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RESOLUTION OF PARAPHYLY IN CAESALPINIOID LEGUMES

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ABSTRACT

The exceptionally large, diverse, and economically important plant family Leguminosae has traditionally comprised three subfamilies, the Caesalpinioideae, Mimosoideae and Papilionoideae. Following a large-scale molecular based phylogenetic analysis in which subfamily Caesalpinioideae was demonstrated to be highly paraphyletic, the number of subfamilies recognised was increased to six, with four new subfamilies being segregated from within the Caesalpinioideae, and the Mimosoideae being subsumed into the redefined Caesalpinioideae (as the mimosoid clade). The Caesalpinioideae, and delimitation of genera therein, has therefore been a key focus of the international legume taxonomic community in recent years.

Two of the largest genera in the Caesalpinioideae *sensu* traditional are *Bauhinia* and *Caesalpinia*; the former comprises part of the newly created subfamily Cercidoideae, whilst the latter is retained within the Caesalpinioideae *sensu novo*. Both *Bauhinia* and *Caesalpinia* have historically been most commonly treated as large, pantropical and polymorphic genera, but have in the light of molecular phylogenetic evidence been revealed to paraphyletic. A number of generic segregates have been consequently delineated from within each of them, but polymorphism has persisted, suggesting the existence of further paraphyly.

The aim of this study is to address this remaining paraphyly, using a combined morphological, molecular and biogeographical approach to investigate generic limits and define segregate genera.

The work herein creates a new segregate genus from within *Bauhinia s.l.*, based upon morphological, molecular, palynological, and biogeographical evidence. Details of

the composition of two further generic segregates of *Bauhinia s.l.* are presented, their geographical distributions described, and the relevance of this to the generic limits explored. The status of the putative segregate genus *Lasiobema* is examined, with novel data on a poorly known species of the genus presented. The monophyly of *Mezoneuron,* a segregate genus of *Caesalpinia s.l.*, is demonstrated with morphological and molecular data, and infrageneric relationships are explained. Preliminary findings reconstructing the evolutionary and biogeographical history of the genus are discussed.

This study represents substantial progress towards resolving generic limits within two of the major groups of the Caesalpinioideae (*sensu* traditional), and provides data upon which further such studies can be built, setting the framework for identification and resolution of the remaining paraphyly.

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1.1 BACKGROUND AND LITERATURE REVIEW

1.2 Introduction

The science of taxonomy is concerned with the description of organisms as identifiable and distinct units, and their classification into groups according to various sets of criteria. The criteria for determining these units have changed over time, as have the methodologies used to classify organisms. Contemporary taxonomic classification adopts as a central tenet the principle of monophyly, seeking to recognise only groups that represent natural evolutionary units.

Family Leguminosae (Fabaceae) is the third largest flowering plant family in the world, after the Orchidaceae and Compositae (Asteraceae), and one that has been subject to considerable taxonomic flux, particularly at the genus and supra-generic level in recent years. Traditionally considered to comprise three subfamilies, the Caesalpinioideae, Mimosoideae, and Papilionoideae, the family has recently undergone a major reconfiguration that has increased the number of subfamilies recognised to six (LPWG, 2017). The Papilionoideae has remained essentially unchanged in this reclassification, whereas four new subfamilies have been created from within the Caesalpinioideae, and the Mimosoideae has been subsumed as the mimosoid clade into the newly recircumscribed Caesalpinioideae.

Two of the largest genera within the Caesalpinioideae, as formerly circumscribed, are *Bauhinia* (*sensu lato*) and *Caesalpinia* (*sensu lato*). These large, pantropical genera have been demonstrated with the use of molecular data to be paraphyletic, necessitating their segregation into smaller, monophyletic genera. The work here presented contributes to the resolution of paraphyly in these broadly defined genera, presenting detailed morphological, biogeographical, and molecular evidence for segregation of particular monophyletic genera.

Term	**Definition**
Apomorphy	Derived character state
Clade	The taxa forming a monophyletic group, including the most recent common ancestor and all of its descendent taxa
Cladistics	Method for grouping taxa into hierarchically nested sets; often used as a synonym for phylogenetic systematics
Crown node	Most recent common ancestor of the sampled species of the clade of interest
Homology	Character state shared due to common ancestry
Homoplasy	Non-homologous character state i.e. character state shared due to reason other than common ancestry (such as convergence, parallelism, reversal)
Monophyletic group	A group of organisms that includes ALL of (and only) the descendants of a most recent common ancestor
Paraphyletic group	A group containing some but not all of the descendants of a most recent common ancestor; that which remains when a clade is excluded from a monophyletic group
Polyphyletic group	A group containing taxa that do not share a single most recent common ancestor (a group derived from more than one ancestor)
Stem node	Most recent common ancestor of the clade of interest *and* its sister clade
Synapomorphy	Shared derived character state; apomorphy shared by the members of a monophyletic group

Table 1. Definition of key terminology in systematics and phylogenetics

1.3 A history of systems of biological classification

Artificial Systems

Biological classification systems date back as far as 300 BC (Steussy, 2009), when the naturalist and philosopher Theophrastus (c. 372–287 BC) in one of his great works, *The Enquiry into Plants* (translated into English 1916), made one of the first ever attempts to classify plants into different types. He categorised them as ‘trees’, ‘shrubs’, ‘undershrubs’ and ‘plants’, as well as recognising Monocotyledons and Dicotyledons, and differences in ovary position and types of corollas (Sivarajan, 1991). Theophrastus’ system was probably the earliest example of an artificial classification, a system which is formed by grouping according to similarity in certain characters considered to be taxonomically significant. The selected characters are thus afforded particular weight by the taxonomist, but not because they are in any way more indicative of close relationships between the taxa; in fact, artificial systems do not aim to represent evolutionary relationships.

The most comprehensive and widely accepted artificial system of plant classification was designed by Swedish botanist Carolus Linnaeus (1735) (Steussy, 2009). Linnaeus’ classification was devised with 24 classes, based almost entirely on the number, arrangement and extent of fusion of the sexual parts, in particular the number of stamens, relative length of stamens, fusion of staminal filaments, fusion of anthers, and fusion of androecium and pistil (Sivarajan, 1991). This system was adopted almost universally, partly due to its ease of use. An artificial system such as that of Linnaeus considers the parts of the plant in isolation, lacking any holistic view of the organism or the relationship of the parts to one another. The major disadvantage of this approach, despite being easily accessible, is the lack of predictive value. In other words, it does not represent a tool enabling organisms to be grouped alongside their close relatives, or enable prediction of the relationships of a taxon based upon its morphology.

Natural Systems

Natural systems, by contrast, are based upon multiple characters considered together, relative to one another, and they enable the grouping of organisms by hierarchical ranks. These have greater predictive value than artificial systems, in terms of the interrelatedness of organisms, although this has only been understood in the light of evolutionary theory that has arisen latterly. John Ray (1623–1705) developed one of the first credible natural plant classifications in his *New Method of Plants* (Ray, 1682) (Huxley, 2007), based upon his belief that as many characters as possible should be used in classifications. Although his system was flawed in an evolutionary sense, in that it placed trees, shrubs and herbs into separate groups he did nonetheless observe that certain characters, such as plant height, were not useful for classification and should be excluded, and, like Theophrastus, grouped plants as to whether they produce one or two seed leaves – the Monocotyledons and Dicotyledons. Another of Ray's extremely important contributions to the natural sciences was in first proposing the concept of species, which he defined as a group of individuals sharing a number of characteristics that would be passed on to their progeny.

Bernard Jussieu (1699–1777) was another of those who advocated a method based on multiple characters. However, he did not publish his theories, and it was his nephew, Antoine-Laurent Jussieu (1748–1836), who reworked his uncle's system and published it in his *Genera Plantarum* (de Jussieu,1789). This publication, more than that of Ray, marked the beginning of a new era of classification, the shift from artificial to natural. Following de Jussieu, many classification systems were devised that were essentially modifications of this system. These were particularly prolific in the period 1825–1845, during which 24 such systems were introduced (Lawrence, 1951).

Phyletic and Phylogenetic Systems

With emergence of the theory of evolution by natural selection first formally proposed by Darwin in 1859, taxonomists began to develop new ways of thinking about classification. They started to develop systems that would reflect relationships by descent, known as phyletic systems.

The first system of classification of plants that was built using the principle that organisms are related to each other through descent was produced by the German botanist, August Wilhelm Eichler (1883). This system encompassed the entire plant kingdom, which he divided into two subgroups, the Cryptogamae and Phanerogamae, and was the first to identify Angiospermae and Gymnospermae as separate groups (Lawrence 1951).

A number of other important and widely-recognised systems arose following that of Eichler, including those of Bentham & Hooker (1862–1883), Engler & Prantl (1887–1915), Hutchinson (1926, 1934, 1959. 1973), Cronquist (1988), Takhtajan (1958–2009). The system of Bentham and Hooker presented in a series of volumes comprising their Genera Plantarum (1862-1883) was one of the most important ever produced, and many herbarium collections are, or have been, arranged according to this classification, which provided detailed descriptions of all genera (Turner, 2016). It had the advantage of being highly predictive, so that an unidentified taxon could be placed with relative ease within the system. Engler and Prantl's classification improved in one respect upon that of Bentham and Hooker by being the first to incorporate the ideas of organic evolution, and therefore the first to move towards phylogenetic classification, and dividing up large and non-natural families such as the Euphorbiaceae and Urticaceae of Bentham into smaller units (Singh, 2010). However, a significant shortcoming of their system was the assumption of simplicity of form indicating early branches of evolution.

The system of Hutchinson (1926, 1934, 1959, 1973) was complex, and based upon 24 principles on the themes of General Principles, General Habit, General Structure of Flowering Plants, and Flowers and Fruits (Singh, 2010). Hutchinson's system was an improvement over those of previous authors in many ways, being more phylogenetic than that of Engler and Prantl (1887–1915), and maintaining high standards of description, as well as keys for the identification of families (Singh, 2010). It did, however, have some major disadvantages, the primary one being that it only went as far as family level for most groups. In addition, there was a lack of explanation for his evolutionary concepts, and his division into smaller families of some larger groups that have subsequently been supported as monophyletic.

Takhtajan was an international authority on the origin and phylogeny of flowering plants, who adopted complex analyses to create his widely used series of classifications published between 1958 and 2009. He was strongly influenced by Hutchinson, amongst others, and his approach adopted phylogenetic principles, particularly in his final version. The comprehensive system of Cronquist (1988) agreed largely with that of Takhtajan, and was also advanced in that it was largely based upon phylogenetic principles.

The aim of cladistics is to reconstruct evolutionary branching patterns to interpret the relationships between taxa. The use of the term within evolutionary science originated from Rensch (1954, 1959), who referred to the branching events of evolution as ‘cladogenesis’ (Steussy 2009). Hennig (1966), is considered to be the founder of cladistics in the sense of its application to taxonomic relationships, proposing the idea that organisms should be grouped and named only when they represent evolutionarily real entities. A distinction can be made between Darwinian classification, which requires the use of two criteria, similarity and common descent, and Hennigian classification, which accepts only common descent, and monophyly (Hörandl, 2006). The use of cladistics in the study of evolutionary relationships has come to be called phylogenetic systematics, or phylogenetics (Steussy 2009), and is contemporarily usually conducted through the analysis of molecular data (DNA sequences). Analyses of this type have a central role in modern taxonomy and systematics.

1.4 Concepts and methods in taxonomy

Taxonomic units in Linnaean classification

The Linnaean binomial system of biological nomenclature universally governs the way in which organisms are named and classified today. The concept of binomial classification, although widely attributed to Linnaeus, was in fact first proposed by Gaspard Bauhin who, in his *Pinax Theatri botanici* (1623) advocated the use of generic and specific names and whittled down polynomial descriptions into a specific name of just one to four words (Huxley, 2007). The importance of the contribution of G. Bauhin to the development of the contemporary nomenclatural system is reflected in the naming of the large and important genus *Bauhinia* L., studied here, in recognition of the scientific contribution of G. Bauhin and his brother, Jean Bauhin (also a botanist), the often bilobed leaves of this genus being perceived as suggestive of a brotherly relationship.

This principle was developed by Linnaeus into the hierarchical system of classification proposed in his *Species Plantarum* (1753) (Humphries & Huxley, 2007), which had at its core the binomial system, replacing the previous cumbersome method of naming which listed a number of descriptive terms to form a polynomial. Linnaeus' revolutionary binomial system was voted at the 1905 Vienna International Botanical Congress to be adopted as the basis for the nomenclature of flowering plants, and is still used as such today. The system, introducing the binomial method, consists of eight ranks: domain, kingdom, phylum, class, order, family, genus, and species. Despite its benefits, and still being the system utilised for all biological classification up to the present day, it is imperfect. The major limitation inherent in the structure of the Linnaean system is that the number of ranks is fixed and finite, and the system is therefore rigid in terms of the number of hierarchical ranks that can be formally recognised. Depending on the way in which ranks are assigned, not all clades can be named in a large and complex group (i.e., one runs out of (formal) ranks quickly) – then informal, intermediary ranks such as section and subsection must be resorted to. Phylogenies derived from molecular data, in which many nested clades require a greater number of ranks than are available in the Linnaean hierarchy, pose a problem in the Linnaean system, and the use of informal clade names becomes inevitable.

A further potential disadvantage of the Linnaean system, which may particularly confuse non-specialists, is the implication that taxa of the same rank are presumed to be somehow equivalent in an evolutionary sense. The reality is that these ranks are not (as may erroneously be assumed) actual phylogenetic entities, but rather are subjective and hypothetical definitions. This can lead to misunderstanding of the status of taxa, and an incorrect assumption that taxa of the same rank are comparable in some biologically meaningful way (Cantino & de Queiroz, 2010).

An alternative system, that of phylogenetic nomenclature, was proposed in the 2010 *Phylocode* (Cantino & de Queiroz, 2010). The *Phylocode* aimed to establish a means by which taxonomic units could be named without the need to simultaneously assign a hierachical rank (although it is designed to be used in conjunction with rank-based codes). The major advantage of phylogenetic nomenclature is that it allows clades to retain their names when recircumscribed, thus ensuring much greater nomenclatural stability. A system of phylogenetic nomenclature also facilitates the naming of clades as they are discovered, without the associated need to rename related clades according to their relative position (Cantino & de Queiroz, 2010). Despite the disadvantages of the Linnaean hierarchy, and the potential of a phylogenetic nomenclature system such as *Phylocode* for overcoming these, Linnaean ranking remains the universal system in place for the naming and classification of organisms, albeit with some systems adopting the use of a backbone of Linnaean ranks together with a series of informal names for recognisable clades within them.

Two of the most fundamental units of Linnaean classification, and those which are of most relevance to the current study, are the genus and species, although the question of whether these concepts represent ‘real’ biological entities (as opposed to human constructs) has been the subject of much debate. Tournefort is regarded as the father of the generic concept (Steussy, 2009), as he categorised all of the plants in his *Institutiones Rei Herbariae* (Tournefort, 1700) by genus, according to the principle that five of the six parts of a plant (roots, stems, leaves, flowers, fruits, seeds) should be considered together for generic classification (Steussy 2009). The subsequent generic concepts of Linnaeus, which specified the use of three characters, stemmed from those of Tournefort (Steussy, 2009). The concept of the genus is, to a greater extent even than the species, a problematic one.

