifts is associated with the genus *Crudia* (Figs. III.1, III.2). Models from BAMM reveals 20 distinct configuration shifts from the 95% credible sets (Fig. III.3). Only the nine shift configurations with the highest posterior probability are considered. One configuration assigns no shifts at a frequency of 49%. The other eight configurations with high posterior probability do assign one or more shifts to the tree with smaller frequencies. Taken together, these eight configurations consistently reveal three major shifts in the phylogeny (Fig. III.1).

III.3.2 – Characterizing niche differences

The first five principal axes of the PCA represent 95% of the environmental variation, but because the fourth (9.05%) and fifth (6.16%) axes explain less than 15% of the variance, only the first three are represented (Fig. III.4). The first (PC1, 38.94%), second (PC2, 25.16%) and third (PC3, 15.94%) components together explain c. 80 % of the total variation among the BioClim variables.

We took the four most strongly correlated BioClim variables for each axis (in bold, Table III.1). Variables strongly correlated with the first axis based on eigenvalues and on the variable correlation plots (Figs. III.4d, e, f) are BioClim 1 (Annual Mean Temperature), BioClim 3 (Isothermality), BioClim 16 (Precipitation of Wettest Quarter) and BioClim 19 (Precipitation of Coldest Quarter). Variables strongly correlated with the second axis based on eigenvalues are BioClim 2 (Mean Diurnal Range (Mean of monthly (max temp - min temp))), BioClim 7 (Temperature Annual Range), BioClim 13 (Precipitation of Wettest Month) and BioClim 15 (Precipitation Seasonality). Variables strongly correlated with the third axis based on eigenvalues are BioClim 4 (Temperature Seasonality), BioClim 5 (Max Temperature of Warmest Month), BioClim 8 (Mean Temperature of Wettest Quarter), and BioClim 11 (Mean Temperature of Coldest Quarter).

Accordingly to the permutational test, group dispersion is non-homogeneous (presented in Fig. III.5). Dispersion homogeneity within each group graphically shows three distinct continents. The values of average distance to median for Africa, America and Asia are respectively 3.807, 2.855 and 3.516. PERMANOVA indicates that, based on environmental features, the three continents are different with a significant *p-value* of 10^{-4} (Table III.2). However, pair-wise comparisons do not identify any differences in the degree similarity between continents (e.g., we cannot say if African environmental features are closer to Asian or American ones, likewise for all possible combinations).

III.4 – Discussion

III.4.1 – No significant diversification rate shift is associated with the genus Crudia

Based on its higher species richness compared to closely allied Detarioideae genera, we expected the genus *Crudia* to have experienced at least one shift in diversification rate during its evolution. However, we did not detect a diversification rate shift for *Crudia* at the subfamily or genus level (Figs. III.1, III.2). In a previous study, de la Estrella et al. (2017) detected at least three shifts in diversification rates through the evolutionary history of the subfamily Detarioideae during the Eocene, the Neogene and the Quaternary. However, they used the relative number of lineages through time as a calculation input to provide ages of diversification shifts. Here, we took an alternative approach to look at the diversification in the Detarioideae subfamily by using the precise number of species per clade as well as the divergence time tree. Our BAMM analysis allows us to detect where (i.e. in which clade, or at which node in the phylogeny) and subsequently when (i.e. during which era) diversification rate shifts occurred in the tree. Unlike de la Estrella et al. (2017), we found an overall increase of diversification rates in the whole Detarioideae tree (Fig. III.1), with extinction rates increasing slightly during the last 20 Ma, slowing down global diversification rates. We also found each of the three diversification rate shifts occurred in a distinct clades during the Oligocene/Miocene transition, instead of during the Eocene, Neogene and Quaternary as previously hypothesized by de la Estrella et al. (2017). These three clades include some of the most species-rich lineages in Detarioideae, but also some species-poor lineages. For example, one of the three clades includes species-rich genera such as *Macrolobium* Schreb. (74 species), *Brownea* Jacq. (21 species), as well as species-poor genera like *Elizabetha* M.R.Schomb. ex Benth (11 species), *Heterostemon* Desf. (6 species), *Paloue* Aubl. (3 species), and even the monotypic genus *Ecuadendron* D.A.Neill. All these genera are located in South American rainforest environments, particularly in the Amazon forest (Lewis et al. 2005).

Diversification rates depend on the relative age of the studied group, and of groups within it, as well as the number of species in each clade. Logically, in two clades with an identical number of species, the more recent one will display a higher diversification rate (i.e., more speciation events, leading to more species, during a similar amount of time). Although *Crudia* is reconstructed as one of the oldest genera within Detarioideae, with fossils dating from the Eocene (Herendeen et al. 1990), it does not show any change in diversification rates. This contrasts with other younger Detarioideae genera (e.g. *Macrolobium*, *Cynometra* s.s) in which diversification rates are the highest. Thus, the relatively high species richness in *Crudia* could be related to species accumulation through time as generally suggested by McPeek et al. (2007), rather than recent diversification rate shifts. Magallon et al. (2001) showed that high species diversity in a given clade is not necessarily associated with an accelerated diversification rate if the clade is sufficiently old, and that flowering plant lineages display a huge disequilibrium in species diversity, most likely due to the accumulation of species through time than a sudden acceleration in diversification rate.

Finally, it should be noted that the existence of currently species-poor lineages that were previously species-rich could lead to biased estimates of species diversity, shifts in diversification rates, and lineage richness (Morlon 2014, Marshall 2017).

III.4.2 – Species niches are different from one continent to another

Based on descriptions from the literature (De Wit 1950, Vieira 1990, Breteler et al. 2008), herbarium specimen data, and field observations, we determined that *Crudia* species are typically located in seasonally inundated habitats throughout its range. We hypothesized that species did not grow in different habitats between continents (i.e. no perceptible differences existed between continents). However, we find that the habitats of African, American and Asian species do not share identical environmental features, showing that niches differ significantly between continents. Niches differ most in terms of annual mean temperature, isothermality, and precipitations during the wettest and coldest quarter. These environmental characteristics may be related to the specific features of each continents (e.g. location of the Intertropical Convergence Zone on the continents, Bush et al. (2007)). Indeed, although they are located in the rainforest tropical biome, areas where *Crudia* species are distributed do not experience identical rainfall patterns or wind exposure due to the presence of mountains chains like the Andes (Liebmann et al. 2004) and Himalayas (Bhatt et al. 2005). When we compared the three continents, our analyses showed that no continent is more or less similar to another, in terms of environmental features. The PERMANOVA is supported by the graphical plot of the dispersion of our data (Fig. III.5). The three clusters do not appear close enough to interpret a significant overlapping. We could not validate the homogeneity of dispersion (prerequisite to conduct a PERMANOVA), however, PERMANOVA is very robust to heterogeneity, which is why we still conducted this test (Anderson 2017). Although *Crudia* species show clear biome conservatism – all species are strictly located within the tropical rainforest biome – they also display a pattern suggesting niche divergence within this globally similar tropical environment. Biome conservatism is a very strong constraint on global species distribution (Crisp et al. 2009) but species niche divergence has been detected within biomes (Losos et al. 2003, Graham et al. 2004, Debandi et al. 2012). Thus, although *Crudia* species evolution is restricted to the tropical rainforest biome, such as most Detarioideae (Schrire et al.

2005a, de la Estrella et al. 2017), species may have experienced niche changes within the same biome.

Although niches differ significantly between continents, niche similarities within each continent could be explained by several scenarios. First, during the Eocene when *Crudia* species dispersed from Africa to Asia and America, respectively around 46 and 42 Ma (Chap. II), the niches on each continent may have been identical. This is supported by the globally warmer climate of the Eocene (Zachos et al. 2001, Rohl et al. 2007), which resulted in a widespread continuous tropical belt from equatorial to northern and southern latitudes, with biological exchanges from one end to the other. At that time continents also had slightly different positions on Earth with landmasses gathered around the equator (Scotese 2001, 2004), which facilitated the presence of widespread and continuous tropical forests (Maley 1996). Tropical environments on different continents were probably more similar during that time than they are at present. Within a continuous and homogeneous forest, niches are more likely to remain constant through time, although local rainfall pattern or temperature variations might alter environments (e.g., monsoon rainfall, Huber et al. (2012)). Testing this hypothesis would require paleoclimate data from the Eocene. However, only data from the Pleistocene onwards is available in the WorldClim database.

A second possibility is that niches on each of the three continents were already different prior to dispersal, and that *Crudia* species were pre-adapted to their new environments. As Donoghue (2008) suggested, it is easier for a species to colonize a new location if it is pre-adapted to its new habitat. So, it is possible that *Crudia* species were already pre-adapted to their new environment, or that they subsequently evolved to fit their new environment after arrival, as suggested by Edwards et al. (2013), who refined this argument by postulating that niche shifts do not necessarily occur prior to dispersal, but can also occur when a species reaches its new environment.

Third, inter-continental niche differences can also be caused by biological pressures on the newly established species. Invasion of foreign environments, especially in the case of long distance dispersal as suggested for *Crudia* (Chap. II), is often accompanied by changes in biotic and abiotic environmental conditions. Invasive species often experience niche shifts when establishing in new regions (Gallagher et al. 2010, Medley 2010), which is frequently associated with rapid adaptation to their new environmental conditions (Broennimann et al. 2007, Prentis et al. 2008).

Ecological niches of *Crudia* species are statistically different through distribution of the genus, giving clues about habitat changes through time, probably related with settlement in new tropical environments (Asia and America) slightly different from the ancestral area of origin (Africa). One scenario is that *Crudia* species may have established on foreign shores following long distance dispersal, experiencing different environmental characteristics such as edaphic features (Fine et al. 2005) or new competitive interactions (Silvertown 2004, Silvertown 2008), which might have played a role in the niche specialization of *Crudia* species. Those scenarios show variability in ecological preferences among species in the genus *Crudia*, and denote their capacity to adapt to newly encountered environmental conditions.

Figure III.1 : Diversification rate shifts as determined by BAMM from the dated Detarioideae phylogeny. Intensity of colours on branches reflects the relative probability density of diversification rates (see color scale).
Clade 1 : *Isomacrolobium, Englerodendron, Anthonotha, Isoberlina* and *Berlinia*.
Clade 2 : *Macrolobium, Heterostemon, Elizabetha, Paloue, Ecuadendron* and *Brownea*
Clade 3 : *Cynometra s.s., Zenkerella* and *Maniltoa*