A genus can be thought of as a group of species that appear to be more closely related to each other than they are to other species (Steussy, 2009). A genus should be monophyletic, and recognisable by multiple characters (rather than a single one) (Singh, 2010). However, the subjectivity entailed in the perception and definition of what makes organisms closely related means that this is not a rigorous or unambiguous scientific premise. Genera are argued by some to be entirely artificial constructs, and by others as more natural than species (Steussy, 2009). Flexibility of interpretation in the application of the genus concept, along with the provision of additional plant material over time, and advances in analytical techniques, has resulted in frequent, often profound, recircumscriptions of genera.

A species can be defined in a number of ways, including according to its morphology, reproductive capacity, genetic distance from other populations or ecological affinities. The morphological species concept has traditionally been the one most employed by taxonomic researchers, by which species are defined according to the unity of their phenotypic characteristics. Modern systematists, however, may adopt a more phylogenetically orientated approach, wherein the terminals on a cladogram are considered to represent species (even in the absence of supporting morphological data).

A commonly used concept of a species is the ‘biological species concept’, which considers a species to consist of a group of interbreeding populations which is reproductively isolated from other such groups (Steussy, 2009). In practice, this information is rarely available to a systematist, particularly in plants, and hybridisation between species with fertile offspring is widespread. A taxonomist when seeking to define species boundaries should, however, prioritise those characters that may confer reproductive isolation over those such as vegetative characters, and in doing so can seek to define taxa according to the biological species concept.

The biological species concept, as well as being difficult to apply in practice, has the shortcoming that it does not incorporate the principle of evolution. The 'evolutionary species' concept addresses this, in which a species is defined as "… a lineage… evolving separately from others and with its own unitary evolutionary role and tendencies" (Simpson, 1961; Steussy, 2009). The evolutionary roles in this sense can be seen as ecological niches (Steussy, 2009).

The particular concept adopted by a systematist can affect the overall number of species defined, for example the evolutionary species concept, being narrower than the biological concept, will result in more numerous species.

Morphological vs. molecular analytical methods

Morphology, anatomy, and chemistry have traditionally been the primary tools for classification, grouping organisms according to their similarity to define genera, and they continue to be instrumental in this process. Since around the turn of the millennium, molecular analysis, especially that of DNA, has played an increasingly important part in taxonomic classification. The efficacy of morphological taxonomy has been demonstrated by the results of molecular phylogenetic analyses: classifications produced using traditional morphological analysis have been largely substantiated by corresponding molecular phylogenies.

However, this is not to suggest that morphological taxonomy is without problems and limitations. The prevalence of homoplasy (when similar character states exist in organisms due to reasons other than shared ancestry, such as parallelism and convergent evolution) has often resulted in the circumscription of genera that, although readily morphologically diagnosable, do not represent natural groupings of species. Further issues are that species boundaries can be extremely difficult to resolve due to issues such as polymorphism, which can result in the description of many species or infraspecifics from within a single biological species, or cryptic speciation in which clear morphological characters to delineate species boundaries are lacking. The increasing use of DNA taxonomy in contemporary systematics has in some cases illuminated these situations, and has led to more frequent discovery of instances of cryptic species (Bickford et al., 2007; Sotuyo et al., 2007; Pillon et al., 2009; Gagnon et al., 2015).

The advent of molecular analysis provides a major comparative tool that facilitates much greater insight into relationships between taxa, generating a wealth of additional data that can be used in conjunction with morphological analysis to define genera and to diagnose paraphyly. It is often cited as a more subjective method of analysis than morphological taxonomy, and to some extent this is true; however there is a degree of subjectivity involved in molecular phylogenetic analyses. A matrix comprising DNA bases derived from Sanger sequencing will usually be aligned using computer software, and the alignment subsequently adjusted manually. The second phase of this alignment process entails a certain amount of subjective decision-making in terms of the way in which one sequence is presumed to have affinity with another. For example, a sequence of bases ATAGGTC from one sample may be presumed to align with a similar sequence, ATCCGTC, from another, but this may be a misinterpretation of the data. This has the potential to introduce a certain amount of error into the analysis. Additionally, selection of outgroups for rooting the tree, and of parameters for setting an analysis (e.g. setting of priors), may result in some introduced bias, although this can be overcome by running multiple analyses using different outgroups and parameters. The information contained in a phylogenetic tree is itself to a certain extent open to interpretation, in that the circumscription of a genus is dependent upon the depth in the tree of the node determined as the crown node. This interpretation may be influenced to some degree by the taxonomist's understanding of the morphology of the species in question, and is therefore not wholly objective.

One of the major advantages of molecular taxonomy is the greater number of characters available for analysis, resulting in what are likely to be more accurate phylogenies (Scotland et al., 2003). Another great advantage may be the presumed lower levels of homoplasy in molecular data compared to morphological data: in other words, the likelihood of identical (or similar) DNA sequences having evolved multiple times between taxa is lower than the likelihood of a physical structure within the plant arising multiple times in different lineages through evolutionary processes. The veracity of this assertion has been questioned by some authors who have presented studies demonstrating that homoplasy can be as high or higher, in molecular data sets than in morphological ones. However, the fact that modern phylogenies usually are built using large data sets involving at least several gene regions, or when Next Generation Sequencing is adopted, entire genomes, provides high capacity for overcoming these issues.

Monophyly, Paraphyly, Polyphyly

The concept of monophyly is a fundamental tenet of modern biological classification, a principle that is accepted by the vast majority of contemporary systematists, and one that has arisen partly in response to the new molecular based paradigm. The definition of monophyly as currently recognised was created by Hennig (1966), who modified the pre-existing definition from describing a group of organisms that have descended from a common ancestor, to "a group of organisms that includes ALL of the descendants of a most recent common ancestor" (Steussy, 2009). A paraphyletic group, by contrast, can be defined as one containing some but not all of the descendants of a most recent common ancestor, whilst a polyphyletic group contains taxa that do not share a single most recent common ancestor, or in other words taxa from more than one clade, and excluding the common ancestor (Sivarajan 1991). It is important to note that one taxonomic group is only monophyletic relative to another, and depending upon the taxonomic level at which it is applied, as ultimately all groups of organisms derive from a single ancestor and are therefore monophyletic (Sivarajan, 1991).

The concept of monophyly has become embedded in the science of classification over the past two to three decades, but until recently its obligate adoption within the discipline was vigorously contested by certain practitioners (Cronquist, 1987; Sosef, 1997; Brummitt, 2002; Nordal & Stedje, 2005). Objections revolved around two central arguments: firstly, the assertion that within a Linnaean system of nomenclature, it is impossible to divide the entire evolutionary tree into monophyletic units (Brummitt & Sosef, 1998; Nordal & Stedje 2005); therefore, we must accept and recognise paraphyletic groups. Secondly, a system that requires monophyly does not give weight to the pragmatic diagnosability of taxonomic entities based upon readily recognisable characters (Brummitt, 2002, 2008; Brickell et al., 2008). Authors with these views therefore believe that absolute monophyly within a Linnaean framework is an impossibility, as well as a significant practical disadvantage. Both of these arguments have validity, and have caused concern amongst researchers. For example, George (2014) argued against the transfer of the genus *Dryandra* into *Banksia* on the grounds that good morphological characters existed to distinguish them. His position was that molecular cladistics should not be allowed to override existing trait-based classifications. This position is defensible: if one of the primary applications of taxonomy is to enable organisms to be easily identified, it is logical to suggest that conventions should be designed to facilitate this aim.

Nonetheless, these arguments have been almost universally rejected by contemporary systematists, and the principle of monophyly as a central guiding principle of modern taxonomy has been overwhelmingly accepted. The justifications for this can be summarised as follows:

- The foremost role of systematists is to understand and interpret as accurately as possible relationships between biological organisms. To circumscribe non-monophyletic groups is to ignore one of the fundamental aims of the discipline, resulting in an inaccurate portrayal of the natural world. This in turn potentially weakens the predictive quality of a classification, and correspondingly its utility in practical applications, such as medicine or agriculture, for which knowledge of the properties, or traits, of an organism is key. As summed up by one author (Scott-Ram, 1990) "Given that evolution has produced a natural system of relationships amongst organisms… then it is the job of systematists to discover these relationships".
- Another fundamental role of taxonomy is to provide a stable name for every organism (Baum & Smith, 2013). To accept a system in which recognising paraphyletic groups is permissible is to promote potential taxonomic instability, as interpretation of taxonomic units becomes more subject to the author's personal opinion.
- Opponents of obligate monophyly may argue that its strict imposition leads to the circumscription of groups that do not display any morphological synapomorphies (shared derived character states – character similarities that occur due to being derived from a common ancestor) to enable their identification. Whilst this situation

may occasionally occur, usually at least one morphological characteristic, or a suite of characters, can be found to distinguish a given taxon. In the small minority for which this is not possible, we should not be in the position of sanctioning compromise of scientific principles in favour of convenience. Moreover, improved technologies and methodologies (such as morphometrics) can provide novel tools with which to locate and identify characteristics that may evade traditional taxonomic techniques. Further, analysis of non-traditional taxonomic characters such as chemistry, chromosomes, wood anatomy and pollen can illuminate taxonomic boundaries where evidence is lacking from macromorphology alone.

- If taken to extreme, non-admission of monophyly regresses us to a system such as that of Linnaeus, in which apparent similarity regardless of true relationships is the sole criterion for classification.
- To be rigorous, the science of systematics should be governed by a set of unambiguous rules, which are followed by all practitioners and are not open to interpretation. Otherwise, we are left with a situation in which subjectivity has the potential to drastically influence the outcome of any taxonomic evaluation. Such subjectivity arguably already plays too large a part in the science of morphological taxonomy!

The concept of a genus in the contemporary sense is governed by the principle of monophyly, as demonstrated by robust molecular phylogenetic evidence. In this context, genera can be considered as more ‘natural’ taxa than they have been regarded in the past, although there is still no strict or universal application of the term that could render all genera equivalent evolutionary units.

Botanical Nomenclature and Type Specimens

"Biology requires a precise, coherent, international system for naming clades and species of organisms." - Phylocode

A system by which each known taxon is identifiable by a single, clearly defined name is an essential tool for communication, and a fundamental goal of any taxonomic classification. Furthermore, nomenclatural and taxonomic stability is a priority, with the objective that the unique name for any given taxon is fixed, and changes to the name are minimised.

The rules governing botanical nomenclature are laid out in the International Code for Algae, Fungi, and Plants (Melbourne Code) (McNeill et al., 2012), which is subject to regular revision following discussions in the Nomenclature Session meetings at the International Botanical Congress, held every five years. These extremely detailed rules ensure that the application of plant names is instigated in a standardised way, such that names will be as stable as possible, and that there can only be a single correct name for a taxon at any given time.

Multiple names may exist for a given taxon but there is only ever one correct current name applicable under these rules. Multiple names for a single species have arisen, for example, for taxa which are widespread and have been treated independently by a number of authors over time, or for taxa whose morphological variability can lead to taxonomic misinterpretation. Sometimes this has led to the creation of multiple infraspecific taxa, which are often prone to taxonomic instability. Establishing the correct current name for any given taxon requires an in-depth understanding of both the taxon in question, and the rules governing botanical nomenclature. In order to identify a correct name, a range of literature must usually be consulted, including the most recent (reliable) monographic, floristic, and nomenclatural publications on the taxon, as well as the protologue of a taxon name.

The type specimen (or specimens) of a taxon name are the primary specimens linked to the creation of the name, and these ultimately define its application. The correct identification and listing of type specimens is essential for establishing and correctly applying taxon names. Where a holotype does not exist (if one has not been designated, or it has been lost), a subsequent author must designate a lectotype or neotype. If the original holotype is deemed to be of insufficient quality to represent the taxon, an epitype (supplementary type) can be designated.

1.5 Taxonomy of the Caesalpinioideae (*sensu* traditional)

The subfamily Caesalpinioideae as formerly circumscribed before the recent major reclassification of the family into six subfamilies (LPWG 2017) comprised c. 2300 species in 171 genera arranged in four tribes. Subfamily Caesalpinioideae now comprises 148 genera with c. 4400 species. The reclassification of the family involved the extraction of three former tribes and one additional species from the Caesalpinioideae, which were instated as four new subfamilies, the Cercidoideae (12 genera, 335 species), the Detarioideae (84 genera, 760 species), the Dialioideae (17 genera, 85 species), and the Duparquetioideae (1 genus, 1 species). The size of the Caesalpinioideae has nonetheless increased significantly with the new circumscription, due to the incorporation of the former subfamily Mimosoideae, now the mimosoid clade, comprising ca. 3,300 species (Table 2).

Subfamily (LPWG, 2017)	**Circumscription pre-2017**	**Circumscription post-2017**
Caesalpinioideae	171 genera, 2,300 species	148 genera, 4,400 species
Mimosoideae	c. 82 genera, 3,300 species	mimosoid clade within Caesalpinioideae
Papilionoideae	480 genera, 13,800 species	503 genera, 14,000 species
Cercidoideae	tribe Cercideae	12 genera, 335 species
Detarioideae	tribe Detarieae	84 genera, 760 species
Dialioideae	tribe Cassieae *pro parte*	17 genera, 85 species
Duparquetioideae	tribe Cassieae (placement uncertain)	1 genus, 1 species

Table 2: Summary of the reclassification of the subfamilies of Leguminosae (LPWG, 2017)

1.6 Taxonomy of the Cercidoideae

Cercideae Bronn (1822) was formerly a tribe of subfamily Caesalpinioideae, one of the three traditionally recognised subfamilies of the Leguminosae. The tribe was created for a single genus, *Cercis* L., and subsequently expanded to encompass two subtribes, the Cercidinae and Bauhiniinae, with up to 29 genera. As part of the major reclassification of the Leguminosae from three subfamilies to six, the Cercideae has been elevated in rank to become one of the new subfamilies, the Cercidoideae (LPWG, 2017).

Since Bentham (1840; 1865) the Cercidoideae has been thought to represent a natural group (Wunderlin, 1979), characterised by the distinctive leaf, which is unifoliolate and entire or bilobed, or bifoliolate, compared with the leaves of most Leguminosae which are trifoliolate, once- pinnate or bipinnate (with few to many leaflets and pairs of pinnae). The hypothesis, based principally on leaf form, that the Cercidoideae represent an early diverging lineage within the family (Wunderlin et al., 1981), has been recently confirmed by molecular phylogenetic analyses (Bruneau et al*.,* 2001; Herendeen et al*.,* 2003; LPWG, 2017) although the precise relationship to other subfamilies remains as yet unresolved; in the latest and best-sampled molecular phylogenetic analysis the Cercidoideae forms a polytomy with the Duparquetioideae, Detarioideae and the clade containing the other three subfamilies (LPWG, 2017).

Despite the readily identifiable nature of the group, the subtribal classification of the Cercidoideae, in its former circumscription as the Cercideae, has been subject to considerable flux. Wunderlin (1979) and Wunderlin et al. (1981), divided the Cercideae into subtribes Cercidinae and Bauhiniinae, based on seed, floral, and fruit characters. Of these, subtribe Cercidinae has been largely stable in its circumscription, usually considered to include the genera *Cercis*, *Adenolobus*, and *Griffonia*, although there have been other configurations such as that of Yakovlev (1972), who placed *Bauhinia* and *Griffonia*, along with *Barklya*, in the Bauhiniinae, leaving only *Cercis* in the Cercidinae. The internal circumscription of the Bauhiniineae, by contrast, has varied enormously from 26 genera (Wunderlin, 1976) to one, *Bauhinia sens. lat.* (Wunderlin et al., 1981), due to the extreme fluidity of the generic limits.

1.6.1 Taxonomy of *Bauhinia sensu lato*

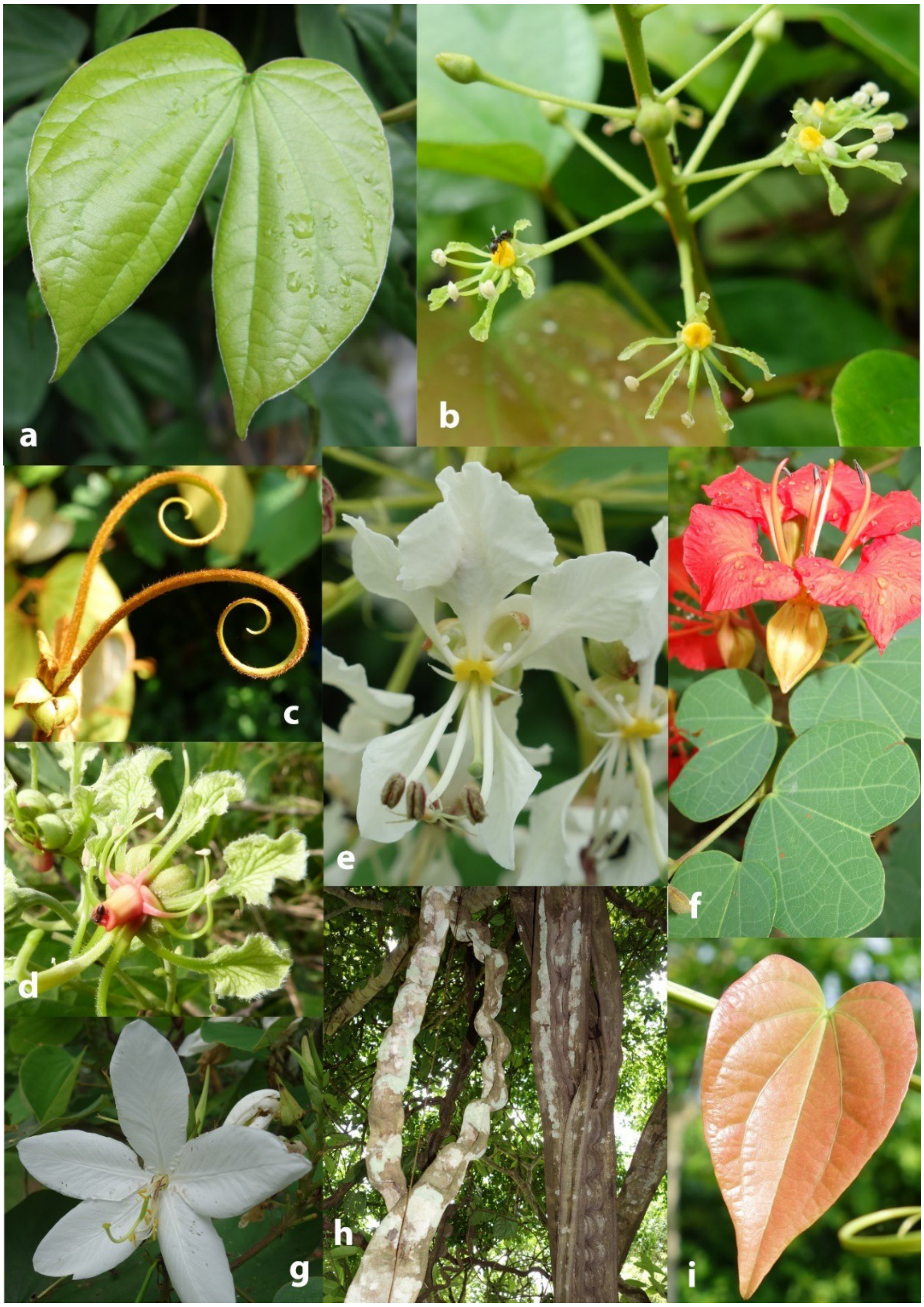


Figure 1. Composite plate showing vegetative and floral forms of *Bauhinia s.l.* (a) Bilobed leaf typical of *Bauhinia s.l.* (b) Flowers of *Lasiobema championii* (c) Tendrils of *Phanera* (d) Flower of *Phanera bracteata* (e) Flower of *Cheniella tenuiflora* (f) Flower and leaf of *Bauhinia galpinii* (g) Flower of *Bauhinia s.s.* (h) 'Monkey-ladder' lianescent stems of *Phanera* (i) Entire leaf form of *Bauhinia s.l.*

The genus *Bauhinia* L. (classified in the subfamily Cercidoideae) was first described in Linnaeus' *Species Plantarum* (1753), based on the type species *B. divaricata* L., in a treatment that included eight species. The circumscription of the genus has hugely expanded since that time to include in its broadest sense 300–350 species, and has always been controversial, diverging radically between different authors and even within the opinion of a single author. Bentham himself (1840) was at first inclined to divide *Bauhinia s.l.* into four genera, stating that "the form of the flower and fruit in the various groups collected under the name of *Bauhinia* is so very different that it seems impossible to retain the genus entire". However, he subsequently (1865) altered his view to adopt the wide generic delimitation of *Bauhinia*, which was generally followed thereafter (de Wit, 1956).

The morphological heterogeneity of the genus in its broad sense has been reflected in the infrageneric classifications devised by various authors, consisting of subgenera, sections, subsections and series, in their efforts to negotiate the diverse group. For example, in his 1825 synopsis, de Candolle recognised five sections within *Bauhinia*: sect. *Casparia*, sect. *Pauletia* Cav., Sect. *Symphopoda* DC., Sect. *Phanera* Lour., and Sect. *Caulotretus* Rich., whilst Baker (1879) defined six sections within *Bauhinia s.l.*., encompassing 37 species. Taubert (1891) subdivided *Bauhinia s.l.* firstly on the number of fertile stamens, stating that his reason for recognising subdivisions of *Bauhinia* as sections rather than distinct genera was due to the lack of single unique synapomorphies to distinguish some of the individual groups. De Wit (1956) took a different view, pointing out that the presence or absence of a single character does not signify relationships between taxa more than does the correlation or combined occurrence of a group of characters. In fact, according to the central tenet of natural classification systems, '…taxa characterised by sets of characters are as a rule more natural than those founded on an isolated 'key-character''.

Two decades later, Wunderlin (1979), whilst defining the genus as pantropical and comprising. c. 225 spp., acknowledged that "It is evident that the large and diverse genus *Bauhinia* should be further subdivided into a number of infrageneric units", and indicated that such a revision was under way in collaboration with Professor Kai and Supee Larsen. However, in the subsequent years he continued to recognise *Bauhinia s.l.*, delineating in 1981 four 'groups' within the genus, the Bauhinia group, Piliostigma group, Barklya group and Phanera group. Shortly thereafter (1983) his synopsis of the arborescent *Bauhinia* species of Central ('Middle') America divided 27 species into three 'species alliances', the Divaricata, Petiolata, and Aculeata alliances. Four years later, he presented another treatment of *Bauhinia* as a single large genus of 300–350 spp., in which were recognised four subgenera, 22 sections, and 30 series (Wunderlin et al., 1987).

De Wit's (1956) comprehensive revision of the Malaysian species of *Bauhinia s.l.* was one of the first major treatments to ascribe the rank of genus to subdivisions that had previously been treated by most authors at lower ranks. Acknowledging the complexity of *Bauhinia s.l.*, de Wit observed that 'When emended to some degree, the sections in *Bauhinia s. ampl.* [in the broad sense] recognised by Bentham and his followers could often be equally well delimited as genera as could *Bauhinia s. ampl…*'. He then elaborated '…*Bauhinia s. ampl.* ought to be reduced to what we may believe to be in close agreement with the Linnaean conception. This made necessary the resurrection of genera usually referred to synonymy of *Bauhinia* and the description of a new genus [*Lysiphyllum*]. The genera I recognise here are, I believe, very natural groups, repeatedly linked, but well distinguished by certain combinations of characters'.

His conspectus elucidated seven (Malaysian or partly so) genera: *Bracteolanthus, Lysiphyllum, Gigasiphon, Piliostigma, Lasiobema, Phanera,* and *Bauhinia.* Other treatments that delineated several genera from within *Bauhinia s.l.* include those of Britton & Rose (1930), who recognised *Alvesia, Caspareopsis, Casparia* and *Schnella* as distinct (Wunderlin 1983), and Verdcourt's (1979) *Manual of New Guinea Legumes* which treated *Lasiobema, Lysiphyllum, Phanera, and Tylosema* as separate from *Bauhinia.*

Some authors continue to adhere to the concept of *Bauhinia* as a single, large, polymorphic genus. For example, Meng *et al*. (2014) and Wang et al. (2014) have continued to treat *Bauhinia s.l.* as a single unit, although Wang et al. did acknowledge that "recent studies on pollen morphology and molecular systematics of *Bauhinia* have suggested that Bauhinia *sensu lato* (*s.l.*) is not monophyletic and should be subdivided into Bauhinia *sensu stricto* (*s.s.*) and other independent genera". In the main, however, the view of *Bauhinia* as a single genus has now been superseded.

Whilst many regional treatments exist, comprehensive revisions of *Bauhinia s.l.* have rarely been carried out, due to the large size of the genus, its morphological complexity, and its wide geographical distribution. Notable revisions of the genus in its entirety, as recognised at the time, include those of Dietrich (1840), who recognised 81 species, Taubert (1891), and Wunderlin et al. (1987). However, during the past two decades, the onset of the use of molecular phylogenetic techniques has enabled studies across a broad spectrum of taxa, and revolutionised understanding of the relationships within the Cercidoideae. The most comprehensive phylogenetic study of the Cercidoideae to date has been that of Sinou et al. (2009), which included representatives of all eight genera within *Bauhinia s.l.* as proposed by Lewis & Forest (2005). The primary aim of Sinou et al. (2009) was to investigate relationships between these proposed segregate genera, rather than interspecific relationships, and in this they advanced our understanding substantially. Their study revealed *Bauhinia s.l.* to be paraphyletic with respect to the monospecific Madagascan genus *Brenierea*, which was resolved as nested within *Bauhinia s.l.* It also supported the recognition of a number of segregate genera, in agreement with the proposal of Lewis & Forest (2005).

Despite these major advances, understanding of the infraspecific relationships, and to some extent the generic delimitations within *Bauhinia s.l.*, is still lacking. Much more densely sampled phylogenetic studies, using a range of molecular markers, are necessary to further illuminate the relationships within this taxonomically complex and ecologically important group.

1.6.2 Segregates of *Bauhinia*: *Phanera* and *Schnella*

Phanera Loureiro (1790) is the largest genus segregated from within *Bauhinia s.l.* The genus was originally created for a single species, *Phanera coccinea* Lour., the presence of 3 stamens per flower noted in the protologue as being a defining character of the genus. Since it was created, *Phanera* has been considered by subsequent authors either as a distinct genus containing up to 130 species (Baker, 1879; de Wit, 1956; Verdcourt, 1979; Zhang & Chen, 1992; Larsen & Larsen, 1997; Lewis & Forest, 2005; Quieroz, 2006; Vaz 2010; Bandyopadhyay, 2012), or as a subgenus or section of *Bauhinia* (de Candolle, 1825; Korthals, 1839–42; Bentham & Hooker, 1865; Larsen et al. 1980, 1984; Hou et al*.,* 1996; Dezhao et al*.,* 2010; Chatan, 2013). During the last 30 years or so, the majority of authors in Asia have subscribed to the latter view.

The species within *Phanera*, even in its broadest circumscription, are consistently homologous in two major traits: all are tendrilled lianas, and possess (2–) 3 fertile stamens. In this, the genus is easily distinguished from *Bauhinia s.s.*, which consists of trees or shrubs, with 1–10 stamens, and from *Schnella*, also a tendrilled liana, that uniformly possesses 10 stamens.

Despite these consistent generic characters, considerable morphological heterogeneity exists within *Phanera s.l.* This is best illustrated by the treatment of de Wit (1956), who recognised *Phanera* as a distinct genus comprising 44 species, which he divided into three subgenera, subgenus *Phanera*, subgenus *Austrocercis*, and subgenus *Biporina*. Of these, subgenus *Biporina* comprised three sections, and subgenus *Phanera* three sections, which were together then further subdivided into six subsections. The morphological basis for his classification was as follows: *Phanera* subgen. *Biporina* de Wit was separated for having porate anthers; *Phanera* subgen. *Austrocercis*, consisting of a single New Guinea endemic species, was distinguished by bud shape, flowers 'semi-papilionaceous', the calyx 2-lobed (vs. at least 3-lobed), and at the base of the vexillum 'a digitate, fleshy body'; *Phanera* subgen. *Phanera,* consisting of 28 species, was distinguished from *Phanera* subgen. *Biporina* by having anther slits, and from *Phanera* subgen. *Austrocercis* by characters contrasting with those listed for that subgenus. Characters used by de Wit to distinguish the sections and subsections of *Phanera* subgen. *Phanera* included: receptacle length; receptacle turbinate or tubular; bud shape; sepal lobing; petal length; length of petal claw; petal shape; petal caducous or not; anther length; ovary indumentum; ovary sessile or stalked.

A similarly complex system designed to navigate the morphological heterogeneity within *Phanera* was that of Wunderlin (1976), who considered the group as a subgenus of *Bauhinia* and proposed that it be divided into 11 sections. Included in these were sections *Lasiobema*, *Lysiphyllum* and *Tylosema*, which were subsequently reinstated as distinct genera by Lewis and Forest (2005).

Following the revelation published by Sinou et al. (2009) of the paraphyletic nature of *Bauhinia s.l.* with respect to *Brenierea* as well as the evidence provided by other molecular based analyses such as that of Hao et al. (2003), the international taxonomic community has broadly accepted the status of *Phanera* as a reinstated "good" genus. Despite this, questions have persisted surrounding the monophyly of *Phanera*, and its correct delimitation, particularly regarding the status of the proposed segregates *Schnella* Raddi (1820) and *Lasiobema* (Korth.) Miq. (1855).