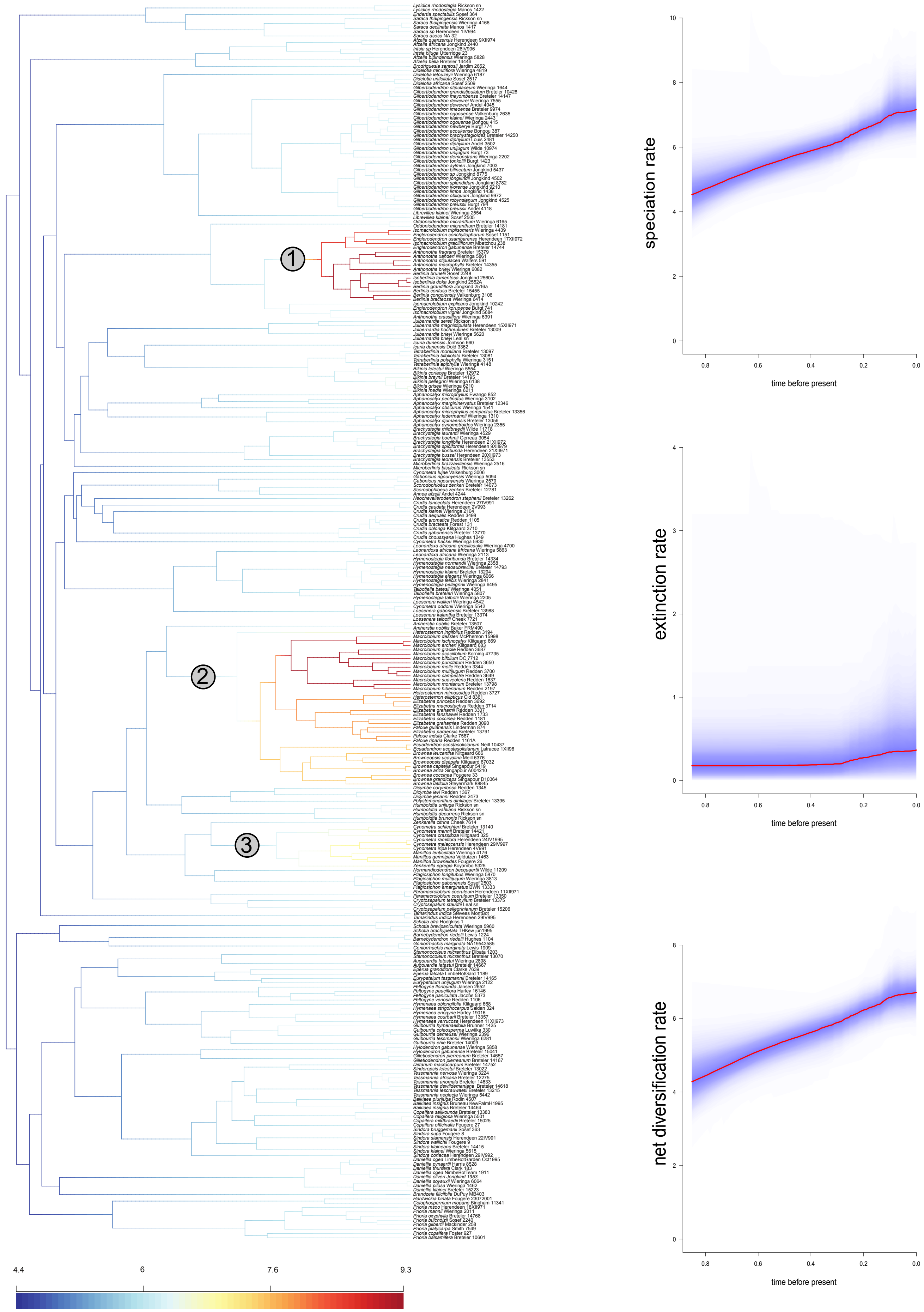


Figure III.2: Diversification rate shifts as determined by BAMM from the dated *Crudia* phylogeny.
Intensity of colors on branches refletcs the relative probability density of diversification rates (see colors at the bottom)

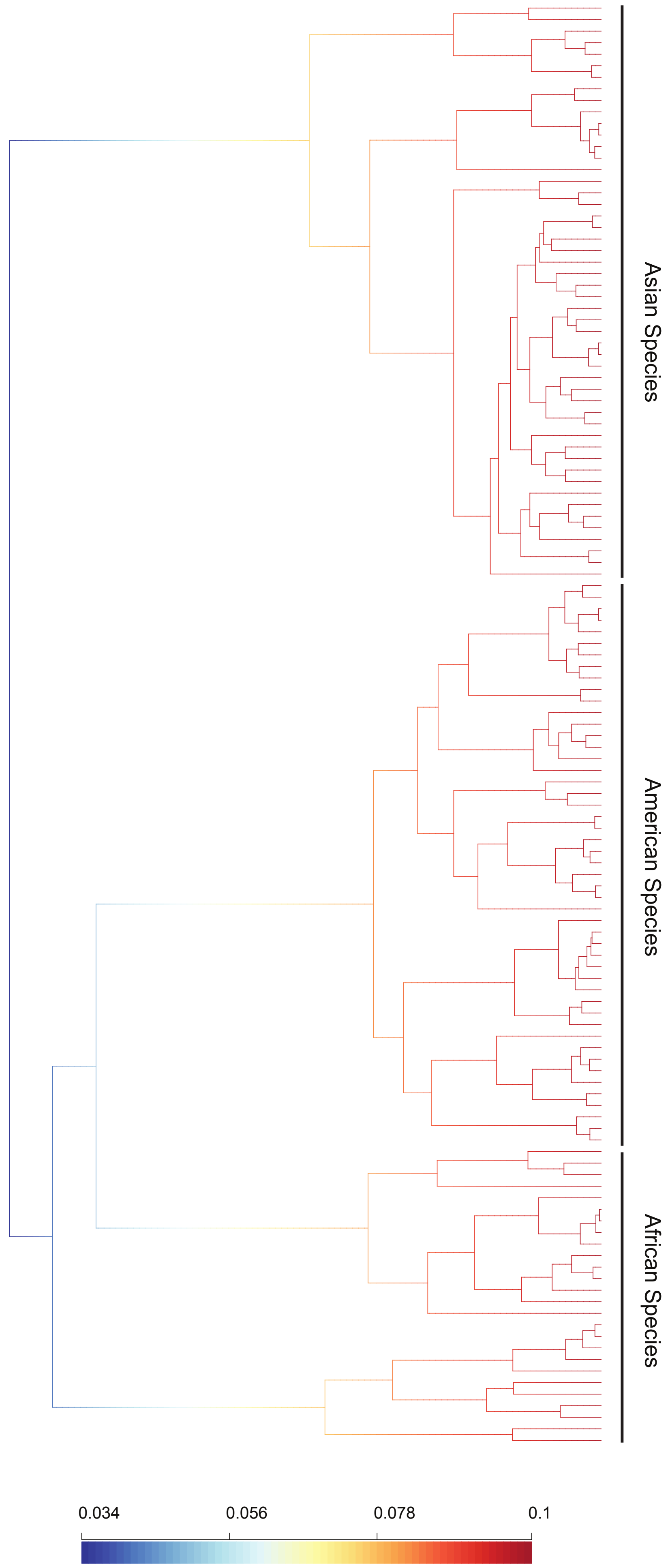


Figure III.3 : Nine first configuration shifts from the 95% credible set sampled by BAMM from the Detarioideae phylogeny

Figure III.4 : Bioclimatic niches of *Crudia* species

a), b), c), projection of PC1, PC2 and PC3

d), e), f), contribution of BioClim variables respectively on each PC

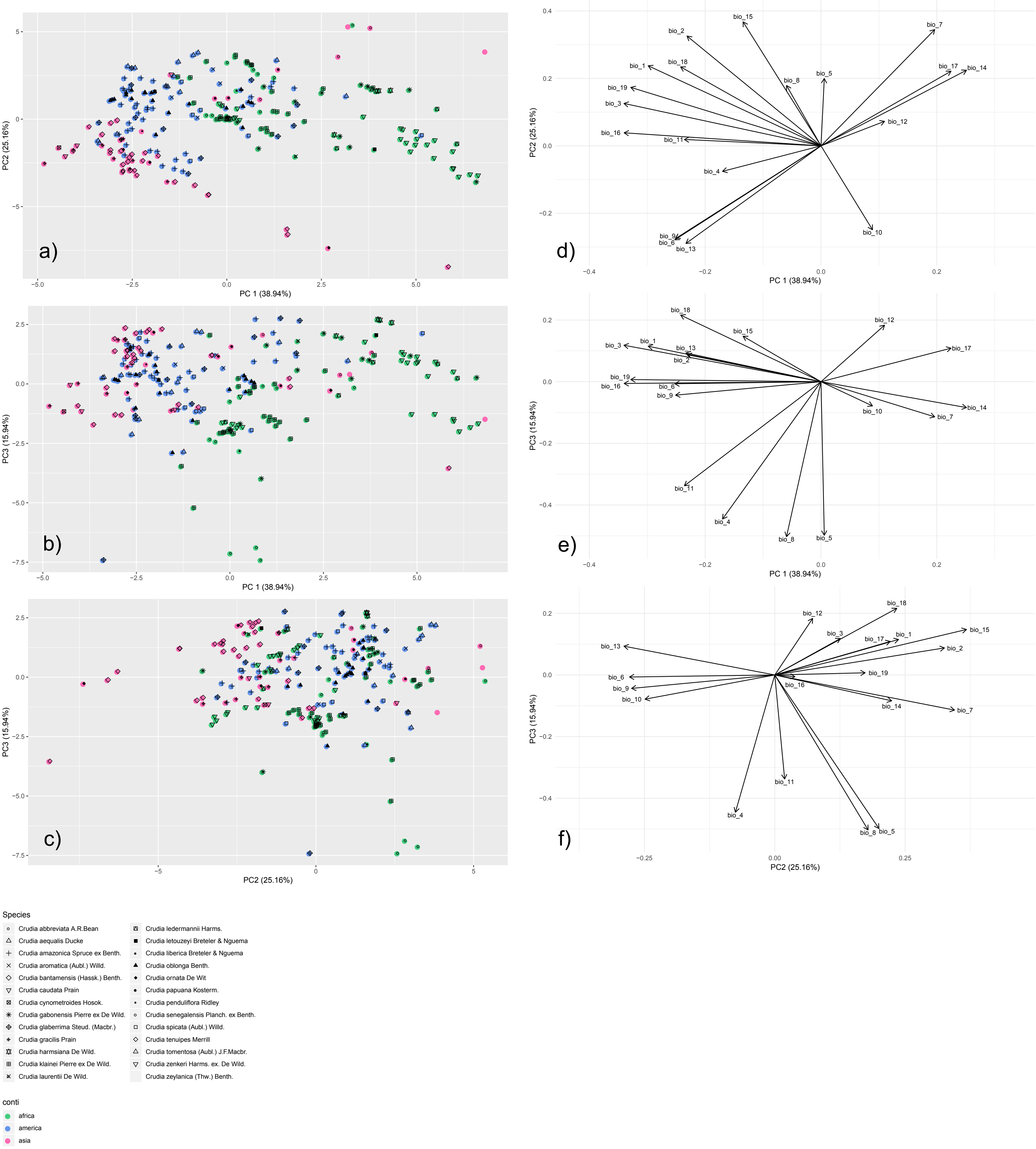


Figure III.5 : Dispersion homogeneity of *Crudia*'s species niches among continents