Lewis and Forest (2005), stopped short of reinstating the New World genus *Schnella* but did point out that it might merit generic status according to a preliminary analysis of the Cercideae by Forest (unpublished data). Subsequently, Wunderlin (2010b), acting on the basis of the molecular evidence provided by Sinou et al. (2009), reinstated *Schnella* as a genus, thus formally separating the lianescent species of the New World from those of the Old World. The two genera are also separated morphologically by stamen number, the species of *Phanera* bearing (2–) 3 fertile stamens, whereas those of *Schnella* have 10.

Nevertheless, the morphological heterogeneity that persists within *Phanera* suggests that further generic segregations may be necessary as additional data are generated and monophyletic units illuminated.

1.6.3 Segregates of *Bauhinia*: *Lasiobema*

The genus *Lasiobema (*Korth.) Miq. (1855), based upon *Bauhinia* sect. *Lasiobema* (Korth, 1839–1842) was created to accommodate two species, *Lasiobema anguinum* Korth. and *Lasiobema horsfieldii* Miq. Up to 20 species have subsequently been treated within *Lasiobema.* Although recognised by some authors as a distinct genus (Bentham & Hooker, 1865; de Wit, 1956; Wunderlin, 1976; Verdcourt, 1979), and assigned generic status by Lewis and Forest (2005), a majority of authors have considered *Lasiobema* to be part of *Phanera* or *Bauhinia* (Baker, 1879; Hou et al*.,* 1996; Hao et al*.,* 2003; Lau et al*.,* 2009; Wunderlin, 2010a), and the taxonomic status of *Lasiobema* remains unresolved. The phylogenetic evidence (Hao et al*.,* 2003, Sinou et al*.,* 2009) and morphological evidence to support the status of *Lasiobema* has thus far proved inconclusive.

The species of *Lasiobema* (at whatever taxonomic rank it is recognised), like those of *Phanera*, are distributed throughout South East Asia, and the genus is closely morphologically allied with *Phanera*. The characters of habit and fertile stamen number, by which *Bauhinia, Phanera*, and *Schnella* are distinguished from one another, are homologous between *Lasiobema* and *Phanera,* both being tendrilled lianas with three fertile stamens. Putative morphological synapomorphies that have been proposed for *Lasiobema* include the presence of a swollen nectariferous disc in the flower (de Wit, 1956), a truncate calyx with reduced sepals (compared with a calyx of 5 strap-shaped lobes split to the mouth of the receptacle in *Phanera*), receptacle turbinate, and flowers small and numerous (de Wit, 1956). De Wit observed potential paraphyly within *Lasiobema*, describing two distinct morphological types: one having a swollen disc and glabrous ovary, the other without a swollen disc, and the ovary densely tomentose. He went on to say that in future the group without a disc and with tomentose ovary will prove to be better treated a genus. No synapomorphies are known to occur in all species that have been attributed to the genus, which further suggests the existence of paraphyly.

Schmitz (1977) attempted to circumscribe generic segregates of *Bauhinia* based solely upon pollen type. Six species were given a new combination (comb. nov.) within *Lasiobema* and added to the four taxa included by de Wit (1956) in the genus. He united these species as possessing the ‘curtisii’ pollen type, with three apertures, longitudinally angled towards the poles, a smooth surface and non-spherical shape (Schmitz, 1973). Schmitz (1977) described *L. harmsianum* (Hosseus) de Wit var. *media* (Craib) Schmitz as having a ‘bracteata’ type pollen.

Few molecular phylogenetic studies have included species of *Lasiobema*. The analysis by Hao et al. (2003), which utilised the nuclear gene region *ITS* to examine interspecific relationships of *Phanera s.l.*, was the most densely sampled molecular study of the genus to date, incorporating 32 species of *Phanera s.l.* of which seven also have a combination within *Lasiobema*. These seven species were indicated to be paraphyletic, and nested within various parts of the *Phanera s.l.* phylogeny, although with low support. The study of Sinou et al. (2009) sampled only a single species belonging to *Lasiobema* (*L. penicillilobum*), which appeared as sister to the clade of *Phanera s.s.*, although this relationship was poorly supported. Evidence from molecular phylogenetic analyses has thus so far been inadequate to demonstrate the monophyly or otherwise of *Lasiobema.*

1.6 Taxonomy of *Caesalpinia sensu lato* and *Mezoneuron*

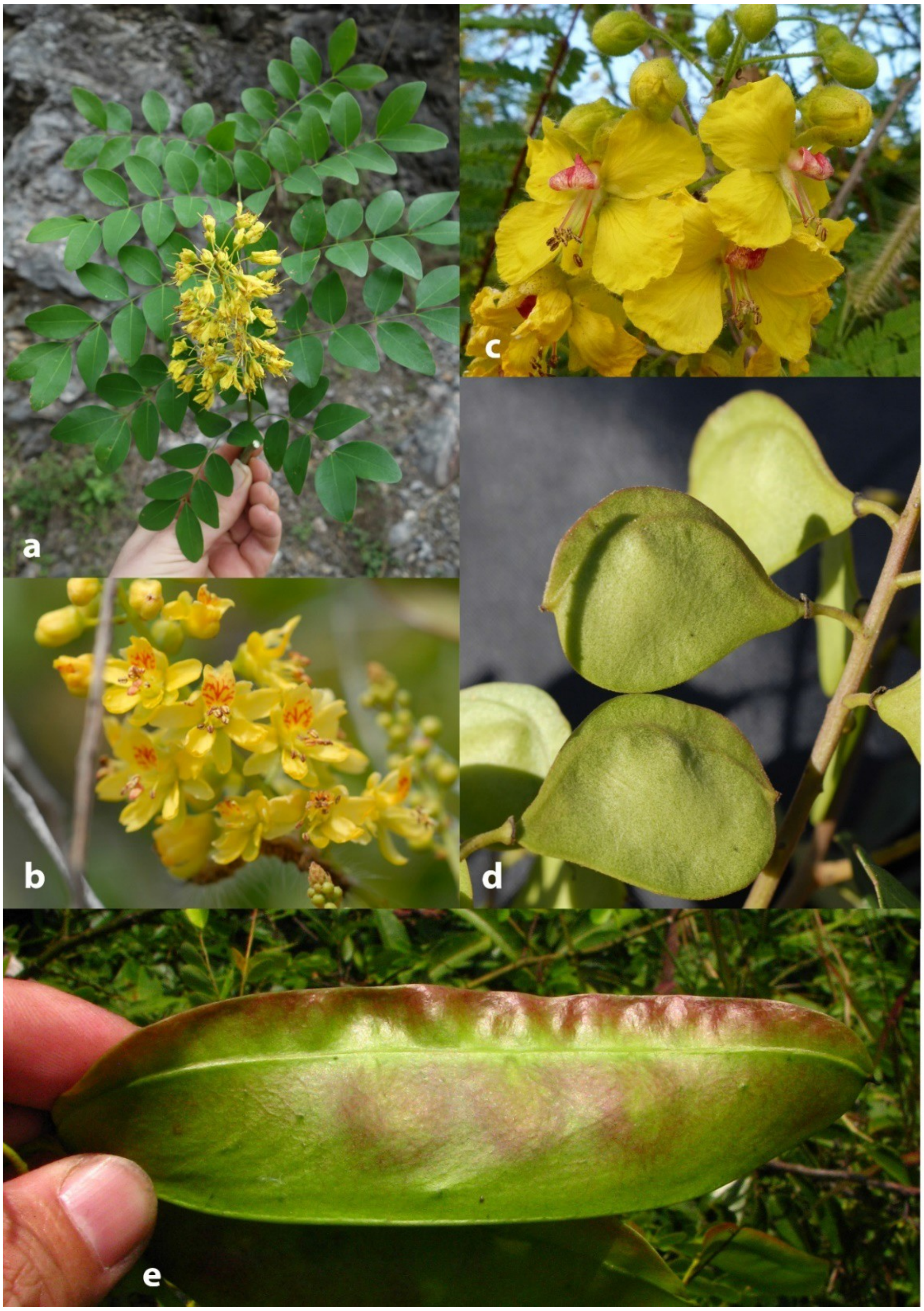


Figure 2. Composite plate showing leaf, floral, and fruit forms of *Caesalpinia s.l.* (a) Leaf and inflorescence of *Caesalpinia szechuenensis* (b) Flowers of *Mezoneuron deverdianum* (c) Flowers of *Caesalpinia mimosoides* (d) Fruit of *Mezoneuron montrouzieri* (e) Fruit of *Mezoneuron andamanicum*

The Caesalpinia group is one of eight informal generic groups into which Polhill and Vidal (1981) divided the tribe Caesalpinieae, and was defined by having a modified (sometimes cucullate) lowermost sepal, flowers generally zygomorphic with stamens crowded around the pistil at least toward the base, and the presence of spines, prickles and glands (Polhill & Vidal, 1981; Lewis & Schrire, 1995; Simpson et al., 2003; Nores et al. 2012). The number of genera in the group as defined at that time was 16, and has subsequently increased to 21 (Lewis, 2005). Of these, *Caesalpinia* L. (1753) *sensu lato* has been the most taxonomically complex and difficult to delimit, due in part to high levels of homoplasy (where similar character states arise for reasons other than shared ancestry, such as convergence or parallelism). It has most commonly been treated either as a single, polymorphic, pantropical genus, particularly by authors of regional accounts (Hattink, 1974; Vidal & Thol, 1976; Lewis, 1987; Lock, 1989; Hou, 1996; Lewis, 1998; Lock & Ford, 2004), comprising up to 150 species (Bentham, 1865), and with up to 30 names in synonymy (Lewis, 1998). The existence of considerable morphological heterogeneity within the broadly circumscribed genus is reflected in the loosely defined infrageneric sections devised by various authors (de Candolle, 1825; Bentham, 1865). Other authors have delineated up to 16 smaller segregate genera from within *Caesalpinia s.l.* (Britton & Rose, 1930). More recently, studies utilising molecular and/or morphological evidence have suggested or confirmed the paraphyletic nature of *Caesalpinia s.l.* (Lewis and Schrire, 1995; Simpson and Miao, 1997; Bruneau et al., 2001; Simpson et al., 2003; Bruneau et al., 2008; Manzanilla & Bruneau, 2012; Nores et al., 2012). Based on this molecular evidence, Lewis (2005) proposed that *Caesalpinia s.l.* may be comprised of eight segregate genera.

The most comprehensive molecular investigation into the Caesalpinia group to date is by Gagnon et al. (2016). This densely sampled analysis utilised one nuclear and five plastid gene regions to generate a phylogeny that largely resolved the questions surrounding generic limits within the Caesalpinia group, finding 26 well-supported genera. Of the eight genera proposed by Lewis (2005) to be reinstated as segregates of *Caesalpinia s.l.*, five (*Tara, Coulteria, Guilandina, Mezoneuron, Libidibia*) were robustly supported as monophyletic in this study, all of which are recognisable by a set of morphological synapomorphies. The remaining three (*Caesalpinia s.s., Poincianella, Erythrostemon*) were not supported as monophyletic, resulting in a reconfiguration of these genera, and the transferral of five species to a newly created genus, *Arquita* E. Gagnon, G. P. Lewis & C. E. Hughes (Gagnon *et al*., 2015).

One of these eight proposed segregate genera is *Mezoneuron* Desf. (1818) which has been treated by different authors since its inception either as part of *Caesalpinia s.l.*, or as a distinct genus. The primary morphological character that distinguishes *Mezoneuron* from *Caesalpinia s.s.* or other segregates of *Caesalpinia s.l.* is the fruit, which is laterally compressed, indehiscent, and bearing a wing along the upper suture. *Mezoneuron* has a disparate distribution, being most diverse in South East Asia, but with species also in Africa, Madagascar, New Caledonia, Australia, and Hawaii. This unusual distribution, coupled with the single supporting synapomorphy, raise questions regarding the status of *Mezoneuron* as a distinct genus.

2.1 SUMMARY AND CRITICAL APPRAISAL OF THE PUBLISHED WORK

2.2 Aims of the Research

1. Conduct a morphological and molecular analysis of *Mezoneuron*, to test the monophyly of the genus and evaluate interspecific relationships.

2. Examine generic limits within *Bauhinia s.l.*: how many genera should be segregated?

3. Evaluate the importance of monophyly in the context of the taxonomy of the Leguminosae, and more generally.

4. Explore the taxonomic relationships within *Bauhinia s.l.* and *Caesalpinia s.l.* in relation to their biogeography and evolutionary history.

2.3 List of papers

1. Clark, R.P., Mackinder, B.A., Banks, H. 2017. *Cheniella* gen. nov. (Leguminosae: Cercidoideae) from S. China, IndoChina and Malesia. *European Journal of Taxonomy* 360: 1–37.

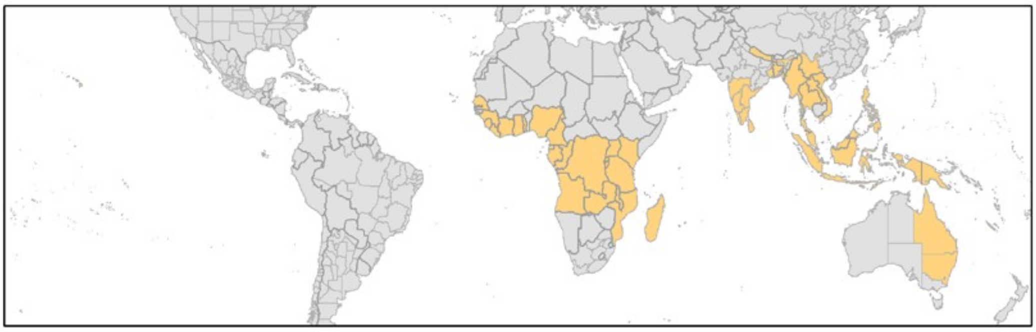
2. Clark, R.P. 2016. A Taxonomic Revision of *Mezoneuron* (Leguminosae: Caesalpinioideae: Caesalpinieae). *Phytotaxa* 274(1): 1–72.

3. Clark, R. & Gagnon, E. 2015. A revision of *Mezoneuron* (Leguminosae – Caesalpinioideae) in New Caledonia, with perspectives on vegetation, geology and conservation. *Phytotaxa* 207(1): 68–92.

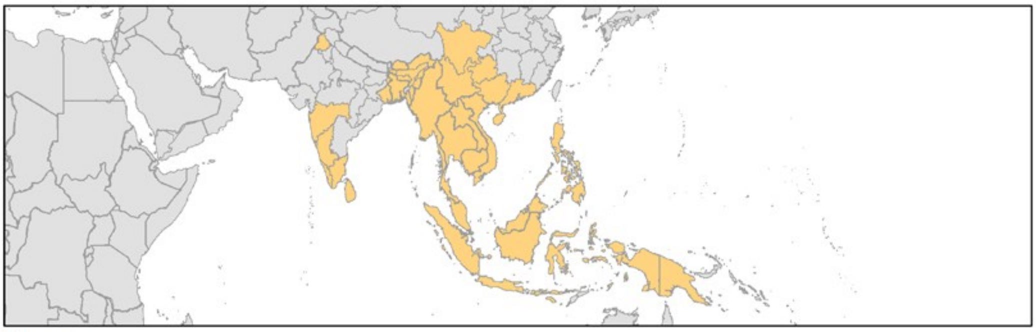
4. Clark, R.P. 2015. *Lasiobema flavum* (Leguminosae: Caesalpinioideae), a new record for the Flora of Thailand. *Thai Forest Bulletin (Botany)* 43: 70–73.

5. Trethowan, L., Clark, R.P., Mackinder, B.A. 2015. A synopsis of the neotropical genus *Schnella* (Cercideae: Caesalpinioideae: Leguminosae) including 12 new combinations. *Phytotaxa* 204(4): 237–252.

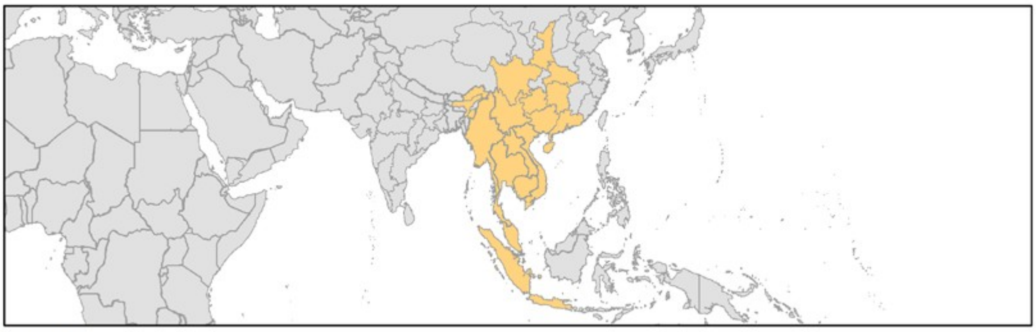
6. Mackinder, B.A., Clark, R. 2014. A synopsis of the Asian and Australasian genus *Phanera* Lour. (Cercideae: Caesalpinioideae: Leguminosae) including 19 new combinations. *Phytotaxa* 166 (1): 49–68.



Mezoneuron



Phanera



Cheniella

Schnella

Figure 3. Distribution maps of the four genera that are the subjects of the published works

Year	**Activity**
2005	Publication of Legumes of the World by Lewis et al., in which 8 potential segregates of *Caesalpinia s.l.* were indicated
2007	One of these potential segregate genera, *Mezoneuron*, was identified as requiring taxonomic and phylogenetic investigation to resolve its status as a monophyletic genus or otherwise. With its centre of diversity in South East Asia, a project on this genus was in line with my regional expertise on legumes Loans of herbarium material requested from eight international herbaria internationally Morphological review of all species of *Mezoneuron* commenced; continued throughout duration of project
2009	Field expedition to New Caledonia to collect herbarium specimens for study, silica-dried material for DNA analysis, and to study the plants *in situ.* Field expedition to Sierra Leone resulted in collection of *Mezoneuron benthamianum*
2010	Extractions of DNA from New Caledonia species conducted. Sequencing of *trnL-F* and *ITS* for some samples carried out
2011	Field expedition to Thailand facilitated collection of *Mezoneuron andamanicum* and *M. enneaphyllum*
2012	X-ray imaging used to investigate wing morphology of *Mezoneuron* fruits
2013	Extractions of DNA from herbarium material undertaken
2015	Publication of Revision of *Mezoneuron* in New Caledonia (Clark & Gagnon, 2015)
2016	Following correspondence with the Red List Authority of New Caledonia, revised conservation assessments for the *Mezoneuron* species of New Caledonia published by them
2016	Publication of Taxonomic Revision of *Mezoneuron* (Clark, 2016)
2016-2017	Further extractions of DNA from *Mezoneuron* samples. Sequencing of 4 plastid and one nuclear region. Phylogenetic analysis of sequences

Table 3. Methodology timeline for studies of *Caesalpinia s.l.*

Year	**Activity**
2005	Publication of Legumes of the World (Lewis et al., 2005), in which 8 potential segregate genera of *Bauhinia s.l.* were outlined
2009	Publication by Sinou et al. of phylogeny of the Cercideae, supporting in most cases the segregation of genera as indicated by Lewis et al. (2005)
2011	Field expedition to Thailand results in discovery of new locality (first country record) for very rare and poorly known species, *Lasiobema flavum*

2012	Review of carpological material in herbarium collections at RBG Kew by B. Mackinder & R. Clark reveals a distinct fruit type, corresponding to *Phanera* subgenus *Corymbosae.* Further investigation reveals additional morphological characters, biogeographical data, and molecular based phylogenetic evidence distinguishing the group Palynological study of *Phanera* subg. *Corymbosae* initiated (with H. Banks). Study reveals novel pollen type to characterise the group
2013-2014	CSYS ('Sandwich') student employed at RBG Kew to develop web page content for tribe Cercideae for Legumes of the World Online project. Student managed by R. Clark
2014	Publication of the Synopsis of *Phanera* (Mackinder & Clark, 2014). Identified the need for publication of new nomenclatural combinations in *Schnella*, following reinstatement of the genus by Wunderlin (2010)
2015	Publication of the Synopsis of *Schnella* (Trethowan, Clark & Mackinder 2015).
2016	Field expedition to Guangxi, China, results in new collections of *Phanera* subg. *Corymbosae*, including flowers in alcohol for anatomical study Anatomical study of floral structure of *Phanera* subg. *Corymbosae* reveals novel synapomorphy for the group
2017	Publication of *Cheniella* gen. nov. (based upon *Phanera* subg. *Corymbosae*) (Clark, Mackinder & Banks, 2017)

Table 4. Methodology timeline for studies of *Bauhinia s.l.*

2.4 *Bauhinia sensu lato*

Bruneau et al. (2001) and Sinou et al. (2009), showed that the genus *Bauhinia s.l.* is paraphyletic with respect to the monospecific Madagascan endemic *Brenierea*, and therefore should be divided into smaller, monophyletic genera. The morphological evidence needed to (re)instate several of these smaller genera already existed, having been laid out in the taxonomic literature; however, a level of variation remains within some currently delineated genera, suggesting that further paraphyly persists within these groups.

The focus of my research has been to address the uncertainty concerning classification of *Bauhinia s.l.*, specifically generic limits within the segregate *Phanera s.l.* The ultimate aim of this is to create a stable taxonomy that reflects evolutionary relationships between the component taxa, which can be used to aid identification of and communication about these taxa.

2.3.1 Segregates of *Bauhinia*: *Cheniella*

Phanera Lour. (1790) is the most speciose genus that has recently been reinstated at generic rank from within *Bauhinia s.l.* based upon a synthesis of morphological and molecular data (Lewis & Forest, 2005; Sinou, 2009), but polymorphism persists within the genus. A review carried out for this study of palynological and molecular data for *Phanera*, in conjunction with a careful evaluation of the morphological heterogeneity within the genus, revealed strong evidence that the species of *Phanera* subsection *Corymbosae* are a natural group that warrant generic status. Paper 1 describes the genus *Cheniella* to accommodate them, based upon robust morphological, palynological, molecular, and geographical data, and comprising 10 species. This work therefore separates a distinct evolutionary unit from within *Phanera*, reducing the polymorphism therein, and removing a degree of paraphyly from the genus. The paper provides a synoptical and comparable description of each species of *Cheniella*, including a comparative table of characters, as well as a key to the species, and a composite illustration (line drawing) including elements of several of the species. These enable identification of the genus, and of the species that comprise it. In the broader context, this represents a set of additional tools by which to identify elements of the large and morphologically complex group *Bauhinia s.l.*

A preliminary conservation assessment based on herbarium specimen data and the available literature is presented for each species of *Cheniella*, and these are the first ever created for these species. These assessments highlight the status of certain species as potentially at risk of extinction, as well as forming the basis for future more comprehensive conservation assessments. Details of the distribution of each species are presented, the synthesis of which reveals the centre of diversity of the genus to differ from that of *Phanera.* This information, combined with the conservation assessments, will enable researchers to target future collecting efforts, which will further elucidate the range and threat status of the species.

Analyses carried out for this study reveal novel micromorphological data, showing *Cheniella* to be characterised by a pollen type that is unique within the Leguminosae. This extends our palynological knowledge of *Bauhinia s.l.* as well as of the family overall. Our work also describes the fused staminodal ring that is an apparently unique synapomorphy for the genus, previously poorly documented for these species, and unknown within the rest of the Leguminosae. The implications of the staminodal disc for pollination, and of a further synapomorphy of the elongated hypanthium also described in the published work, are discussed in the paper. The description and analysis of these floral and pollen structures provides new insights into the poorly understood pollination systems of *Bauhinia s.l.*

The treatment creates a new name (new combination) for each taxon within the genus, and lists the basionym for each. This clarifies the former taxonomic position of each taxon, and unambiguously provides the correct current name for each. This is essential for any communication relating to the taxa. For each taxon name in the treatment, the type specimen (or specimens) are listed in full. For *Cheniella touranensis*, which had no holotype designated in the original description, a lectotype was designated as part of this study.

Discussion of the taxonomic status of *Cheniella glauca* and *C. tenuiflora* contributes to the body of philosophical debate regarding the nature of taxonomic boundaries, and our collective approach to their delineation and status. Upranking of the taxon *Bauhinia* (*Cheniella*) *glauca* subsp. *tenuiflora* to the level of species gives a more accurate understanding of species numbers within *Bauhinia s.l.*

The study provides valuable new data for a poorly known and apparently very rare species, *C. ovatifolia*, including a new country record (Vietnam), and the first illustration of the species.

A systematic arrangement of the species of *Cheniella* is presented in this published work, based upon morphological similarities and geographical range of the species. A preferable approach to constructing a systematic arrangement is through interpretation of a molecular-based phylogenetic tree; however, such data were not available for this study. The *Corymbosae* species sampled by Hao et al. (2003), although strongly supported as a monophyletic clade, were poorly resolved at the inter-species level, with high support on only one of the branches, and two polytomies. We therefore deemed this phylogeny to be inadequate evidence on which to judge the systematic relationships within the genus, and hence relied upon morphological and biogeographical characters.

2.3.2 Segregates of *Bauhinia*: *Phanera* and *Schnella*

Phanera has been historically recognised as a distinct genus by some authors, most notably de Wit (1956) who delineated 44 species of Malesian *Phanera*, and also by Wunderlin (1976; 2010a; 2011), Verdcourt (1979), Queiroz (2006) and Vaz (2010); however, the vast majority of authors have treated it as a subgenus of *Bauhinia* (Bortoluzzi et al., 2006; Chen, 1988; Larsen et al., 1980, 1984; Wunderlin et al., 1981; Wunderlin & Eilers, 2009). Since the broadly sampled phylogenetic treatment of Sinou et al. (2009), the morphological evaluation by Lewis et al. (2005), and unpublished molecular analysis of Lewis & Forest (2005) in which eight generic segregates were suggested, the reinstatement of *Phanera* at generic rank has been widely accepted._

The genus *Schnella* (1820) was accepted by various authors in the subsequent years, before being reduced to a section of *Bauhinia* by Bentham (1865). Since then, *Schnella* has been upheld at generic rank by certain authors, whilst being subsumed within *Bauhinia*, or considered synonymous with *Phanera* by others. More recently, the molecular phylogenetic analyses of Hao et al. (2003), Lewis & Forest (2005) and Sinou et al. (2009) have provided some evidence that *Schnella* represented a clade separate to *Phanera s.s.* Based on this evidence, Wunderlin (2010b) formally reinstated *Schnella* as a genus, publishing 28 new combinations. Palynological evidence (Banks et al., 2013, 2014) and morphological characters (primarily stamen number) also support the status of *Schnella* as a distinct genus.

The reinstatement of *Phanera* and *Schnella* resulted in the need for new combinations in each genus for many taxa described in *Bauhinia*. In Papers 5 and 6 we present all accepted names, synonyms, and excluded names for *Phanera* and *Schnella*, including, respectively, 19 and 12 new combinations not made by previous authors.

Complete and up-to-date rendering of accurate accepted names of all taxa included within any genus is the foundation for understanding the composition of the genus, as a fundamental tool for taxonomists, and for anyone who needs to know the identity of an organism. This is particularly true of genera with long and complex taxonomic and nomenclatural histories, such as *Bauhinia s.l.*, in which there are often a large number of names available for any given taxon. If the names are not explained and listed, enormous confusion can arise as to the appropriate identity for a given taxon, which can result in taxonomic instability. Clarification of, and presentation of, currently accepted names and synonymy for all taxa included within *Phanera, Schnella,* and *Cheniella* (within a single publication for each) avoids doubt or ambiguity regarding the taxonomic limits of these genera, and removes nomenclatural confusion. Additionally, in providing full and accurate lists of current names, the published work makes information regarding the size and composition of each genus accessible to a wide user community.

The lists of names for these treatments were compiled using a combination of internet resources, and a wide range of literature, with the aim of detailing as comprehensively and accurately as possible the names for each taxon.

Phytogeography is a key element of the segregation of genera from within *Bauhinia s.l.*, and is particularly relevant to the delineation of both *Phanera* and *Schnella. Phanera* has been formerly recognised as a widespread taxon occurring in both the New World and Old World, but the segregation of the c. 40 species from South America as the genus *Schnella* results in *Phanera* becoming circumscribed as a genus restricted to Asia and Australasia. The occurrence of each species by country is detailed in Papers 5 and 6, with the addition of a map showing relative species density by country for *Schnella*. The species distributions were assessed using a combination of the published literature, and herbarium specimens at RBG Kew.

The published papers describe the taxonomic history of the respective genera. The synopsis of *Phanera* includes a table comparing the defining characters of *Bauhinia s.s.*, *Phanera*, *Schnella*, and a further proposed segregate genus, *Lasiobema.*

2.3.3 Segregates of *Bauhinia*: *Lasiobema*

Lasiobema is a putative segregate genus of *Bauhinia s.l.*, whose monophyly has not yet been successfully demonstrated. Paper 4 presents the first record of the species

Lasiobema flavum in Thailand based upon a collection made by the author. This very poorly known species has previously been collected from only two localities in Peninsular Malaysia. By recording a new locality for the species, the paper improves understanding of its distribution and conservation status, and contributes to ongoing efforts to fully document the flora of the Thailand. A preliminary conservation assessment is provided. The taxonomic description given in this published work expands upon the previously available description of the species with additional morphological details. These data can contribute to elucidating the monophyletic nature or otherwise of the proposed genus.

The new specimen was collected on a limestone hill, as were the two previous collections of the species from Malaysia, indicating that *Lasiobema flavum* may be an obligate limestone species; were it able to grow on other substrates, further collections would probably exist.