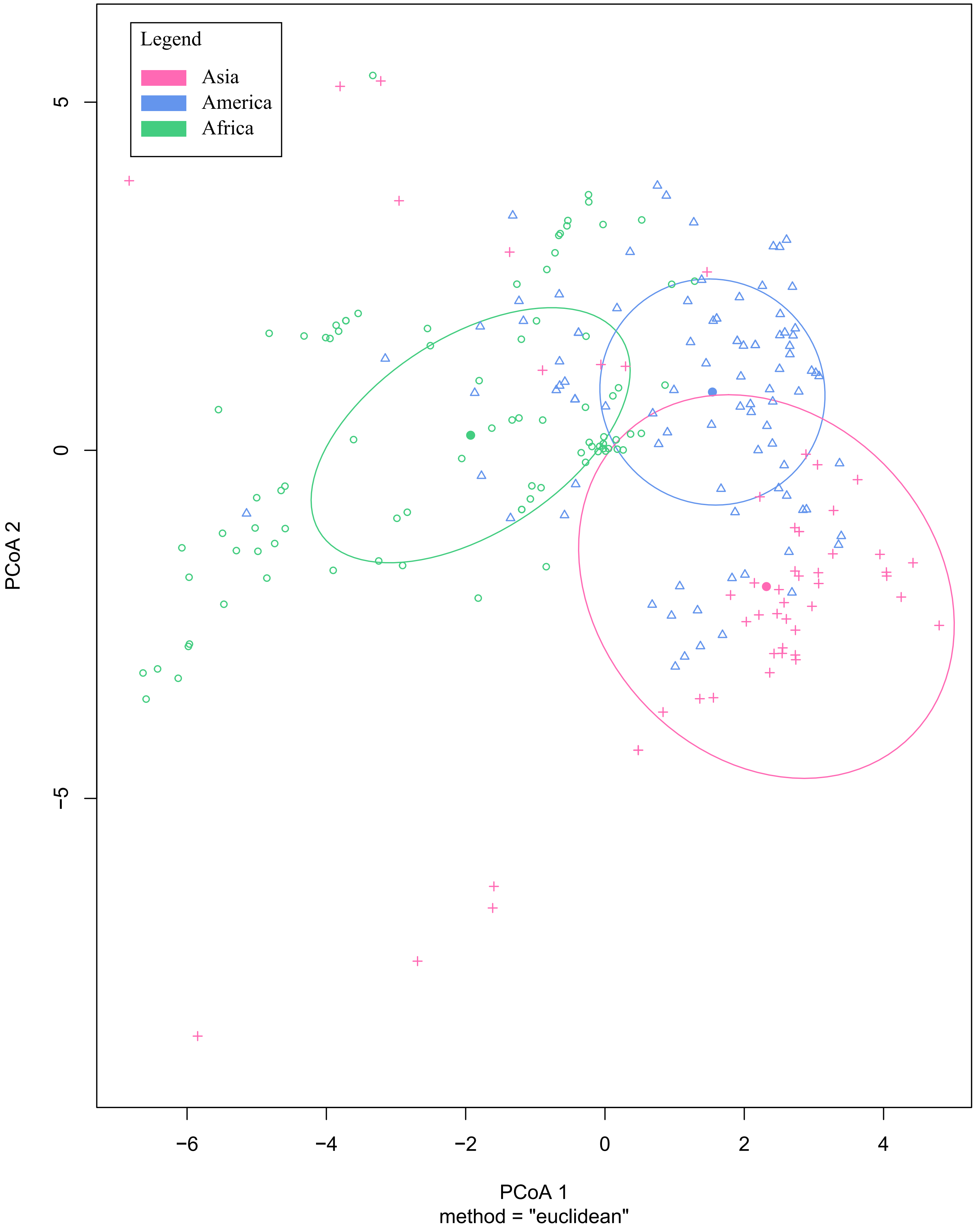


Table III.1 : Eigenvalues for BioClim variables depending on Principal Component

		Principal Component Space				
		CS1	CS2	CS3	CS4	CS5
BioClim Variables	bio 1	**-0.30**	0.24	0.12	-0.04	0.13
	bio 2	-0.23	**0.33**	0.09	-0.08	0.21
	bio 3	**-0.34**	0.13	0.12	0.03	-0.03
	bio 4	-0.17	-0.08	**-0.45**	0.21	0.18
	bio 5	0.01	0.20	**-0.50**	0.00	0.01
	bio 6	-0.25	-0.28	-0.01	0.14	**0.22**
	bio 7	0.20	**0.34**	-0.11	-0.12	-0.08
	bio 8	-0.06	0.18	**-0.50**	0.12	0.03
	bio 9	-0.25	-0.27	-0.04	0.15	0.21
	bio 10	0.09	-0.25	-0.08	-0.04	**0.68**
	bio 11	-0.24	0.02	**-0.34**	0.22	**-0.23**
	bio 12	0.11	0.07	0.18	**0.67**	-0.04
	bio 13	-0.23	**-0.29**	0.09	0.17	-0.17
	bio 14	0.25	0.22	-0.08	-0.14	**0.33**
	bio 15	-0.13	**0.37**	0.15	**0.27**	0.10
	bio 16	**-0.34**	0.04	-0.01	**-0.26**	-0.06
	bio 17	0.22	0.22	0.11	**0.44**	0.13
	bio 18	-0.24	0.23	0.22	-0.06	0.31
	bio 19	**-0.33**	0.17	0.01	-0.03	-0.13

Table III.2 : PERMANOVA values

	Df	SumsOfSqs	MeanSqs	F.Model	R^2	Pr(>F)
Continents	2	1087	543.52	37.643	0.24661	1e-04***
Residuals	230	3321	14.44		0.75339	
Total	232	4408			1.00000	

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Conclusion

Cette thèse, articulée autour de l'étude des espèces du genre *Crudia*, a permis de mettre en évidence la nécessité d'accroitre la quantité et la qualité des données pertinentes, notamment par la collecte de spécimens et l'obtention de séquences d'ADN menant à la reconstruction de l'histoire évolutive de ce genre. Mieux connaitre et savoir délimiter les espèces, à l'aide des caractères morphologiques, moléculaire et écologiques, en reliant les données provenant de différents domaines complémentaires (e.g. écologie, taxonomie, climatologie, géologie), nous a permit de comprendre l'évolution du genre dans son ensemble, ce qui n'avait jamais été réalisé jusqu'à présent. Nous avons également pu reconstruire l'évolution des patrons de distribution des espèces au cours du temps, mettant ainsi en lumière l'importance des phénomènes passés dans la formation des patrons de diversité actuels. Cette étude est novatrice, car c'est le premier travail considérant le genre *Crudia* dans son ensemble; toutes ces nouvelles données et interprétations lèvent le voile sur les patrons observés dans ce genre auparavant méconnu.

Révision taxonomique des espèces asiatiques du genre *Crudia*

Le travail du taxonomiste est de définir un seuil, parfois arbitraire, où une espèce commence lorsqu'une autre s'arrête, en fonction des caractères portés par les organismes qu'il étudie. Dans le premier chapitre de cette thèse, nous nous sommes basés exclusivement sur l'observation des caractères morphologiques des individus de *Crudia* qui se trouvent exclusivement distribuées dans la région asiatique, en appliquant le concept d'espèce morphologiques pour tester si les précédentes délimitations des espèces étaient valides ou non, et sur quelles bases nous pouvions concevoir de nouvelles délimitations d'espèces. Cette réévaluation des délimitations d'espèces avait pour objectif de mener à un meilleur aperçu de la richesse spécifique du genre *Crudia* dans la région asiatique, par une nouvelle estimation du nombre d'espèces, ainsi qu'à pouvoir proposer de nouveaux statuts de conservation des espèces en prenant en compte de leurs aires de distribution.

Nous suspections dès le départ que le grand nombre d'espèce asiatiques (auparavant 35), comparativement à ce qui est observé en Afrique et en Amérique (respectivement 10 et 9), était dû à une surévaluation du nombre d'espèces, lié aux études indépendantes sur les espèces asiatiques réalisées par de nombreux auteurs successifs. Partant de ce principe, nous avons également considéré que les anciens statuts de conservation seraient invalides et que de nouveaux devraient être proposés. La révision des espèces asiatiques a effectivement entrainé, comme nous le pensions, une réduction significative du nombre d'espèces auparavant décrites, en passant de 35 à 15 incluant la description d'une nouvelle espèce, *Crudia curvosa*, basée principalement sur un nombre stable de folioles ayant une morphologie caractéristique.

Cette nouvelle délimitation des espèces est basée non pas sur la pilosité des organes végétatifs, contrairement à ce qui était utilisé dans les études précédentes (De Wit 1950, Kostermans 1962), mais plutôt sur le nombre de folioles et leur forme. De nouveaux caractères, tels que la courbure de la nervure centrale, ont été utilisés pour discriminer les espèces entre elles. En réévaluant ainsi les délimitations des espèces, nous avons concomitamment proposés de nouveaux statuts de conservations, considérant à la fois la nouvelle distribution géographique de chaque espèce et les données à propos de l'état de conservation des environnements où se retrouvent les espèces de *Crudia*. Majoritairement, il ressort que les espèces ont un statut vulnérable ou en danger critique, principalement lié à la dégradation de leur environnement forestier par les activités humaines.

Le travail de taxonomie a été réalisé à l'herbier de Kew, en se basant sur plus de 120 spécimens asiatiques disponibles – il s'agit d'un des plus grands regroupements de spécimens du genre *Crudia* parmi les principaux herbiers mondiaux. Cependant, bien que le maximum d'information ait été tiré de ces spécimens, il s'agit toujours d'une vue parcellaire sur la diversité réelle des organismes. A l'avenir, le travail de taxonomie pourrait bénéficier d'une observation d'autres spécimens, mieux conservés et récoltés au cours de la dernière décennie, pour asseoir la délimitation des espèces. Particulièrement, des spécimens récemment collectés et conservés dans les herbiers en Asie pourraient être d'une grande utilité.

Nous n'avons pas réussi à trancher sur la légitimité d'une espèce, *Crudia wrayi*, auparavant décrite comme valide, à présent considérée comme douteuse. En effet, les caractères portés par les spécimens associés à cette espèce sont extrêmement fluctuants, sans oublier les descriptions et illustrations disponibles dans la littérature, qui sont également très variables. Cependant, il est possible que la consultation de spécimens supplémentaires permette de trouver un cadre descriptif plus précis et de redéfinir les limites de cette espèce. Ainsi, cela permettra de trancher entre l'existence d'une espèce à morphologie variable ou un problème d'identification de plusieurs espèces distinctes mais actuellement réunies sous un même nom.

Une des espèces nouvellement délimitée, *Crudia gracilis*, montre un polymorphisme plus élevé comparativement aux autres espèces, en particulier au niveau de la forme et du nombre des folioles. De plus, cette espèce possède une aire de distribution étendue, allant de la péninsule malaise à la Nouvelle Guinée. Il serait judicieux de réaliser une étude ultérieure prenant en compte le polymorphisme génétique, ainsi que de nouvelles études morphologiques sur d'autres spécimens, pour vérifier qu'il s'agit bien d'une espèce possédant des caractères plus variables que les autres, organisée en sous-populations distinctes.

Parallèlement, l'utilisation de la morphométrie géométrique sur l'appareil végétatif pourrait être un outil clé afin de discriminer les espèces entre elles (Cope et al. 2012) : en se basant sur les formes et les mesures des organes observées, il est possible de grouper les spécimens présentant les mêmes patrons morphologiques, et tester ainsi si la morphométrie seule peut permettre de distinguer les espèces entre elles (Gonzalez-Andres et al. 1996, Plotze et al. 2005, de la Estrella et al. 2009). Sachant que la délimitation des espèces du genre *Crudia* dans son ensemble est majoritairement basée sur des caractères qualitatifs liés à l'appareil végétatif (Breteler et al. 2008) (Chap. I), la géométrie morphométrique pourrait venir renforcer les délimitations entre les espèces en traitant les caractères d'un point de vue quantitatif. Ainsi, un grand nombre de descriptions utilisent la forme des folioles ou des stipules comme caractères discriminants entre les espèces; en quantifiant statistiquement la variabilité de ces caractères et en les associant à une espèce précise, il serait plus simple de discriminer les espèces entre elles. De manière similaire, l'utilisation de la morphométrie pourrait permettre de mieux placer les fossiles de *Crudia* dans la phylogénie et ainsi affiner la datation de l'histoire évolutive du genre. L'application de méthodes de morphométrie à la caractérisation des fossiles est régulièrement utilisée afin de préciser leur affinité taxonomique (e.g. Jacques et al. (2011), De Meulemeester et al. (2012), Dewulf et al. (2014)). En effet, en comparant les mesures du fossile à celles des espèces actuelles (e.g. forme des folioles, longueur des pièces florales, etc.), il est possible d'associer plus efficacement les fossiles à une espèce actuelle précise, plutôt qu'à un clade complet de manière générale (comme cela a été fait dans notre étude, où le fossile utilisé est associé au clade américain et non à une espèce en particulier). Ainsi, le placement du fossile serait bien plus précis, ce qui engendrerait une datation de l'arbre et des branchements entre les espèces plus exacte. En améliorant la précision du placement d'un fossile dans la phylogénie, les erreurs de calibration seront réduites et les âges reconstruits aux nœuds internes de la phylogénie seront plus fiables (Ho et al. 2009).

L'ajout de données provenant d'autres organes de ces arbres, tels que les fruits ou les fleurs, serait bénéfique pour venir compléter le travail de taxonomie majoritairement focalisé sur l'appareil végétatif. Tout particulièrement, les fleurs conservées en alcool seraient une alternative pérenne, comparée à la conservation des fleurs sous forme d'échantillons d'herbiers, qui se dégradent très rapidement lors de la dessiccation et perdent leurs pièces florales.

A l'avenir, une classification infragénérique prenant en compte des synapomorphies pourrait être proposée. Une tentative d'organisation en sections et sous-section a déjà été réalisé par De Wit (1950) sur les espèces Malaises : ce travail pourrait être le point de départ à une étude plus vaste, conduite à l'échelle du genre au complet. Nous avons déjà montré que le genre possède une structure phylogénétique interne correspondant peu ou prou aux continents sur lesquels se retrouvent les espèces (Chap. II) : une classification infragénérique permettrait de conceptualiser ces séparations et d'inclure de nouvelles informations diagnostiques à propos des espèces.

Dans une optique plus large, cette étude montre de l'intérêt de prendre en compte l'ensemble de la variabilité d'un groupe pour mieux en évaluer la diversité spécifique et les statuts de conservations des espèces qui en découlent. En effet, définir un statut de conservation est une opération délicate, prenant en compte de nombreux paramètres (Moritz 2002), car au sein d'une espèce, il existe des variants naturels agissant comme réservoir de diversité génétique, essentiels à conserver pour le maintien de l'espèce, mais qui ne semblent pas nécessairement à première vue totalement typiques de l'espèce caractérisée. Ainsi, au lieu d'avoir une espèce très typique, certains individus peuvent s'écarter de la « norme » (dans le sens statistique du terme) plus que d'autres, sans pour autant appartenir à une espèce différente. Pour éviter ce biais, il est nécessaire de posséder de nombreux spécimens représentatifs de l'étendue de la variabilité au sein de l'espèce, afin de statuer clairement si l'espèce est en danger ou non. Il faut également penser à considérer non seulement l'espèce en tant que telle, mais également son habitat et environnement immédiat, car si ceux-ci sont eux-mêmes menacés de manière plus large, l'espèce est alors en danger. Dans notre étude, nous avons apporté de nouveaux éléments à propos de la délimitation et de la distribution des espèces, qui pourront être utilisés ultérieurement afin de protéger les espèces et leur habitat *in situ* et de mettre à jour officiellement leur statut de conservation auprès de l'IUCN.

Biogéographie et systématique phylogénétique du genre *Crudia*

Dans le deuxième chapitre, nous nous sommes focalisés sur la reconstruction de la systématique phylogénétique de *Crudia*, afin de pouvoir étudier l'histoire biogéographique du genre complet, mais également les relations entre les espèces. Nous avons également cherché à comprendre l'origine des distributions observées des espèces, en reliant des phénomènes climatiques et géologiques passés aux patrons phylogénétiques observés.

Nous nous somme interrogés sur l'existence d'une structure phylogénétique infragénérique, ainsi que de savoir quelle était l'aire ancestrale de *Crudia*. Nous nous sommes également posé la question de savoir quels scénarios évolutifs et biogéographiques étaient les plus probables et quels phénomènes biogéographiques (vicariance, dispersion) étaient à même d'expliquer la distribution pantropicale du genre.

Dès le départ, nous considérions l'Afrique comme berceau du genre, car l'aire ancestrale estimée pour de nombreux autres genres de Detarioideae correspond également à ce continent. De même, nous nous attendions à une structuration du genre en fonction des continents actuellement occupés par les différentes espèces. Enfin, connaissant l'âge des Légumineuses, nous suspections que la vicariance gondwanienne comme explication des distributions observées serait à écarter au profit d'autres phénomènes biogéographiques comme la dispersion longue distance.

Nous avons effectivement montré que le genre *Crudia* est monophylétique et possède une origine africaine, comme la plupart des Detarioideae. Tandis que les espèces asiatiques et américaines forment deux clades séparés, les relations entre les espèces africaines restent plus délicates à définir. Le placement d'un fossile dans la phylogénie, ainsi que la datation des groupes externes, permet de dater l'apparition du genre *Crudia* au cours de l'Éocène, postérieurement à la séparation des masses continentales africaines et américaines. Cela implique que la distribution actuelle du genre ne peut être expliquée par la vicariance gondwanienne, mais plutôt que *Crudia* a subit deux évènements de dispersion indépendants, depuis l'Afrique vers l'Asie et vers l'Amérique du Sud, soit par voie terrestre via les boréotropiques en suivant un phénomène de dispersion par diffusion, soit par voie maritime via une dispersion longue distance, probablement liée à la capacité des graines à flotter à la surface de l'eau. Plus récemment, les lignées contenant les espèces actuelles de *Crudia* se sont diversifiées au cours de la transition Miocène/Oligocène.

En revanche, nous n'avons pas réussi à déterminer clairement certaines relations interspécifiques. L'échantillonnage des espèces africaines de *Crudia* est incomplet et pourrait grandement bénéficier de l'ajout de spécimens supplémentaires des espèces récemment décrites par Breteler et al. (2008) telles que *Crudia letouzeyi* et *C. liberica*. De plus, l'espèce *Crudia gabonensis*, largement distribuée en Afrique de part et d'autre du Dahomey Gap, s'avère potentiellement polyphylétique : il serait pertinent d'ajouter plus de spécimens formellement identifiés dans une nouvelle analyse phylogénétique, afin de vérifier si effectivement la délimitation de cette espèce doit être réévaluée. Plus de spécimens intégrés dans une phylogénie pourraient également montrer des patrons clairs quant à l'existence de sous-groupes contraints par la géographie (e.g. Gagnon et al. (2014)). Une étude populationnelle de *Crudia gabonensis*, basée sur d'autres marqueurs moléculaires issus des nouvelles techniques de séquençage (e.g. Fontaine et al. (2004), Olsson et al. (2017)) pourrait révéler s'il existe ou non des flux de gènes au sein de l'espèce et trancher sur la validité de l'espèce.

Nous n'avons également pas pu intégrer d'information sur les modes de pollinisation des espèces de *Crudia*, faute de données relatives à ce sujet. Cela aurait été pertinent pour avoir une idée des mécanismes d'échanges de flux de gènes entre populations éloignées, pour mieux cerner si celles-ci sont capables de s'hybrider. Il est probable que les fleurs des espèces de *Crudia* soient pollinisées par un vecteur biotique tel que les insectes, suite à la présence (notée à travers la littérature) de certaines fragrances se dégageant souvent des fleurs. Le type de pollinisateur pourrait être un paramètre essentiel dans la compréhension du patron de distribution disjointe des espèces, particulièrement sur les flux de gènes entre populations éloignées, si les pollinisateurs jouent un rôle de dissémination du pollen sur des longues distances, à l'échelle du continent (i.e. au sein de l'Afrique et de l'Amérique du Sud indépendamment, ou entre les îles dans le Pacifique). L'étude de l'introgression de certains gènes via les échanges de pollen serait une piste pour mieux comprendre la structuration des populations des individus appartenant aux différentes espèces du genre *Crudia*.

D’autre part, la capacité des graines de *Crudia* à être transportées par l’eau pourrait aussi un indice sur les potentiels flux de gènes entre populations distantes. Malheureusement il n’existe à l’heure actuelle aucune étude ayant retracé la dispersion effective des graines sur de longues distances, à travers les océans. De tels échanges de matériel génétique entre des endroits éloignés pourraient expliquer que certaines espèces possèdent des aires de distribution étendues, qui semblent morcelées (e.g. l’aire de distribution de *Crudia gabonensis* est divisée en deux par le Dahomey Gap ; *Crudia caudata* est distribuée dans la péninsule malaise et sur l’île de Bornéo ; *Crudia spicata* se retrouve dans les Antilles et dans la forêt amazonienne).

Certain clades de l’arbre phylogénétique souffrent d’un manque de résolution : en particulier, les clades les plus dérivés présentent de nombreuses polytomies, probablement à cause d’un manque de caractères discriminants entre les espèces. Les différentes espèces de *Crudia* montrent une grande similitude dans leurs séquences d’ADN, même pour des marqueurs rapidement divergents comme ITS et ETS. A l’avenir, il pourrait être judicieux d’utiliser les nouvelles techniques de séquençage afin de rechercher certaines zones du génome hyper variables, permettant de mieux discriminer les espèces entre elles et de résoudre les polytomies comme celle présente dans le clade des espèces asiatiques.

Nous avons eu l’opportunité d’utiliser un nouveau marqueur nucléaire apportant de la résolution, à savoir le marqueur ETS dont les amorces ont été produites *de novo* pour notre étude. Ce marqueur pourra certainement se révéler utile dans les études phylogénétiques chez d’autres membres des Detarioideae, car il possède une variabilité équivalente à celle de l’ITS (déjà beaucoup utilisé) tout en produisant des alignements de séquences comportant un nombre réduit d’indels.

La littérature reliée aux études de biogéographie comporte de plus en plus d’éléments en faveur des dispersions longue distance pour de nombreux groupes taxonomiques indépendants, reliés aux distributions observées des espèces. Alors que la vicariance gondwanienne semblait être l’explication favorisée dans le cadre du patron de distribution pantropicale de *Crudia*, nous avons démontré ici qu’il n’en est rien et que les phénomènes de dispersion passés, reliés à des conditions climatiques et géologiques connues, expliquent proprement la distribution des espèces. Notre étude démontre l’importance de prendre en compte les phénomènes passés ponctuels, rares, mais néanmoins essentiels au façonnement de la diversité du monde vivant actuel (Renner 2004) : le cas du genre *Crudia* vient parfaitement illustrer cette tendance qu'ont certains clades à subir des évènements ponctuels de dispersion qui façonnent leur histoire évolutive. Dans un contexte plus large, il serait intéressant d'aborder la question d'un point de vue statistique, afin de savoir si ces évènements de dispersion ponctuels sont réellement si inhabituels, ou bien s'ils sont présents à divers degrés dans tous les clades du vivant. Ainsi, on pourrait par exemple se demander si cette tendance à la dispersion se retrouve de manière identique chez toutes les familles d'angiospermes, ou bien si certaines familles présentent des prédispositions à la dispersion tandis que d'autres ne subissent pas ce type de phénomènes.

La richesse spécifique du genre : causée par les facteurs environnementaux ?

Certains genres de Detarioideae possèdent une richesse spécifique plus élevée que d'autres : il s'agit là d'un constat purement mathématique (Lewis et al. 2005). Dans ce troisième chapitre, nos objectifs étaient de déterminer si la richesse spécifique élevée du genre *Crudia* était liée à des changements dans les taux de diversification au cours du temps. De plus, nous avons cherché à identifier si les différentes espèces réparties sur trois continents possédaient des niches écologiques similaires, dans un contexte de conservatisme de niche au travers d'un même biome.

Nous nous sommes posé la question de savoir si les taux de diversification montraient une accélération, en relation avec la plus grande richesse spécifique observée chez *Crudia*. Puis, nous avons voulu savoir si les espèces possédaient des environnements similaires selon le continent qu'elles occupaient, et quels paramètres environnementaux définissaient les niches écologiques des espèces.

Nous avons donc testé l'hypothèse selon laquelle la richesse spécifique du genre *Crudia* était directement liée à un accroissement des taux de diversification, ainsi que pour d'autres genres possédant un nombre d'espèces élevé, à l'échelle des Detarioideae ; parallèlement, nous avons testé l'hypothèse selon laquelle les niches écologiques des espèces seraient similaires entre les continents.

C'est avec surprise que nous en sommes venus à la conclusion que, finalement, les espèces de *Crudia* n'avaient pas subit de changement de taux de diversification au cours de leur histoire évolutive, mais que la richesse spécifique du genre provenait vraisemblablement d'une accumulation des lignées au cours du temps plutôt que d'un brusque saut de diversification. De même, nous avons démontré que les niches évolutives n'était pas similaires entre elles selon le continent considéré, bien que les espèces se retrouvent toutes dans le même biome.

D'autres études (Broennimann et al. 2012, Alexandre et al. 2017) mentionnent la possibilité de comparer les niches entre elles afin de savoir lesquelles sont les plus similaires; si nous avons déjà mis en évidence que les environnements des trois continents présentent bien des différences, en revanche, nous n'avons pas réalisé de tests de manière à savoir si les niches au sein des continents présentaient des similitudes plus élevées entre elles, comparativement aux niches des autres continents. Cette lacune peut s'expliquer par le manque de données au sein de chaque espèce (e.g. il n'existe qu'un seul point d'occurrence pour *Crudia cynometroides*) ainsi que par l'absence de données pour certaines espèces (e.g. aucun point d'occurrence n'est disponible pour *Crudia blancoi*, qui se trouve à l'extrême Nord des Philippines et fait partie des espèces les plus périphériques dans l'aire de distribution asiatique). En l'absence de données supplémentaires, nous avons choisi de ne pas conduire ces tests, afin de ne pas réaliser de conclusion partielle hâtive.

D'autres tests auraient pu être conduits sur les données à notre disposition, particulièrement, ceux ayant pour but de détecter un recouvrement de niche. Comme dit précédemment, les niches entre continents sont différentes; en revanche, il serait pertinent de se demander si les niches se recouvrent entre elles au sein de chaque unité géographique, c'est-à-dire si elles présentent de fortes similitudes environnementales, et si c'est bien le cas, quelles sont les modalités de ce recouvrement. Cela permettrait de tester, par exemple, pour les espèces asiatiques, si les espèces ayant des niches qui sont les plus semblables entre elles sont situées dans des zones géographiques communes, ou bien si la localisation géographique est indépendante de l'indice de recouvrement. Évaluer les recouvrements de niches pourrait être réalisé à l'aide de diverses méthodes, comme celle développée par Broennimann et al. (2012), qui fait intervenir les indices *D* et *I* de recouvrement (pour plus de détails, voir Warren et al. (2008)) : plus ces indices sont élevés, plus le recouvrement des niches entre elles l'est également. Il est cependant nécessaire de délimiter précisément les aires de distribution respectives des espèces de *Crudia* sur les différentes continents, afin d'éviter de surestimer l’espace correspondant à chaque niche (Anderson et al. 2010) et de s’assurer que l’étendue géographique considérée à priori corresponde à une réalité biologique potentielle pour les espèces (VanDerWal et al. 2009). Ces pré-requis nécessitent cependant de posséder un nombre suffisant de points d’occurrences pour chaque espèce, afin de circonscrire au mieux une aire potentielle pouvant correspondre aux niches : dans notre cas, certaines espèces sont sous-échantillonnées et il serait difficile de produire une extrapolation fidèle de leurs aires de distribution respectives préalablement à l’analyse. D’autre part, les indices de recouvrement de niche sont comparés par paires entre les espèces, mais le déséquilibre dans nos données (i.e. une seule occurrence pour une espèce, face à plus d’une dizaine pour une autre) pourrait engendrer un biais dans l’interprétation des valeurs obtenues.