The preliminary conservation assessment for this study determined the species to be Endangered, according to IUCN (2014) criteria, based upon its apparently very limited range, and restriction to limestone peaks, which are at risk of destruction from quarrying for lime. However, the flora of the limestone peaks of Thailand and Peninsular Malaysia is poorly studied, and a full survey of the peaks in the vicinity of the collection localities of the species would possibly reveal further populations. Detailed local surveys in Malaysia and Thailand would be necessary for a full conservation assessment to be carried out.

2.4 Caesalpinia *sensu lato*: *Mezoneuron*

Mezoneuron is one of the proposed segregate genera of *Caesalpinia s.l.* It has been separated primarily on the basis of the characteristics of the fruit, which is distinct from those of other members of *Caesalpinia s.l.* in being winged and indehiscent.

In accordance with the accepted principles of systematics, to be suitable for recognition at the generic level, *Mezoneuron* should be demonstrated to be monophyletic. Prior to the study in Paper 2, the monophyly of *Mezoneuron* had not been tested using phenotypic evidence, and only partially tested with molecular phylogenetics. Analysis to test the apparent synapomorphy of the fruit type and to evaluate for additional synapomorphies is carried out in Papers 2 and 3 of this work, thus assessing the morphological evidence for the monophyly of the group.

The study in Paper 2 presents the first ever complete taxonomic revision of the 24 species of *Mezoneuron*, across its geographical range. The revision, and that of the New Caledonian species in Paper 3, each include a key to the species, and for each species: a full morphological description, details of distribution and a distribution map, habitat details, and a preliminary conservation assessment. Paper 2 also presents a systematic arrangement of all species in the genus, and a discussion of the range of variation in fruit morphology across the genus in the context of its distribution and evolution. Paper 3 additionally provides colour photographs, a composite illustration of the taxa, and discussion of vegetation and geological substrates types of New Caledonia, and the habitat preferences of each species.

The previously existing descriptions of the species assigned to *Mezoneuron* appear in numerous pieces of literature since the genus was first described in 1818. These descriptions have been extremely variable in quality, length, and detail.

Standardised descriptions of the species were not available in the literature, and no single key existed to all species in the genus. The species of *Mezoneuron* in New Caledonia previously have been little studied; the only taxonomic descriptions available were the original protologues, which were published many decades previously, and were brief and lacking in detail. The studies in Papers 2 and 3 provide detailed and standardised species descriptions, and keys to all the species, essential tools for identification of the taxa.

The morphological data on which Papers 2 and 3 were based were gathered from herbarium specimens housed in 16 herbaria, especially those with rich Asian and New Caledonian collections. This was to ensure that multiple specimens of each species were studied, thus encompassing the full range of morphological variation within, and full distribution range of each taxon. The set of specimens used was augmented by using online digital images. Type specimens were consulted wherever possible to ensure accurate understanding of the taxon concepts. For some species, only few specimens were available, and limited information could be assembled, such as *M. nhatrangense* which is endemic to Vietnam and known from only three herbarium collections in a single locality, the most recent from 1932.

The summaries of the distribution and known localities of the species of *Mezoneuron* that are provided in these works distinguish widespread and common species from those that are rare or have a restricted range. This information, along with phenological information, further enables identification of the species, and makes it possible to devise future targeted collecting strategies, particularly of rare species. Providing habitat details can allow species that are most at risk from habitat destruction to be recognised and appropriately protected.

As part of this research, a preliminary conservation assessment was generated for each species of *Mezoneuron*, based upon herbarium specimen records, and additional data where available. In the modern global context of ever-increasing anthropogenic threats to habitats and to the continued survival of plant species, conservation assessments are an essential tool for detecting and monitoring at-risk taxa, so that protection measures can be implemented where necessary to avoid population declines, and taxon extinctions. For almost every species in the treatments herein, the conservation assessments provided are the first ever published. These assessments of rarity and conservation status enable prioritisation of conservation measures, and inform further research. The assessments carried out for this study reveal five species to have a threatened status (from Vulnerable to Critically Endangered), in addition to the single species already formally assessed by IUCN as Critically Endangered (*M. kauaiense*), and two species which are Data Deficient.

The conservation assessments of the New Caledonian species were updated between publication of Papers 2 and 3. Following the preliminary conservation assessments of the species in Paper 3, full IUCN Red List Assessments for Plants of New Caledonia were carried out by the relevant Red List Authority for the country. These full assessments were carried out based upon those published in the current work, and in discussion with the present author. The resulting assessments downgraded the category of threat for two species (less threatened), whilst two species were considered Data Deficient. This reflects the incomplete nature of the data available when creating the original assessments, and highlights the fact that conservation assessments based upon herbarium specimens with limited additional data should be considered as preliminary.

Preliminary conservation assessments for this study were carried out in the absence of certain data that would be desirable to incorporate, such as known threats, or measured changes to population numbers over time. Inclusion of old herbarium specimens in the generation of Extent of Occurrence (EOO) and Area of Occupancy (AOO) figures may result in an overestimate of the contemporary population size, if populations have declined since the date of collection. Nevertheless, preliminary conservation assessments based upon herbarium specimen data give an extremely valuable and often accurate picture of the rarity and threat level of a taxon, and provide a baseline from which to recognise vulnerable taxa and to seek further data with which to carry out a full assessment.

Accurate lists of current names with full synonymy, as presented in these works, provides an essential communication tool. Additionally, a full list of exsiccatae is given in both Papers 2 and 3. These numbered exsiccatae allow identification of duplicate specimens housed in herbaria not consulted by the author. In many cases, the specimens utilised in this study represent historical records of distribution, which can be examined in the context of current distribution to determine range reductions over time. The listing of type specimens for each taxon in these studies is essential to inform the correct application of the taxon names. The designation of four lectotypes, two epitypes, and one neotype in the treatment of Paper 2, and two lectotypifications in Paper 3, removes ambiguity regarding the application of the taxon names, enabling users to accurately define the taxon concept, and to confidently identify specimens.

The first ever systematic arrangement of all species of *Mezoneuron* is presented Paper 2. This arrangement was devised by inferring infrageneric relationships based upon morphological characters and geographical distribution of the species. It informs our knowledge of the inter-species relationships, and is a tool for researchers and curators working with collections of the genus. The alternative option, to present the species in alphabetical order, would have produced a less functional tool for the end user. The nature of systematics is such that the expectation is to publish a treatment in the knowledge that it may be subject to potential future change in light of new data. A taxonomic revision nonetheless should represent scientific advance, without the assumption of ‘complete’ knowledge.

The investigation in Papers 2 and 3 into the variation in fruit morphology within *Mezoneuron* highlighted the existence of two fruit types, which are correlated with geographical distribution patterns. This contributes to our understanding of the possible evolutionary patterns and inter-species relationships within the genus, and constitutes evidence that can be interpreted through future biogeographical analyses.

Of the 24 species currently recognised in *Mezoneuron*, five (as circumscribed in Paper 3) are endemic to New Caledonia. This is a taxonomically and evolutionarily significant subgroup of *Mezoneuron* in terms of distribution and morphology. The species are ecologically interesting, occurring within a range of habitat types, and on different substrates including ultramafics. Ultramafics present challenging conditions for plant growth, and often harbour many species that are restricted to this substrate and therefore narrowly distributed. Understanding the ecology of the endemic species of *Mezoneuron* is an important element of understanding the genus as a whole. The morphology of the fruit of the New Caledonian species poses questions regarding the evolutionary position of these species within the genus, as well as in relation to the putative sister genus, *Pterolobium.* These questions were highlighted in the Paper 3, indicating the possibility that *Mezoneuron* may be paraphyletic, and that further investigation, including molecular analysis, was necessary to test this possibility.

The morphological analysis integral to this study indicated one Asian species (*M. sinense*) as being probably misplaced within *Mezoneuron*, thus erecting a hypothesis that has since been successfully tested and proven correct by the current author using molecular phylogenetic analysis, thus further elucidating species numbers within the genus.

The species of *Mezoneuron* in New Caledonia are morphologically highly homogeneous, rendering the delimitation of species units problematic, with obscure species boundaries and poorly defined character sets. Where the species in question belong to a geographically distinct area, morphological homogeneity can be an indication of the recent evolutionary origin of a group. Two previously described species of *Mezoneuron* from New Caledonia, *M. deverdiana* and *M. montrouzieri*, proved to be particularly problematic in terms of delimitation during this study. Following extensive examination of the available herbarium material, and field observations, I concluded that no clear morphological characters could be found to distinguish them and that *M. deverdiana* should therefore be sunk into synonymy with *M. montrouzieri.* Although this decision was justified, based on the data available, subsequent molecular phylogenetic analysis by the present author has revealed the existence of two distinct evolutionary units within this complex, necessitating the reinstatement of the species *M. deverdiana.* Subsequently, I have identified certain small (generally non-discrete) morphological differences that can be used to distinguish the two species, principally ovary indumentum, leaflet number, bract size, and fruit size.

As a morphological analysis, these published works complemented the work of Gagnon et al. (2013), in which a phylogeny of *Caesalpinia s.l.* based upon the plastid gene region *rps16*, which included 11 species of *Mezoneuron*, was published. Since the publication of the papers presented for this study, I have commenced a molecular phylogenetic study to further test the monophyly of *Mezoneuron* and its intrageneric relationships. I have also started a biogeographical analysis. The preliminary results of these analyses are discussed in Section 4 of this Critical Appraisal, and a paper presenting these results is in an advanced state of preparation.

3.1 FURTHER DISCUSSIONS AND RESULTS ARISING FROM THE PUBLISHED WORKS

3.2 Phylogenetic analysis of *Mezoneuron*

Paper 2 of the works herein aimed to evaluate the monophyly of *Mezoneuron* through examination for synapomorphic traits. The study revealed a lack of uniquely homologous characteristics, although the occurrence of a winged fruit was shown to be universal within the genus, but not exclusive to it. The genus was demonstrated to be characterised by a suite of characters, in addition to the fruit type, which mirrors the situation in many other genera of *Caesalpinia s.l.*

The large scale phylogenetic analysis by Gagnon et al. (2016) of the Caesalpinia group incorporated 10 of the 24 species of *Mezoneuron* from most of its geographical range. This study utilised six gene regions, one nuclear and five plastid, to provide robust support for *Mezoneuron* as a monophyletic group sister to a clade containing *Pterolobium.* However, the study did not sample from any of the species of the genus from New Caledonia, and was limited in terms of the number of species sampled.

Since the publication of the work on which this thesis is based, I have carried out a molecular phylogenetic analysis of *Mezoneuron* which included eight species not sampled for previous published studies. The aim of this analysis was to further test the monophyly of the genus, and to evaluate the disjunct distribution of the genus within the evolutionary context. For a total of 30 samples of *Mezoneuron*, one nuclear and four plastid gene regions were sequenced, representing 19 of the 24 species of the genus. This includes all six species of *Mezoneuron* endemic to New Caledonia, and two species from South East Asia not sampled by Gagnon et al. (2016). Additional sequences were downloaded from Genbank for inclusion in the analysis. The resulting sequences were concatenated into a single matrix, and analysed using Maximum Likelihood (RaxML-HPC2 v. 8.2.10 (Stamatakis 2014) on XSEDE, via the CIPRES Science Gateway (Miller et al. 2010)) and Bayesian methods (using MrBayes 3.2 (Ronquist et al. 2012) via the CIPRES Science Gateway (Miller et al. 2010)). A time-calibrated phylogenetic analysis was carried out using BEAST 1.8.4 (Drummond et al., 2012), and a preliminary biogeographical analysis using Lagrange.

The preliminary results of my phylogenetic analysis strongly support *Mezoneuron* to be monophyletic in both the Maximum Likelihood and Bayesian analyses, sister to a clade containing *Pterolobium* and the species of an informal Ticanto clade (Figure 4).

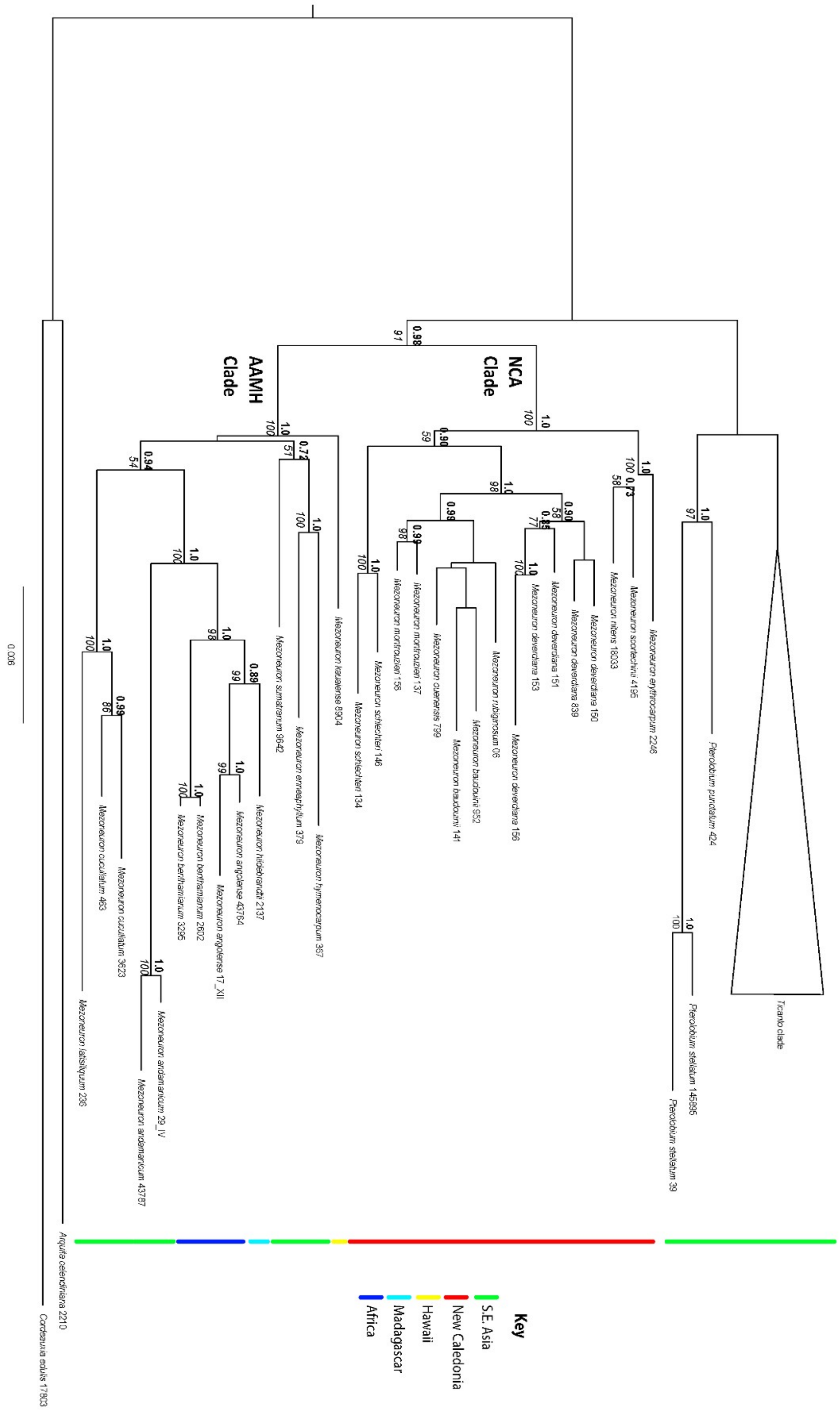


Figure 4. Maximum Likelihood tree of *Mezoneuron* and its sister taxa, *Pterolobium* and the informal Ticanto group, based on consensus of nuclear (*ITS*) and plastid (*matK*, *rps16*, *trnL-F*, *trnD-T*) data. Bootstrap support values are displayed below the branches, italicised, and Bayesian Posterior Probability (PP) values are shown above the branches, in bold. Where no value is shown, this indicates Bootstrap of <50% or PP of <0.5.