Enfin, nous aurions pu modéliser les distributions des espèces en utilisant des méthodes prédictives comme Maxent (Phillips et al. 2006, Phillips et al. 2008, Elith et al. 2011) en ayant au préalable défini les zones potentielles de distribution de chaque espèce. Cela aurait pu apporter des éléments complémentaires dans le cadre de l’évaluation des statuts de conservation des espèces et venir renforcer nos premières estimations.

Nous aurions pu aussi utiliser des critères écologiques et environnementaux pour délimiter les espèces (Wiens 2007). Tout particulièrement, les modèles de niche d’espèces semblent être indiqués lorsqu’il est question d’apporter de nouvelles données intervenant dans la délimitation des espèces, en plus des caractères morphologiques ou moléculaires habituellement utilisés, qui peuvent permettre jusqu’à la reconnaissance d’espèces cryptiques (Raxworthy et al. 2007, Ruiz-Sanchez et al. 2010).

Bien que les espèces de *Crudia* se retrouvent uniquement en milieu tropical, il n’existe pas à proprement parler une définition précise des conditions environnementales requises pour qu’elles puissent s’implanter dans une localité donnée et y prospérer (e.g. préférences édaphiques liées au pH, régime de précipitations, etc.). L’utilisation de modèles de niches, prenant en compte les paramètres abiotiques environnementaux, pourrait permettre de mieux appréhender l’espace correspondant aux habitats des différentes espèces. Ces modèles de niche, correctement calibrés, peuvent être utilisés pour extrapoler l’habitat des espèces (Araujo et al. 2007, Crimmins et al. 2013) dans un contexte de changements climatiques et d’activités anthropiques accrues (Guisan et al. 2005), ou encore évaluer la richesse spécifique de certains groupes taxonomiques, connaissant leurs optimums environnementaux (de la Estrella et al.

2012). Cela permettrait *à posteriori* de mieux comprendre les modalités d'implantation des espèces de *Crudia* à leurs emplacements actuels respectifs et d'appliquer une stratégie de conservation sur les sites géographiques correspondant aux habitats potentiels extrapolés des espèces.

Enfin, l'étude du conservatisme de niche phylogénétique pourrait constituer la suite logique de l'étude des niches écologiques de *Crudia*, mais aussi des Detarioideae en général. Le conservatisme de niche phylogénétique est le principe selon lequel les lignées ont tendance à conserver leur niche ancestrale suite à des processus écologiques et évolutifs (Harvey et al. 1991, Munkemuller et al. 2015), à ne pas confondre avec le signal phylogénétique, où deux espèces sœurs auront une plus forte probabilité de posséder des niches semblables, comparativement à deux espèces prises au hasard dans la phylogénie (Blomberg et al. 2002, Munkemuller et al. 2015). Dans le cadre des Légumineuses, il est généralement admis que la niche ancestrale correspond au biome succulent au niveau de la famille (Lavin et al. 2004, Schrire et al. 2005a, Schrire et al. 2005b), mais que la sous famille des Detarioideae aurait plutôt une niche ancestrale correspondant au biome de forêt tropicale humide (Schrire et al. 2005b, de la Estrella et al. 2017). Nous avons précédemment montré que, bien que les espèces de *Crudia* se retrouvent toutes dans le biome de forêt tropicale humide, elles possèdent des divergences de niches selon le continent où elles se situent. Il serait pertinent de se demander si ces divergences de niches se retrouvent également chez d'autres lignées à l'échelle des Detarioideae, et pour cela, l'étude du conservatisme de niche phylogénétique pourrait être un moyen de répondre à cette question, en apportant une dimension évolutive aux études de niches. De même, cela pourrait être un moyen de voir si les divergences de niches observées chez *Crudia* sont typiques d'une lignée en particulier, si elles sont fréquentes à travers l'histoire évolutive des Detarioideae ou au contraire plutôt exceptionnelles.

Enfin, dans un contexte plus large, les études de diversification sont en plein essor depuis que les méthodes bayésiennes peuvent s'y appliquer (Rabosky 2014). Bien qu'il reste encore du chemin à faire au niveau de la méthodologie, particulièrement pour éviter de surestimer les phénomènes de diversification lors de données manquantes (Marshall 2017), les études de diversification à large échelle sont un des moyens de mieux comprendre l'évolution des lignées (Koenen et al. 2013), reliée à la présence de caractères clés ou de facteurs environnementaux potentiellement explicatifs des patrons de diversité observés. Notre propre étude vient s’inscrire dans ce cadre théorique afin d’apporter de nouvelles conclusions quant à l’évolution du genre *Crudia*, en montrant qu’une haute richesse spécifique n’est pas nécessairement synonyme de diversification intense.

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Supplementary material 1

Specimen sampling of *Crudia* (and outgroup) used in phylogenetic analysis, with new identification when necessary and voucher information.

DOI : 10.5886/dpabji

http://data.canadensys.net/ipt/resource?r=crudia-specimens

Supplementary material 2

GenBank accession number of specimen used to conduct phylogenetic bayesian analysis of Detarioideae (reduced dataset with 105 specimens).

Species	Specimen	matK-trnK	rpL16	trnG-trnG2G	ITS
Afzelia africana	Jongkind 2440 (WAG)	KX161926	KY313126	KY312862	KY306485
Afzelia quanzensis	Herendeen 9-XII-97-4 (US)	KX161930	KY313129	-	KY306488
Amherstia nobilis	Baker 490 (K)	EU361849	KY313132	KY312865	KY306489
Annea afzelii	Andel 4244 (WAG)	KX161933	KY313134	KY312867	KY306491
Anthonotha crassifloliaa	Wieringa 6391 (WAG)	KX161936	KY313136	KY312869	KY306493
Anthonotha xanderi	Wieringa 5861 (WAG)	KX161941	KY313141	KY312872	KY306497
Aphanocalyx obscurus	Wieringa 1541 (WAG)	KX161949	KY313148	KY312879	AF513666
Aphanocalyx pectinatus	Wieringa 3102 (WAG)	KX161950	KY313149	-	AF513668

Augouardia letestui	Breteler 14667 (WAG)	EU361862	KY313130	KY312880	AY955796
Baikiaea insignis	Breteler 14464 (WAG)	KX161954	KY313150	KY312882	KY306500
Barnebydendron riedelii	Hughes 1104 (K)	KX161955	KY313153	KY312885	KY306502
Berlinia bracteosa	Wieringa 6414 (WAG)	KX161960	KY313155	KY312886	KY306504
Berlinia grandiflora	Jongkind 2516 (WAG)	EU361882	KY313159	KY312890	KY306508
Bikinia pellegrini	Wieringa 6138 (WAG)	KX161972	KY313165	KY312896	KY306512
Brachystegia spiciformis	Herendeen 9-XII97-9 (US)	EU361888	KY313173	KY312903	KY306518
Brandzeia filicifolia	Du Puy 403 (K)	EU361870	KY313174	KY312904	KY306519
Brodriguesia santosii	Jardim 2652 (MO)	KX161983	KY313175	KY312905	-
Brownea leucantha	Klitgaard 666 (K)	KX161992	KY313176	KY312910	KY306525
Browneopsis disepala	Klitgaard 67032 (K)	KX161995	KY313182	KY312911	KY306526
Colophospermum mopane	Bingham 11341 (K)	EU361915	KY313185	KY312913	AY955788
Copaifera mildbraedii	Breteler 15025 (WAG)	EU361917	KY313186	KY312914	AY955814
Copaifera officinalis	Fougere 27 (MT)	EU361918	KY313187	KY312915	AY955816
Copaifera religiosa	Wieringa 5501 (WAG)	KX161999	KY313188	KY312916	-
Copaifera salikounda	Breteler 13383 (WAG)	EU361919	KY313189	KY312917	AY955815
Crudia bracteata	Forest 131 (K)	KX162002	KY313192	KY312920	KY306531
Crudia caudata	Herendeen 2-V-99-3 (US)	KX162003	KY313193	KY312921	KY306532
Crudia choussyana	Hughes 1249 (K)	EU361921	KY313194	-	KY306533
Crudia gabonensis	Breteler 13770 (WAG)	KX162004	-	KY312922	KY306534
Crudia klainei	Wieringa 2104 (WAG)	KX162006	KY313195	-	KY306535
Crudia lanceolata	Herendeen 27-IV-99-1 (US)	KX162007	KY313196	KY312923	KY306536

Crudia oblonga	Klitgaard 3710 (K)	KX162009	KY313197	KY312924	KY306537
Cryptosepalum tetraphyllum	Breteler 13375 (WAG)	KX162014	KY313200	KY312926	KY306540
Cynometra hankei	Wieringa 5930 (WAG)	KX162017	KY313202	KY312928	KY306542
Cynometra lujae	Valkenburg 3006 (WAG)	KX162021	KY313204	KY312930	KY306544
Cynometra malaccensis	Herendeen 29-IV-99-7 (US)	KX162023	KY313205	KY312931	KY306545
Cynometra schlechteri	Breteler 13140 (WAG)	KX162029	KY313209	KY312935	KY306549
Daniellia soyauxii	Wieringa 6064 (WAG)	KX162044	KY313216	KY312942	KY306554
Daniellia thurifera	Clark 183 (K)	KX162045	-	KY312943	KY306555
Detarium macrocarpum	Breteler 14752 (WAG)	KX162046	KY313217	-	AY955817
Dicymbe levi	Redden 1367 (US)	KX162050	KY313220	KY312944	KY306558
Didelotia unifoliata	Sosef 2517 (WAG)	KX162064	KY313224	KY312948	KJ777189
Ecuadendron acostasolisianum	Neill 10437 (MO)	EU361938	KY313228	KY312952	KY306562
Elizabetha macrostachya	Redden 3714 (US)	KX162072	KY313233	KY312955	FJ817516
Elizabetha paraensis	Breteler 13791 (WAG)	EU361941	KY313234	KY312956	KY306567
Elizabetha princeps	Redden 3692 (US)	KX162073	KY313235	KY312957	FJ817519
Endertia spectabilis	Sosef 364 (WAG)	EU361943	KY313236	KY312958	KY306568
Englerodendron conchyliophorum	Sosef 1151 (WAG)	KX162074	KY313237	KY312959	KY306569
Englerodendron gabunense	Breteler 11174 (WAG)	KX162075	KY313138	KY312960	KY306570
Englerodendron korupense	Burgt 741 (WAG)	KX162077	KY313238	KY312961	KY306571
Englerodendron usambarense	Herendeen 17-XII-97-2 (US)	EU361944	KY313239	KY312962	KY306572
Eperua grandiflora	Clarke 7639 (US)	EU361946	KY313241	KY312964	AY955807
Eurypetalum unijugum	Wieringa 2122 (WAG)	KX162082	KY313244	KY312967	KY306574