Within *Mezoneuron*, two clades are recovered, each with 100% bootstrap, and 0.99 or 1.0 posterior probability (PP). One (the AAMH clade) contains the species distributed in South East Asia, together with those from Africa, Madagascar, and Hawaii; the other (the NCA clade) is comprised of species found in Australia (in one case also extending into New Guinea), together with the endemics of New Caledonia. Within the AAMH clade, species relationships are generally well-resolved with robust support. A significant finding within this clade is the position of the Asian species *M. andamanicum* as sister to the Africa and Madagascar species. Within the Australasian clade, the three Australian (and New Guinean) species sampled are resolved with strong support (100% bootstrap, 1.0 PP) as sister to the New Caledonian endemic species. Within the New Caledonian clade, further subclades are resolved (with support levels between 56% bootstrap, 0.89 PP to 100% bootstrap, 1.0 PP), which elucidate the inter-species relationships.

As discussed by Clark & Gagnon (2015) and Clark (2016), two morphological patterns can be distinguished within *Mezoneuron*: one type bearing a large, usually multi-seeded fruit with a broad wing, and relatively large flowers, the second type bearing a small, single-seeded fruit with a narrow wing, and flowers of (usually) <1 cm diameter. These morphological types correspond with the discrete geographical clades revealed in the phylogeny here presented, the large-fruited type exclusive to the Asia-Africa-Madagascar-Hawaii clade, and the small-fruited type restricted to the Australasia-New Caledonia lineage.

The preliminary results of my phylogenetic analysis uphold the findings of the morphological studies presented in the published works herein, in terms of the monophyly of the genus, of the infrageneric relationships, and of the relationship of the genus to other elements of *Caesalpinia s.l.* These results also agree with those of the molecular phylogenetic studies of Gagnon et al. (2013, 2016).

The morphological analysis here presented, and the molecular phylogenetic studies by Gagnon et al. (2013, 2016) and by the present author, demonstrate the utility of both of these approaches as complementary tools for understanding and unravelling the taxonomy and evolution of living organisms. In order to maximise certainty regarding the status of taxonomic entities, and relationships between organisms, analysis should include a large number and diversity of characters. Molecular analysis is particularly advantageous in this respect, in that it can include hundreds or thousands of informative characters, which with the adoption of new technologies (Next Generation Sequencing) can become tens or hundreds of thousands. Such data-rich analyses can provide highly robust phylogenies that should resolve inter-organismal relationships.

In light of the modern technologies and techniques available for decoding the tree of life, the relevance of traditional morphological taxonomic methods may be questioned. The number of morphological characters available is considerably smaller than those present in DNA, and a further disadvantage of morphological taxonomy is that it is inevitably to some extent subjective, as reflected in the historical taxonomic complexity of groups like *Bauhinia s.l.* and *Caesalpinia s.l.* However, the strengths of morphological taxonomy complement those of molecular phylogenetics to give a holistic understanding of organismal interrelatedness and of the organisms themselves. The phenotype of an organism presents additional characters to those that are intrinsic within its DNA, and utilisation of both types of characters should be employed to maximise the effectiveness of a systematic study. Complete understanding of organisms, and of the relationships between them, requires knowledge of all component parts, including the measurable physical characteristics.

Morphological taxonomies erect hypotheses that can be tested using molecular techniques: without them and the herbaria which house the specimens essential to morphological studies, the questions that enable directed approaches to molecular phylogenetic testing would not exist. We need to be able to visually recognise taxa in order to construct appropriate questions as to their possible relationships. This is exemplified in *Bauhinia s.l.* and *Caesalpinia s.l.*, in which the phylogenetic testing of relationships depends upon these groups having been conceptualised through (nearly 250 years of) baseline morphological taxonomy.

Moreover, for phylogenetic identification methods such as DNA barcoding to be feasible, the taxonomic identities of organisms must first be reliably established, and reliably identified samples of these organisms used to establish a library of sequences against which new samples can be matched. This must be achieved with traditional morphological taxonomic methods. Morphological data are also necessary for the interpretation of molecular phylogenies - a DNA sequence alone is meaningless without knowledge of the organism that it represents. Moreover, morphological features provide a wealth of information about aspects of the organism that cannot be inferred from a phylogenetic tree, such as ecological adaptation, which can be essential in understanding and predicting distributions and providing accurate conservation assessments.

3.2 Biogeography of the Leguminosae, the Caesalpinioideae and the Cercidoideae

Taxon	**First fossil evidence**	**Origin**	**Age**
Leguminosae (caesalpinioid)	*Sindora*-like pollen	Canada, Colombia, Siberia	Maastrichtian, 75-65 MA
Leguminosae (caesalpinioid)	Fruit, *Leguminocarpon gardneri* (Chandler) Herendeen & Crane	Reading Formation, England	Late Paleocene, c. 56 MA
Cercidoideae	*Bauhinia*-like leaves	Ningming Formation, South China; Coatzingo Formation, Mexico	Oligocene, c. 38-29 MA
Mezoneuron	Fruit	Reading Formation, England; Claiborne Formation, North America	Middle Eocene, c. 45 MA

Table 5. Key fossils of Leguminosae

3.2.1 Biogeography of the Leguminosae

Until recently, the prevailing hypothesis of the origin of the Leguminosae was that the family arose ca. 84–74 MA in the Campanian or Maastrichtian of the Upper Cretaceous (Morley, 2000), in West Gondwana (Schrire et al., 2005) before the breakup of that continent. Africa and South America were last in contact around 100–90 MA, thus the crown age of legumes must be at least as old as this for the hypothesis to be valid (although the potential for dispersal over islands and ridges may have persisted until as late as 65 MA) (Raven & Axelrod, 1974; Morley, 2000; 2003; Schrire et al., 2005. The earliest reliable fossil evidence of the Leguminosae is of caesalpinioid pollen (pertaining to the Caesalpinioideae in its pre-2017 circumscription) resembling that of the extant genus *Sindora,* from the Maastrichtian (74–65 MA) of Canada, Colombia, and Siberia (Herendeen & Crane, 1992); this, therefore, is currently understood to be the maximum age of the family, and the West Gondwana hypothesis must be rejected. However, it should be noted that evaluations of the age of the Leguminosae are ongoing, and a possible earlier stem age for the family has been proposed in the fossil-calibrated analysis of Magallon et al. (2015) in which the stem age for the Leguminosae was projected to be 92.1 MA (+/- ca. 20 million years).

Unequivocally identified fossil fruits of the Leguminosae, again caesalpinioid, are first known from the late Palaeocene (Herendeen & Crane, 1992). A fossil fruit *Leguminosites gardneri* Chandler (1961), later transferred to *Leguminocarpon gardneri* (Chandler) Herendeen & Crane (1992), is documented from the Reading Formation of southern England which dates to the late Palaeocene, c. 56 MA (Lavin et al., 2005). Further possibly caesalpinioid fruits are known from the Claiborne Formation of the early Eocene (c. 50–56 MA) (Herendeen & Crane, 1992). Fossil evidence of the mimosoid and papilionoid groups appears shortly after this, around 55–50 MA (Herendeen & Crane, 1992; Lavin et al., 2005), showing that legumes diversified during the Early Tertiary, soon after their presumed origin. By the middle Eocene (c. 50 MA), the fossil record evidences the presence of most of the major lineages of legumes in North America, Europe, Africa, and Asia (Schrire et al., 2005).

With the rejection of the West Gondwana hypothesis, the previously widely adopted explanation for the global distribution of legumes being the result of vicariance must also be rejected. The presence of legumes throughout every continent on earth must therefore have arisen through multiple dispersal events, including across long distances. The currently most widely-accepted alternative to the West Gondwana hypothesis for the origin of the Leguminosae was presented by Schrire et al. (2005), centred around the Tethys Seaway, a seasonally dry to arid tropical belt that existed during the Tertiary, positioned between two zones of wetter tropical climate to the north and south. The Tethys Seaway spanned the circumference of the globe, spanning the land masses that now represent southern North America, North Africa, and South East Asia (Figure 5). Early-diverging legume clades (c. 60–55 MA) apparently became distributed across the Tethys Seaway during the Tertiary, before dispersing north and south to South America, Africa, and Madagascar (Schrire et al., 2005). Estrella et al. (2017), however, have proposed that the arid Tethys Seaway explanation may not be appropriate for all groups of legumes, presenting an analysis that suggests a southern hemisphere African-South American origin of the Detarioideae, in the early Palaeocene (68–64 MA). Another geographical feature that may have facilitated the dispersal of the Leguminosae is the Early Eocene North Atlantic Land Bridge (NALB), consisting of two bridges between Greenland and Europe, and two between Greenland and North America, thus linking the land masses of Europe and North America. The area during this period was populated by the boreotropical flora (Tiffney, 1985; Milne, 2006), frost-intolerant tropical vegetation, which may have been suitable habitat for members of the Leguminosae adapted to wetter tropical (rather than arid or seasonally dry) conditions. The existence of many closely related genera of legumes between different areas of the tropics is most likely explained by a combination of these hypotheses.

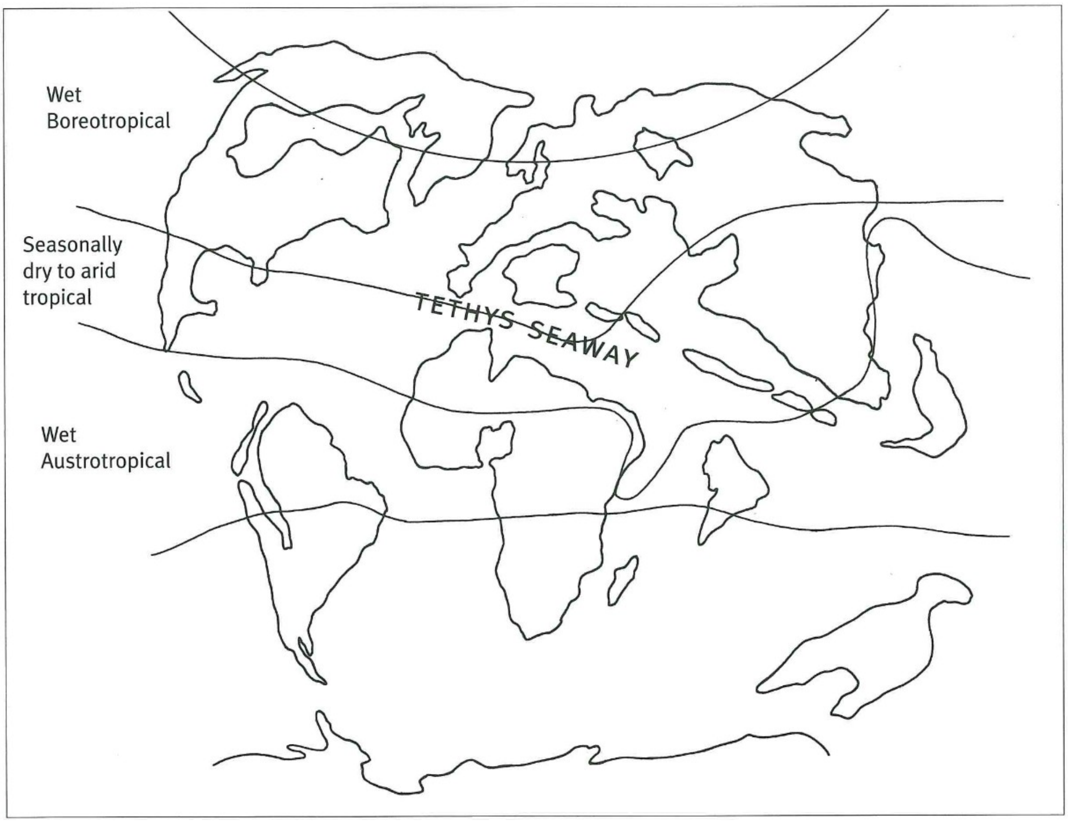


Figure 5. Palaeocene map reconstructing the Tethys Seaway (reproduced with permission from Schrire et al., 2005)

3.2.2 Biogeography and ecology of the Cercidoideae

To understand the origin and dispersal of the subfamily Cercidoideae, and the taxonomic elements that comprise it, it is necessary to examine the fossil evidence of the group in the context of our knowledge of past climatic and geological processes, its present-day distribution, and phylogenetic relationships. The Cercidoideae is currently diverse throughout the tropics, including the Asia-Australia-Pacific region, South America, Central/ North America, and Africa-Madagascar, whilst the genus *Cercis* is present in the warm-temperate Northern Hemisphere, including Europe (Schrire et al., 2005; LPWG, 2017). As the putatively earliest diverging extant lineage of legumes, the origin and initial dispersal of the Cercidoideae is likely to have followed a similar pattern to that of the family as a whole.

Fossil evidence of the Cercidoideae is largely absent from the early legume record, and despite the distinctive leaf shape of the subfamily their representation in the fossil record is not apparent until well after that of other fossil legumes, relatively late in the evolutionary history of the family. Although there have been reports of leaves of *Cercis* from Late Cretaceous and early Cenozoic sediments, the identities of the vast majority of these have not been reliably verified (Wang et al., 2014). The oldest reliable fossil evidence of *Bauhinia* and *Bauhinia*-like leaves derives from the late Eocene – Oligocene (ca. 38–29 MA) Ningming Formation in South China (Wang et al., 2014) and the Oligocene Coatzingo Formation of Mexico (Calvillo-Canadell & Cevallos-Ferriz, 2002; Wang et al., 2014).