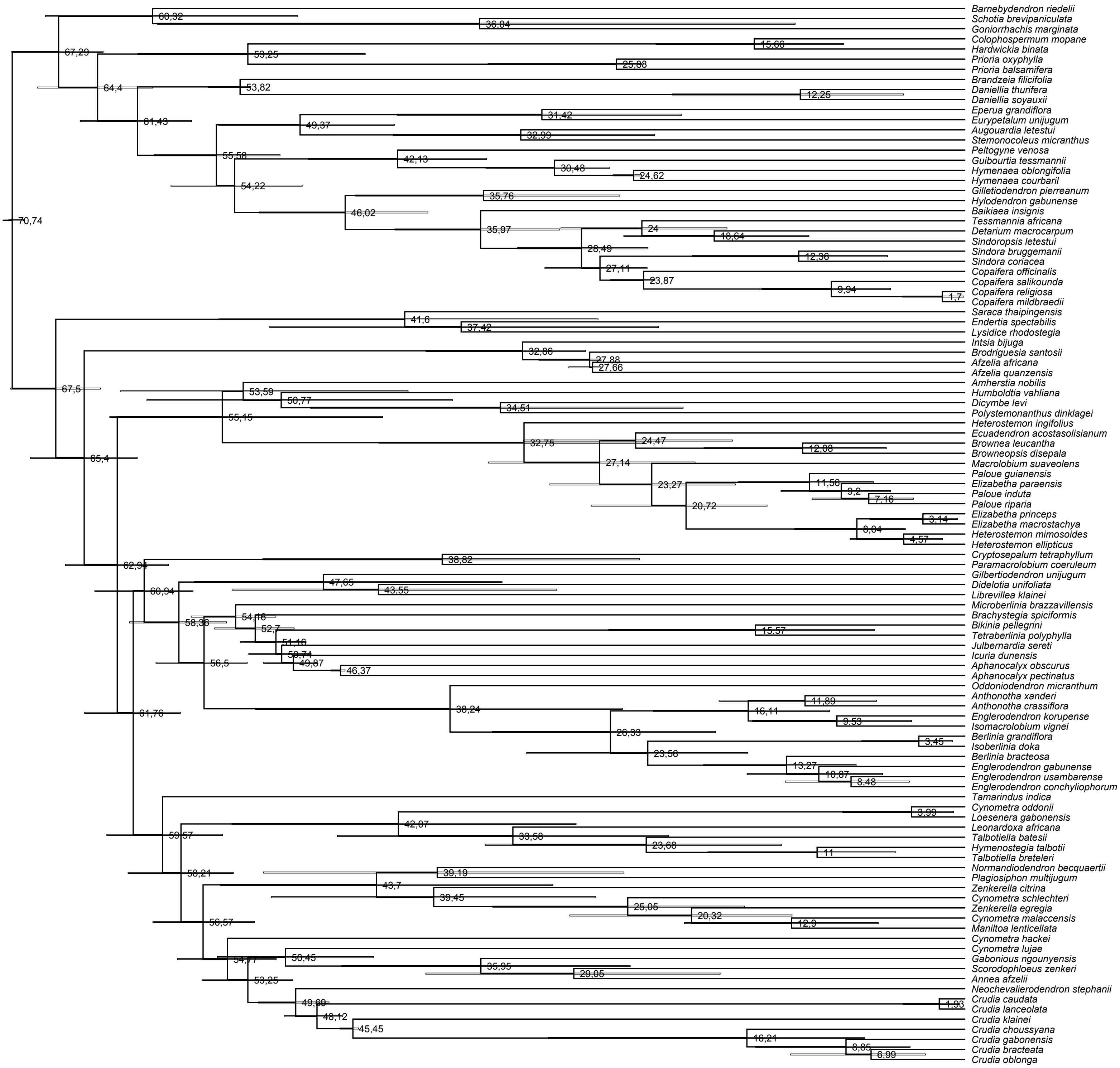
Gabonius ngouniensis	Wieringa 5094 (WAG)	KX162084	KY313245	-	KY306576
Gilbertiodendron unijugum	Wilde 10974 (WAG)	KX162165	KY313274	KY312996	KJ777274
Gilletiodendron pierreanum	Breteler 14167 (WAG)	EU361957	KY313275	KY312997	KY306578
Goniorrhachis marginata	Bruneau sn (K)	-	KY313276	KY313000	KY306580
Guibourtia tessmannii	Wieringa 6281 (WAG)	KX162177	KY313283	KY313005	-
Hardwickia binata	Fougere sn (MT)	EU361967	KY313284	KY313006	AY955789
Heterostemon ellipticus	Cid 8361 (NY)	-	-	KY313007	KY306581
Heterostemon ingifolius	Redden 3194 (US)	KX162178	KY313285	KY313008	FJ817525
Heterostemon mimosoides	Redden 3727 (US)	KX162179	KY313286	KY313009	FJ817528
Humboldtia vahliana	Rickson sn (OSC)	EU361970	KY313290	KY313013	KY306585
Hylodendron gabunense	Wieringa 5858 (WAG)	KX162184	KY313292	KY313015	-
Hymenaea courbaril	Breteler 13357 (WAG)	EU361972	KY313293	KY313016	-
Hymenaea oblongifolia	Klitgaard 668 (K)	EU361973	KY313295	KY313018	-
Hymenostegia talbotii	Wieringa 2205 (WAG)	KX162199	KY313305	KY313028	KY306596
Icuria dunensis	Jonhson & Avis 660 (WAG)	KX162201	KY313307	KY313030	-
Intsia bijuga	Utterridge 23 (K)	EU361981	KY313308	-	KY306597
Isoberlinia doka	Jongkind 2552 (WAG)	EU361982	KY313310	KY313032	AF513691
Isomacrolobium vignei	Jongkind 5684 (WAG)	-	KY313314	KY313037	KY306603
Julbernardia seretii	Rickson sn (OSC)	KX162214	KY313319	-	KY306606
Leonardoxa africana africana	Wieringa 2113 (WAG)	EU361992	KY313323	KY313042	KY306607
Librevillea klainei	Sosef 2505 (WAG)	KX162219	KY313324	KY313044	KJ777275
Loesenera gabonensis	Breteler 13988 (WAG)	KX162221	KY313326	-	KY306610

Lysidice rhodostegia	Manos 1422 (K)	EU361995	KY313330	-	KY306614
Macrolobium suaveolens	Redden 1637 (US)	KX162240	KY313343	KY313060	KY306625
Maniltoa lenticellata	Wieringa 4176 (WAG)	KX162245	KY313346	KY313063	KY306627
Microberlinia brazzavillensis	Wieringa 2516 (WAG)	EU362003	KY313348	KY313064	AF513697
Neochevalierodendron stephanii	Breteler 13262 (WAG)	EU362006	KY313349	KY313065	KY306629
Normandiodendron bequaertii	Wilde 11209 (WAG)	EU362007	KY313350	KY313066	KY306630
Oddoniodendron micranthum	Wieringa 6165 (WAG)	KX162247	KY313352	KY313068	KY306632
Paloue guianensis	Lindeman 1980/874 (U)	KX162250	KY313355	-	KY306633
Paloue induta	Clarke 7587 (US)	EU362015	KY313356	KY313069	KY306634
Paloue riparia	Redden 1161A (US)	EU362016	KY313357	KY313070	FJ817546
Paramacrolobium coeruleum	Breteler 13350 (WAG)	KX162252	KY313358	KY313071	KY306635
Peltogyne venosa	Redden 1106 (US)	KX162257	KY313363	KY313076	-
Plagiosiphon multijugus	Wieringa 3813 (WAG)	KX162269	KY313367	KY313080	KJ777283
Polystemonanthus dinklagei	Breteler 13395 (WAG)	EU362028	KY313368	KY313081	-
Prioria balsamifera	Breteler 10601 (WAG)	KX162273	KY313369	KY313082	KY306639
Prioria oxyphylla	Breteler 14768 (WAG)	KX162279	KY313373	KY313088	KY306642
Saraca thaipingensis	Wieringa 4166 (WAG)	KX162286	KY313377	KY313094	-
Schotia brachypetala	Wieringa 5960 (WAG)	KX162289	-	-	KY306647
Scorodophloeus zenkeri	Breteler 12780 (WAG)	EU362041	KY313380	KY313097	KY306648
Sindora bruggemanii	Sosef 363 (WAG)	EU362043	KY313382	KY313099	AY955824
Sindora coriacea	Herendeen 29-IV-99-2 (US)	EU362044	KY313383	KY313100	KY306650
Sindoropsis letestui	Breteler 13022 (WAG)	EU362049	KY313389	KY313106	AY955818

Stemonocoleus micranthus	Breteler 13070 (WAG)	EU362051	KY313390	KY313107	AY955795
Talbotiella batesii	Wieringa 4051 (WAG)	-	KY313392	KY313109	KY306652
Talbotiella breteleri	Wieringa 5807 (WAG)	KX162296	KY313393	KY313110	KY306653
Tamarindus indica	Stevees sn (MT)	KX162298	KY313395	-	KY306655
Tessmannia africana	Breteler 12275 (WAG)	EU362057	KY313396	KY313112	KY306656
Tetraberlinia polyphylla	Wieringa 3151 (WAG)	EU362061	KY313405	KY313121	AF513705
Zenkerella citrina	Cheek 7614 (K)	EU362066	KY313407	KY313123	KY306664
Zenkerella egregia	Kayombo 5325 (MO)	KX162320	KY313408	KY313124	KY306665

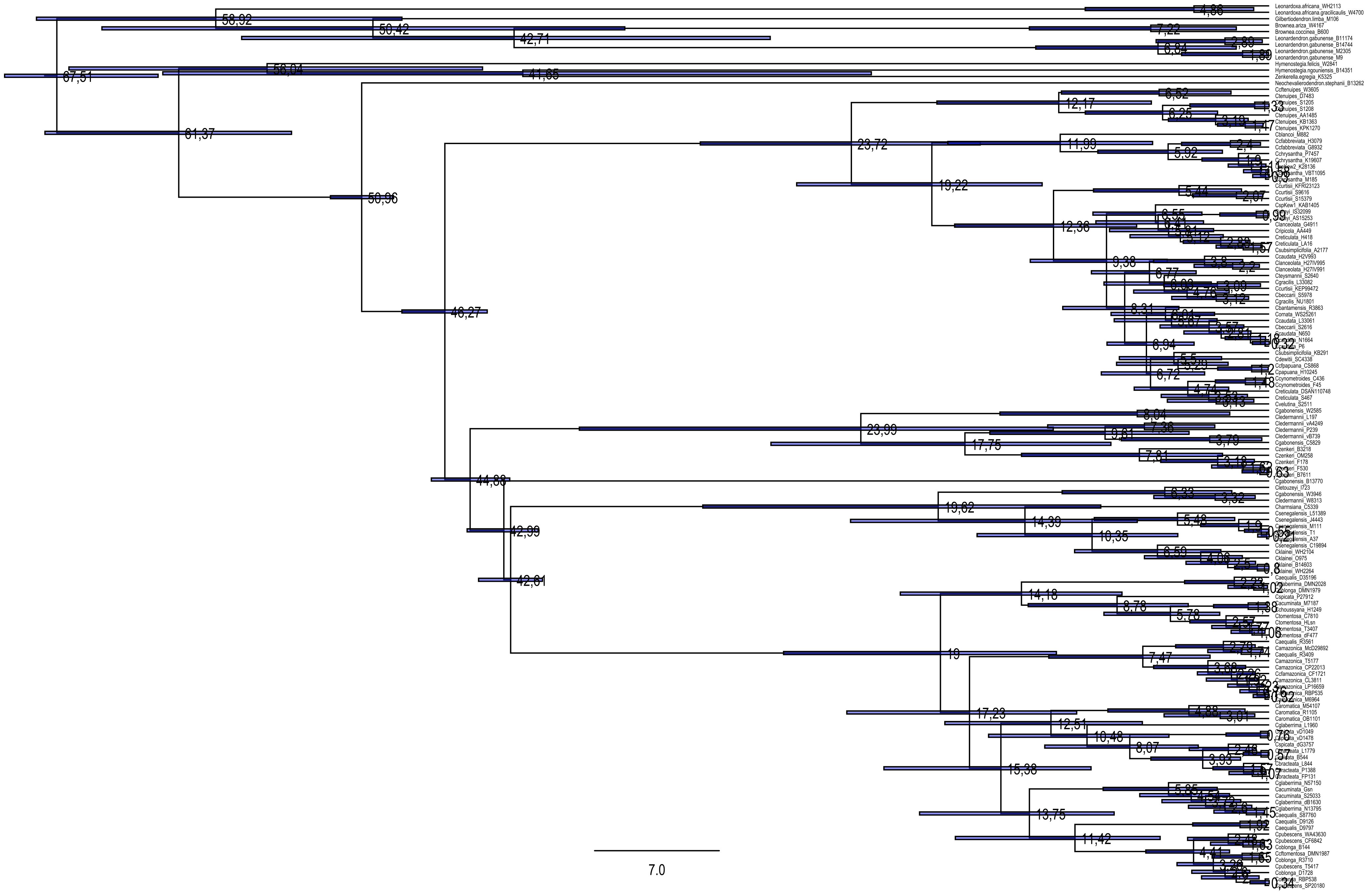
Supplementary material 3

Divergence time calibrated tree of Detarioideae subsampling using sequences data from de la Estrella et al. 2017. Horizontal blue bars are showing 95% HPD of the age node span. Node ages are in Ma



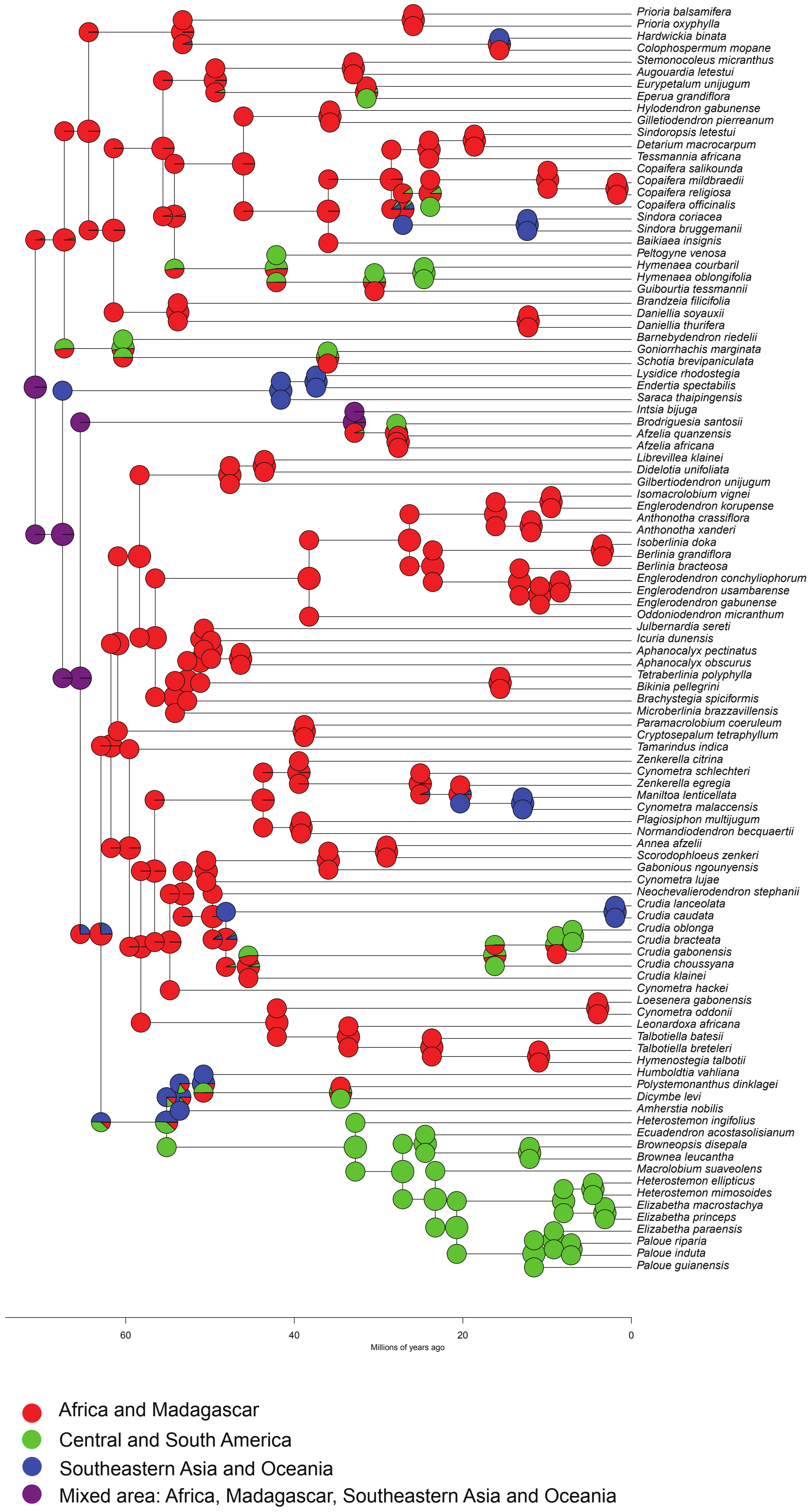
Supplementary material 4

Divergence time analysis of *Crudia* and outgroups



Supplementary material 5

Biogeographical scenario inferred by BioGeoBEARS displaying ancestral range estimation for the Detarioideae



Supplementary material 6

Species occurrences and identified voucher specimens

Species	Continent	Longitude	Latitude	Voucher ID*	Herbarium
Crudia abbreviata A.R.Bean	Asia	141.11666666666667	-8,6333333	Ridsdale NGF33512	K
		142.16666666666666	-13.4166667	Hyland 3079	K
		142.64083333333332	-12.4552778	Gray 08932	K
Crudia aequalis Ducke	America	-58.0219	-2.74889	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1374454	NY
		-66.1142	1.27592	http://n2t.net/ark:/65665/377e2294c-17ce-43cc-8b93-8fb17efc5873	US
		-66.391667	1.091667	http://data.biodiversitydata.nl/naturalis/specimen/U.1241120	U
		-66.41	1.16	http://n2t.net/ark:/65665/35d57cdc9-f167-4f49-991e-32319607c48e	US
Crudia amazonica Spruce ex Benth.	America	-54.7405	-2.44961	http://sweetgum.nybg.org/vh/specimen_details.php?irn=540013	NY
		-54.961	-2.59367	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373647	NY
		-55.8661	-1.76556	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373630	NY
		-55.8676	-1.7716	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373640	NY
		-56.3781	-1.4616	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373627	NY
		-56.6558	-4.70099	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373643	NY
		-57.7183	-3.38361	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373657	NY
		-59.9016	-3.17154	http://sweetgum.nybg.org/vh/specimen_details.php?irn=452158	NY
		-59.9619	-3.25327	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373656	NY
		-60.0507	-3.20432	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373632	NY

	-60.6667	-7.5833	http://n2t.net/ark:/65665/3504ae484-99fd-4020-8eac-aa7cc033b080	US
	-61.03	-2.4275	http://sweetgum.nybg.org/vh/specimen_details.php?irn=2987045	NY
	-61.29	-4.7086	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373637	NY
	-61.3731	-3.8983	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373645	NY
	-61.6268	-3.55354	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373650	NY
	-62.9508	-0.7589	http://n2t.net/ark:/65665/329cfd9c8-4a29-42cc-9cb6-aa193a64859d	US
	-62.9703	-0.8744	http://n2t.net/ark:/65665/3cca36b89-2bd8-487d-824f-dbf19e4d6ad5	US
	-63.3333	-8.8167	http://n2t.net/ark:/65665/30b66f4f1-cb3f-43dc-9051-f168c49835f9	US
	-63.9111	-0.3525	http://n2t.net/ark:/65665/3ecc40aa6-6018-42a6-96b7-566b84118481	US
	-64.3	-0.4	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1371021	NY
	-64.4073	-9.28371	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373626	NY
	-64.8042	-3.22083	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373634	NY
	-64.8793	-3.44917	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373625	NY
	-65.0	-2.0	http://n2t.net/ark:/65665/30b64d09a-0224-4338-847b-50e58942022d	US
	-65.28	-7.47	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373649	NY
	-65.5853	-1.8581	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373641	NY
	-65.7556	-2.62923	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373631	NY
	-66.3833	-0.4167	http://n2t.net/ark:/65665/339ce2f75-de32-4537-b538-d8fd3794b8d3	US
	-66.9944	-1.8861	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1371065	NY
	-67.0	-3.0	http://n2t.net/ark:/65665/318dd91b1-	US

				1c12-4bdd-ac29-72a140b3f2df	
		-67.5707	-3.72761	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373639	NY
		-67.83	-2.83	http://n2t.net/ark:/65665/3076b0786-c59f-446b-a8e2-5095e37de5f1	US
		-70.166667	0.5	http://data.biodiversitydata.nl/naturalis/specimen/U.1241122	U
Crudia aromatica (Aubl.) Willd.	America	-53.05	5.05	http://coldb.mnhn.fr/catalognumber/mnhn/p/p03111145	P
		-56.616667	3.433333	http://data.biodiversitydata.nl/naturalis/specimen/U.1259039	U
		-56.788889	2.325	http://data.biodiversitydata.nl/naturalis/specimen/L.3884751	L
		-59.0237	4.75292	http://n2t.net/ark:/65665/3b5fd39e6-dda1-482b-977c-1aebb18e1ece	US
Crudia bantamensis (Hassk.) Benth.	Asia	112.75	-0.683333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982026	L
		112.833333	-0.716667	http://data.biodiversitydata.nl/naturalis/specimen/L.1982010	L
		116.31944444444444	0.2497222	Lee SL403	K
		116.819556	-1.099389	http://data.biodiversitydata.nl/naturalis/specimen/L.3894794	L
		116.833333	-1.133333	http://data.biodiversitydata.nl/naturalis/specimen/L.3814807	L
		116.939731	-0.989192	http://data.biodiversitydata.nl/naturalis/specimen/L.3895583	L
		117.0	-1.0	http://data.biodiversitydata.nl/naturalis/specimen/L.1982132	L
		117.495833	4.933333	http://medialib.naturalis.nl/file/id/L.1982028/format/large	L
		117.7875	4.6375	http://data.biodiversitydata.nl/naturalis/specimen/L.1982425	L
		117.808333	5.470833	http://data.biodiversitydata.nl/naturalis/specimen/L.1982029	L
		117.916667	5.833333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982021	L
		117.983333	5.866667	http://data.biodiversitydata.nl/naturalis/specimen/L.1981978	L

		118.341667	4.341667	http://data.biodiversitydata.nl/naturalis/specimen/L.1982423	L
		118.466667	4.633333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982422	L
Crudia caudata Prain	Asia	101.75	6.5	http://data.biodiversitydata.nl/naturalis/specimen/L.1982149	L
		109.95	-1.25	http://data.biodiversitydata.nl/naturalis/specimen/L.1982153	L
		114.416667	4.283333	http://data.biodiversitydata.nl/naturalis/specimen/L.3884887	L
Crudia gabonensis Pierre ex De Wild.	Africa	10.031667	2.803333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639669	WAG
		10.450000	-2.233333	http://medialib.naturalis.nl/file/id/WAG.1639646/format/large	WAG
		11.133333	2.816667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639668	WAG
		11.623611	-0.163056	http://medialib.naturalis.nl/file/id/WAG.1639655/format/large	WAG
		13.475	0.831667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639640	WAG
		14.85	0.633333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639663	WAG
		-3.583333	5.7	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639636	WAG
		-8.171667	5.641667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639637	WAG
		9.058333	4.070000	http://medialib.naturalis.nl/file/id/WAG.1639666/format/large	WAG
		9.68	-2.230556	http://data.rbge.org.uk/herb/E00217250	K
		9.875	-1.9283	http://n2t.net/ark:/65665/3c883fc86-edbc-4757-8292-270aa683a25c	US
		9.875	-1.928333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639647	WAG
		9.98333	2.98333	http://coldb.mnhn.fr/catalognumber/mnhn/p/p00187908	P
Crudia glaberrima Steud. (Macbr.)	America	-73	-7.5	http://sweetgum.nybg.org/vh/specimen_details.php?irn=66273	NY
		-49.6833	-0.75	http://n2t.net/ark:/65665/3e61fd454-	US

				6a38-4960-9c40-c0b5e107728c	
		-49.7326612	-0.7998302	http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=1371525	NY
		-58.7833	7.33333	http://n2t.net/ark:/65665/3b2aa7bd6-a5ea-475e-af9e-2ecfc694208d	US
		-59.5	7.75	http://data.biodiversitydata.nl/naturalis/specimen/U.1259123	U
		-61.733333	8.066667	http://medialib.naturalis.nl/file/id/L.1982082/format/large	L
		-63.0225	-7.4927	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373659	NY
		-68.7933	-3.57785	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373660	NY
		-68.7933022	-3.5778475	http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=1373660	NY
		-72.7	-9.1167	http://sweetgum.nybg.org/vh/specimen_details.php?irn=61613	NY
		-76.17	-0.03	http://n2t.net/ark:/65665/3273a10ad-c9e0-438d-adfb-5fdbf43a3c70	US
		-83.61667	10.85	http://coldb.mnhn.fr/catalognumber/mnhn/p/p03111057	P
Crudia gracilis Prain	Asia	112.05	0.833333	http://data.biodiversitydata.nl/naturalis/specimen/L.3894125	L
		118.333333	4.966667	http://medialib.naturalis.nl/file/id/L.1982030/format/large	L
		112.666667	-1.250000	http://medialib.naturalis.nl/file/id/L.1982368/format/large	L
		113.766667	-1.933333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982366	L
		114.31666666666666	4.4333333	Dransfield 6799	K
		114.683333	4.2	http://data.biodiversitydata.nl/naturalis/specimen/L.1982139	L
		117.283333	2.083333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982416	L
		145.416667	-5.166667	http://medialib.naturalis.nl/file/id/L0018867_MLN/format/large	L
		145.58333333333334	-5.1666667	Katik NGF46837	K
Crudia harmsiana De Wild.	Africa	14.933333	0.616667	http://medialib.naturalis.nl/file/id/WA	WAG

				G.1639601/format/large	
		15.283333	-4.3	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639604	WAG
		15.416667	-4.216667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639603	WAG
		15.533333	-4.283333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639608	WAG
Crudia klainei Pierre ex De Wild.	Africa	10.183333	0.266667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639576	WAG
		2.7	6.466667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639600	WAG
		-4.1	5.283333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639565	WAG
		-4.116667	5.333333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639548	WAG
		-4.133333	5.283333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639571	WAG
		-4.133333	5.333333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639549	WAG
		-4.266667	5.316667	http://medialib.naturalis.nl/file/id/WAG.1639567/format/large	WAG
		-4.333333	5.25	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639558	WAG
		8.78333	4.88333	http://coldb.mnhn.fr/catalognumber/mnhn/p/p00187958	P
		9.316667	0.325	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639575	WAG
		9.333333	0.55	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639578	WAG
		9.450000	0.416667	http://medialib.naturalis.nl/file/id/WAG0249261_MLN/format/large	WAG
		9.466667	1.283333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639586	WAG
		9.716667	4.066667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639622	WAG
		9.716667	4.266667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639598	WAG
		9.808333	2.228333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639590	WAG

		9.823333	2.235	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639587	WAG
		9.85	2.3	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639615	WAG
		9.866667	2.283333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639597	WAG
		9.868333	2.28	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639616	WAG
		9.8855	-0.811528	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639580	WAG
		9.896667	2.881667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639618	WAG
		9.9	2.91667	http://coldb.mnhn.fr/catalognumber/mnhn/p/p00187953	P
		9.916667	2.916667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639556	WAG
		9.916667	2.966667	http://medialib.naturalis.nl/file/id/WAG.1639624/format/large	WAG
		9.91667	2.96667	http://coldb.mnhn.fr/catalognumber/mnhn/p/p00187955	P
		9.933333	-2.7	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639573	WAG
		9.941667	3.003333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639595	WAG
Crudia penduliflora Ridley	Asia	114.383333	-2.183333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982137	L
Crudia laurentii De Wild.	Africa	24.45	0.766667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639543	WAG
Crudia ledermannii Harms.	Africa	10.533333	-2.55	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639532	WAG
		10.75	3.116667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639540	WAG
		11.6812	-0.5859	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639536	WAG
		8.8	5.01667	http://coldb.mnhn.fr/catalognumber/mnhn/p/p06835047	P
		9.679167	-2.238833	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639531	WAG
		9.9	2.85	http://data.biodiversitydata.nl/naturali	WAG

				s/specimen/WAG.1639535	
Crudia letouzeyi Breteler & Nguema	Africa	14.316667	2.366667	http://data.biodiversitydata.nl/naturalis/specimen/WAG0266175	WAG
Crudia liberica Breteler & Nguema	Africa	-10.75	6.933333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639524	WAG
Crudia oblonga Benth.	America	-49.6395	-1.61232	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1371544	NY
		-49.8	-0.95	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373653	NY
		-51.75	-0.833333	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1374457	NY
		-51.9333	1.6667	http://n2t.net/ark:/65665/32ee3bd7e-e2ce-4849-99b2-d91cfe3fe9f1	US
		-52.1333	1.1833	http://n2t.net/ark:/65665/33e02510f-6291-418d-aa65-7b60ee133da7	US
		-52.28	4.53	http://n2t.net/ark:/65665/3fc7491bf-3ad4-492d-aa51-5097bfddc1b5	US
		-52.3667	2.8833	http://n2t.net/ark:/65665/3f8fec55c-f5b6-4fc8-89c8-46f967d7a030	US
		-52.4667	3.1667	http://n2t.net/ark:/65665/372253e0e-b457-488c-b9a2-7981dcd2ba7a	US
		-52.6333	2.2833	http://n2t.net/ark:/65665/3ce1246ce-bf3b-415c-a0dc-6dd27a9ac193	US
		-52.65	2.2833	http://n2t.net/ark:/65665/32e912fdf-882a-41eb-bcca-11234e2bf83d	US
		-52.6842	5.0336	http://n2t.net/ark:/65665/3d399879b-a503-44bd-8e6f-571ee9777cfd	US
		-54.7405	-2.44961	http://sweetgum.nybg.org/vh/specimen_details.php?irn=278654	NY
		-58.0219	-2.74889	http://n2t.net/ark:/65665/3f2a50c49-cd07-4f4f-9e2c-367512160035	US
		-58.7269878	-2.3065914	http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=1373664	NY
		-59.0	-1.0	http://n2t.net/ark:/65665/34094039e-3201-4591-ad99-228d1c582bbd	US
		-59.5	-1.5	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373668	NY
		-59.75	-1.75	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1374453	NY

		-59.8	-1.5833	http://n2t.net/ark:/65665/3e0cd348d-7423-4cdb-955c-3d49631bbc4f	US
		-59.8472	-1.51567	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1374456	NY
		-60.0892	-3.0747	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1371143	NY
		-67.0963	2.06386	http://n2t.net/ark:/65665/34723d727-d523-4b1e-a553-0ce4a219a76f	US
Crudia ornata De Wit	Asia	117.533333	5.483333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982060	L
		117.716667	4.416667	http://data.biodiversitydata.nl/naturalis/specimen/L.1982053	L
		117.945833	4.4625	http://data.biodiversitydata.nl/naturalis/specimen/L.1982054	L
Crudia papuana Kosterm.	Asia	142.25	-10.916667	http://data.biodiversitydata.nl/naturalis/specimen/L.3892357	L
		143.000000	-9.000000	http://medialib.naturalis.nl/file/id/L0018870_MLN/format/large	L
		143.25	-8.916667	http://data.biodiversitydata.nl/naturalis/specimen/L.1982032	L
Crudia senegalensis Planch. ex Benth.	Africa	-11.216667	6.766667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639501	WAG
		-11.266667	6.75	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639504	WAG
		-11.339167	6.785833	http://medialib.naturalis.nl/file/id/WAG.1639509/format/large	WAG
		-15.7	11.9	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639520	WAG
		-4.05	5.383333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639518	WAG
		-8.166667	5.466667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639503	WAG
		-8.6225	5.513333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639507	WAG
		-9.168167	5.451667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639513	WAG
		-9.246667	5.471667	http://medialib.naturalis.nl/file/id/WAG.1639511/format/large	WAG
Crudia spicata (Aubl.) Willd.	America	-49.6395	-1.61232	http://sweetgum.nybg.org/vh/specime	NY

				n_details.php?irn=1371538	
		-50.9667	1.75	http://n2t.net/ark:/65665/3d9eb03f3-54ba-4011-84e9-230ea1dfca5c	US
		-52.95	5.0	http://coldb.mnhn.fr/catalognumber/mnhn/p/p00220829	P
		-53.016667	5.016667	http://data.biodiversitydata.nl/naturalis/specimen/U.1259056	U
		-53.03	5.31	http://n2t.net/ark:/65665/35c7588e8-2a7d-44ec-a968-5b2f2ea852cc	US
		-60.6919	-0.2273	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1370468	NY
		-68.1667	-3.41667	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1371066	NY
		-73.22	18.37	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1801242	NY
Crudia tenuipes Merrill	Asia	112.36	-0.61	http://data.biodiversitydata.nl/naturalis/specimen/L.3885612	L
		115.75	5.35	http://data.biodiversitydata.nl/naturalis/specimen/L.1982391	L
		117.183333	1.916667	http://medialib.naturalis.nl/file/id/L.1982395/format/large	L
		117.183333	1.883333	http://medialib.naturalis.nl/file/id/L.1982396/format/large	L
		117.216667	1.916667	http://data.biodiversitydata.nl/naturalis/specimen/L.1982345	L
		117.408333	4.616667	http://medialib.naturalis.nl/file/id/L.1982385/format/large	L
		117.425	5.825	http://data.biodiversitydata.nl/naturalis/specimen/L.1982379	L
		117.483333	4.408333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982387	L
		117.533333	0.783333	http://data.biodiversitydata.nl/naturalis/specimen/L.1982346	L
		117.55	0.816667	http://data.biodiversitydata.nl/naturalis/specimen/L.1982347	L
		117.7875	4.6375	http://data.biodiversitydata.nl/naturalis/specimen/L.1982404	L
		117.950000	4.416667	http://medialib.naturalis.nl/file/id/L.1982407/format/large	L

		118.004167	4.275	http://data.biodiversitydata.nl/naturalis/specimen/L.1982380	L
		118.333333	4.966667	http://medialib.naturalis.nl/file/id/L.1982409/format/large	L
Crudia tomentosa (Aubl.) J.F.Macbr.	America	-44.8219	-3.9572	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1084016	NY
		-44.93	-4	http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=1391312	NY
		-45.38	-3.6669	http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=1391313	NY
		-45.8917809	-1.8926301	http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=1084437	NY
		-48.5233	-0.716667	http://n2t.net/ark:/65665/39102cf50-535c-4f82-9bf5-e1b483e5ab3a	US
		-48.9911	-0.41865	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1371548	NY
		-49.9008	-4.19112	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373670	NY
		-51.73472	4.45194	http://coldb.mnhn.fr/catalognumber/mnhn/p/p03602909	P
		-56.6558	-4.70099	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373674	NY
		-58.1344	-7.34465	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1373676	NY
		-63.5	-10.5	http://sweetgum.nybg.org/vh/specimen_details.php?irn=1371550	NY
Crudia zenkeri Harms. ex. De Wild.	Africa	10.0	2.816667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639482	WAG
		10.01667	2.96667	http://coldb.mnhn.fr/catalognumber/mnhn/p/p00187910	P
		10.03333	3.23333	http://coldb.mnhn.fr/catalognumber/mnhn/p/p00187915	P
		10.05	3.0	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639483	WAG
		10.05	3.01667	http://coldb.mnhn.fr/catalognumber/mnhn/p/p00187912	P
		10.166667	0.991667	http://medialib.naturalis.nl/file/id/WAG.1639460/format/large	WAG
		10.266667	1.616667	http://data.biodiversitydata.nl/naturali	WAG

		s/specimen/WAG.1639475	
10.3	0.55	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639457	WAG
10.366667	0.683333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639459	WAG
10.383333	0.666667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639446	WAG
10.4	0.6	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639468	WAG
10.416667	3.083333	http://medialib.naturalis.nl/file/id/L.1982373/format/large	L
10.433333	0.583333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639447	WAG
10.45	0.7	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639449	WAG
11.1	0.716667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639458	WAG
11.366667	0.733333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639461	WAG
11.545528	0.7255	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639471	WAG
11.633333	0.633333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639453	WAG
11.6895	1.038	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639465	WAG
11.8	0.8	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639452	WAG
11.833333	0.25	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639463	WAG
12.34707	-0.06277	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639474	WAG
12.619083	0.366639	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639472	WAG
12.8	0.516667	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639469	WAG
12.816667	0.516667	http://medialib.naturalis.nl/file/id/WAG.1639455/format/large	WAG
9.9	2.88333	http://coldb.mnhn.fr/catalognumber/mnhn/p/p00187927	P

		9.983333	2.983333	http://data.biodiversitydata.nl/naturalis/specimen/WAG.1639479	WAG
Crudia zeylanica (Thw.) Benth.	Asia	105.707889	17.499444	http://data.biodiversitydata.nl/naturalis/specimen/L.1982100	L
		106.49594329439844	13.772700090043717	voucher unknown	?