The existing published phylogenies of the Cercidoideae, although few, provide important insights into the evolutionary history of the *Bauhinia s.l.* and of the

Cercidoideae as whole. The results of Sinou et al. (2009) show *Cercis* to be the earliest diverging lineage of the Cercidoideae, with this and *Adenolobus* strongly supported as sister to the remainder of the subfamily, and *Griffonia* appearing as sister to the remainder of *Bauhinia s.l.* The position of these three genera in the phylogeny is in line with their taxonomic history, which has usually grouped them together in subtribe Cercidinae. The present-day distribution of these early diverging cercidoid lineages supports an 'out of Eurasia' hypothesis for the origin of the subfamily; the earliest diverging genus, *Cercis*, is found in Eurasia and North America, whilst *Adenolobus* and *Griffonia* are both African genera. A hypothesis of the Cercidoideae having migrated out of Eurasia into Africa, and arriving later in South America, is in line with the phylogeny of Sinou et al. (2009). *Adenolobus* occurs only in the Nama-Karoo biome of southern Africa, and is presumed to have arrived there via the 'arid corridor' of Succulent Biome that extended down through the Horn of Africa (Schrire et al., 2005). As discussed by Schrire et al. (2005), many clades of legumes appear to have originated in the Succulent Biome that formed part of the semi-arid Tethyan Seaway, before migrating northwards into the boreotropics and southwards into seasonally dry tropical climates, during the Tertiary. Migration of the Cercidoideae into North America from Eurasia could have occurred via the Eocene North Atlantic Land Bridge (NALB) (Tiffney, 1985; Thiv et al., 2011), when the boreotropical flora extended northwards in a frost-free and humid climate belt in the northern mid-latitudes, which peaked during the Paleocene-Eocene Thermal Maximum (PETM), c. 52 Ma (Thomas et al., 2015; Meng et al., 2014).

The Bering Land Bridge that connected Eastern Asia with Western North America during the Paleogene is thought to have been another major route for transfer of plant species between Eurasia and North America (Wolfe, 1975). However, the conditions on this route were probably not warm enough to support the essentially tropical Cercidoideae, and even the genus *Cercis*, which has a northern temperate distribution would probably not have been suited to the cool-temperate conditions of the Bering Land Bridge. The conclusion of Davis et al. (2002) in their phylogenetic and biogeographical analysis of *Cercis* was that its distribution came about either via the route of the NALB, or by long-distance dispersal, depending upon the age attributed to the clades within it. Wen et al. (2009) added to this that the dispersal of *Cercis* most likely occurred from the Old World to the New World.

The historical biogeography of *Bauhinia s.l.*, as for the Cercidoideae, is illuminated by phylogenetic evidence, and appears to agree with the above interpretation of the dispersal of the subfamily as a whole. The study of Meng et al. (2014) presented a time-calibrated phylogeny of 35 species of *Bauhinia s.l.* based upon sequences of the chloroplast gene tRNA-Leu (*trn*L) and the *trn*L-*trn*F intergenic spacer, and the fossil record of *Bauhinia s.l.* According to their phylogeny, all but one of the seven Asian species sampled (except *B. tomentosa*) form a clade that diverged from the African and South American species at ca. 34 MA. The African species form a distinct clade from that comprising the South American species. These results concur with those of Sinou et al. (2009), in suggesting that *Bauhinia s.l.* originated in Laurasia, probably Asia, in the Middle Paleocene, and from there migrated into Africa and to America. This origin and dispersal pattern follows that hypothesised for the legume family, as outlined above.

Biogeographical factors have been integral to the segregation of *Bauhinia s.l.* into smaller genera, particularly *Phanera, Schnella*, and *Cheniella*. Recognition of the paraphyletic nature of *Bauhinia s.l.*, which revealed the necessity of deconstructing the genus into smaller segregates, was achieved with the phylogenetic analysis of Sinou et al. (2009), in which the monospecific Madagascan endemic genus *Brenierea* was demonstrated to be nested within *Bauhinia s.l.*, sister to the *Bauhinia s.s* clade. A key finding of that study was the division of the subgroups previously included in the Bauhiniineae (i.e. *Bauhinia s.l.*) into two distinct and well-supported monophyletic clades. The first clade contains *Lysiphyllum*, *Phanera s.s.*, *Lasiobema*, *Schnella*, *Barklya*, and *Tylosema*, supported with 82% bootstrap, and the second comprises species now attributed to *Bauhinia s.s.*, supported with 98% bootstrap, with *Brenierea* and *Piliostigma* as sister. Both lineages are pantropical. It seems that these pantropical lineages evolved independently, each migrating first out of Eurasia, through Africa, and later into America (via the NALB or long-distance dispersal). The fact that the American species of *Bauhinia s.s.* appear, according to this phylogeny, to be more recently evolved than the rest of the genus, supports this hypothesis.

If following the dispersal pattern hypothesised here, the two possible mechanisms by which the lineages could have attained their pantropical distribution are either by transoceanic dispersal from Africa to America (probably via ocean currents), or by migration (via the NALB) from Eurasia into North America and then to South America. Fossil evidence of *Bauhinia s.l.* from the Oligocene Coatzingo Formation in Mexico supports the latter hypothesis to some degree, although the absence of *Bauhinia* fossils in the North American record represents a lack of support. Given the challenging nature of long-distance dispersal (due to many factors, such as the difficulty for propagules of surviving for long periods in often hostile environments, and the requirement for occurrence of particular conditions to transport them), the overland migration via the NALB is possibly the more likely scenario. Dispersal by faunal elements has been proposed as a mechanism for *Bauhinia* by Meng et al. (2014), who suggested that ‘birds are major agents of *Bauhinia* dispersal’; however, this is unlikely to be the case, as their assertion was based solely on the fact that birds are known dispersal agents for other legumes, with no primary data presented to document bird dispersal of *Bauhinia*, and the fruit and seeds of *Bauhinia* do not possess any attractant for birds (e.g. fleshy fruits, seeds that are brightly coloured or which have aril-mimicking colouration). If birds are discounted as a dispersal mechanism for *Bauhinia*, it must be assumed that the causal agents were wind and water. The ability of seeds of the Cercidoideae to survive long immersion in salt water are undocumented; however, as observed by Thomas et al. (2015), long-distance dispersals may not be highly dependent upon the survival capacity of the propagules in adverse conditions, but may instead come about through very infrequent stochastic occurrences, such as rafting on vegetation floats, or extreme meteorological events. Even if extremely rare, such events may be sufficient to allow establishment of taxa on remote land masses, and may explain a majority of continental disjunctions of plants, given that dispersal occurs over many millions of years.

Another significant finding of Sinou et al. (2009) albeit generated with relatively low sampling, was the resolution of the Asian and American species of *Phanera* (as then circumscribed; now *Phanera s.s.* and *Schnella* respectively) as discrete clades; *Phanera s.s* is restricted in distribution to Asia, whereas *Schnella* occurs only in South America. This phylogenetic and biogeographical evidence was key in the separation of these two groups as different genera, *Phanera s.s.* and *Schnella*, and gives further insights into the evolutionary history of the group. An hypothesis of the Asian species of *Phanera s.s.* having evolved from within the American species (now *Schnella*), or vice versa, can be discounted; the alternative hypothesis in which both lineages evolved separately from a common ancestor is therefore accepted.

In terms of resolving the remaining questions surrounding the evolution of *Phanera* and delimitation of putative segregate genera within it, the biogeographical element is less well defined; *Phanera s.s.*, including further putative segregates, is restricted to South East Asia. Nonetheless, the segregation of *Cheniella* from within *Phanera s.s.* was based partly on biogeographical criteria. Although the ranges of the two genera are largely overlapping, the centre of diversity of *Cheniella* is more northerly than that of *Phanera s.s. Cheniella* is distributed in regions with a seasonally dry climate, whereas *Phanera s.s.* exhibits a preference for moist tropical conditions. The species of *Cheniella* are morphologically similar to one another, suggesting a possible recent origin for the genus, and recent diversification of the species recognised within it.

The status of *Lasiobema*, a further proposed segregate of *Phanera s.l.*, remains unresolved. In the analysis of Sinou et al. (2009), only a single species of *Lasiobema* was sampled, *L. penicillilobum* (Gagnep.) A. Schmitz, which appeared, albeit with low support (77% bootstrap, 0.53 PP) as sister to *Phanera s.s*. Biogeographically, the species of *Lasiobema* are found in South East Asia, their distribution being more or less sympatric with that of *Phanera s.s.*, and thus not constituting evidence to support the generic segregation of this putative group. A more detailed study of the biogeography of these species is warranted.

The habit of the various segregate genera of *Bauhinia s.l.* has been cited as a key character in the circumscription of some of these, and is informative in reconstructing the evolutionary relationships of the Cercidoideae. The genera *Cercis* and *Adenolobus*, sister to the rest of the subfamily, are shrubs and trees, indicating a pleisiomorphic arborescent habit. *Griffonia*, by contrast, which appears as sister to the first clade outlined by Sinou et al. (2009), containing *Gigasiphon*, *Lysiphyllum*, *Phanera s.s.,* *Schnella*, *Tylosema*, *Barklya*, and *Lasiobema*, has a climbing habit. A climbing habit (lianas, scandent shrubs, or trailing herbs) is the dominant habit in this clade, although *Gigasiphon*, sister to the rest of the clade, and the monotypic Australian genus *Barklya*, nested within the clade, are both arborescent, whilst *Lysiphyllum* contains both arborescent and lianescent species. The second major clade indicated in the phylogeny, comprising *Bauhinia s.s.*, and with *Brenierea* and *Piliostigma* as sister, displays an exclusively arborescent habit.

Habit, therefore, is demonstrated to be a significant trait in defining clades and determining evolutionary relationships within the Cercidoideae. Both lianescent and arborescent life forms occur repeatedly across the phylogeny, which suggests a degree of genetic plasticity, enabling switching between the two habits to occur with relative ease within the Cercidoideae. The persistence of the arborescent habit within *Bauhinia s.s.*, and of the lianescent habit within *Phanera* and *Schnella* and the success of both of these lineages in terms of diversity, suggests that each life form must confer significant, but distinct, evolutionary advantages. The separation of habits may have furthered evolutionary separation between the lineages, and enabled their adaptation to distinct evolutionary niches.

Lianas are known from the fossil record since the Devonian period, 359–419 MA. Climbers occur in most extant lineages of Mesangiosperms (a large clade that includes the majority of the angiosperms), and the habit must have evolved repeatedly through the Cretaceous and Tertiary. About 30% of angiosperm families have at least one climbing species, reflecting the evolutionary success of the climbing habit as a life strategy. The climbing habit has also arisen independently in the ferns and gymnosperms (Isnard & Feild, 2015). Although trees have obvious advantages in terms of attainment of height and biomass, and do not rely on the presence of other organisms for growth, lianas have certain advantages over trees in terms of competition for resources. They are able to extend above the height of the tree on which they are growing, allowing them to intercept light, and also to reduce light availability for those on which they are supported. Lianas have greater biomass of foliage per unit of plant biomass compared to trees, and allocate more resources to the production of photosynthetic tissue rather than support tissue. Lianas are effective gap colonisers, and can more easily produce new axes from resprouts than can trees. Lianas are also typically faster growing than trees, especially in high light environments, and are better able to survive falling into a gap than trees (Toledo-Aceves, 2015). It has also been suggested that lianas have low susceptibility to water stress, due to various aspects of their physiology that allow stability of water transport, such as high specific conductivity and strong stomatal control (Isnard & Feild, 2015).

3.2.3 Biogeography of *Caesalpinia sensu lato*

The Caesalpinia group now comprises 26 (–27, *Ticanto* remains unresolved) genera (Gagnon et al., 2016), the increase in number of genera largely due to the segregation of eight genera from within the formerly pantropical *Caesalpinia s.l.* This generic reclassification has been driven by strong evidence provided by phylogenetic and morphological data. There is also a strong biogeographical component to the generic divisions; several of the genera are monospecific or with few species, most of which have a narrowly restricted geographical range or are to some extent defined by their distribution. The highest diversity of the group in terms of number of genera occurs in the Neotropics, with 17 genera, whilst 11 genera occur in Africa, and seven in Asia. Whilst a small number of genera occur on more than one continent, only a single genus, *Guilandina*, is pantropical, and *Caesalpinia s.s.* has been reduced to about nine species restricted to the Neotropics.

According to the phylogeny of Gagnon et al. (2016), the Caesalpinia group consists of two major clades. The first of these contains 15 genera, of which the early diverging genera are distributed between Africa, and Central and South America, whilst the later diverging genera all occur in Asia, or for *Mezoneuron*, also Australasia and Hawaii and/ or Africa. The second clade includes 12 genera, all of which are found exclusively in Africa and/ or the Neotropics, with no representation in Asia. Of all genera in the phylogeny (i.e. in the Caesalpinia group), two (*Haematoxylum* and *Pomaria*), have a disjunct distribution between Africa and the Neotropics, whilst three (*Mezoneuron, Pterolobium, Moullava*) are disjunct between Asia and Africa, and one is pantropical (*Guilandina*). The earliest branching lineages of the Caesalpinia group are in the Neotropics and Africa, which are also the areas of highest current diversity.

A putative explanation for this distribution is that the Caesalpinia group originated in North America in the early Tertiary, and subsequently migrated eastwards into the Old World. Dispersal of this nature from North America and Europe into Asia and Africa is hypothesised as one of the major patterns of disjunct tropical lineages during the early Tertiary (Donoghue, 2008). In a similar pattern postulated for the Cercidoideae, and for the legume family as a whole, this migration is likely to have occurred either along the seasonally dry Tethyan Seaway, as discussed by Schrire et al. (2005), or by means of the Eocene North Atlantic Land Bridge (NALB) (Tiffney, 1985; Thiv et al., 2011), or by a combination of both of these routes. Migration would probably also have been possible into South America via small islands which existed between North and South America during the Tertiary, from the Eocene onwards (Davis et al., 2002a). Subsequent global cooling during the Oligocene and Miocene resulted in extinction of many elements of the boreotropical flora that had existed in North America during the Palaeogene (Nie et al., 2012), hence the absence of extant taxa of

Caesalpinia s.l. in this area in the present day. Alternative scenarios are that *Caesalpinia s.l.* evolved first within the Neotropics, or in Africa, and from either of those migrated via a combination of land connections (including the NALB and island links between North and South America) and long-distance dispersal to the other continents that encompass its present-day range. However, given the position of *Caesalpinia s.l.* as an early diverging lineage of the Leguminosae, its pattern of origin and dispersal is more likely to have followed that inferred for the whole legume family.

The importance of long-distance dispersal in explaining the distribution of plants, particularly the disjunct distributions of single or closely related plant taxa, is now widely accepted (Givnish & Renner, 2004; Pennington et al., 2004; Renner, 2004; Wen & Ickert-Bond, 2009; Thiv et al., 2011; Nie et al., 2012; Thomas et al., 2015). Long-distance dispersal can occur via wind or water (or by birds for some plant taxa), and the relative importance of each mechanism in trans-Atlantic dispersal has been documented (Thorne, 1973; Givnish & Renner, 2004). These studies concluded that water was the more common factor in dispersals across the Atlantic, facilitated by the existence of large, reliable currents in both the easterly and westerly directions (Givnish & Renner, 2004). Seeds of certain taxa of the Leguminosae are known to have the ability to disperse via ocean currents (Murray, R., 2012; Gunn & Dennis, 1999). Within *Caesalpinia s.l.* the phenomenon of long-distance dispersal via water is best developed in members of the genus *Guilandina*, particularly in *Guilandina bonduc* L. (the 'grey nicker nut') which floats by means of an intercotyledonary cavity, and under test conditions has been shown to survive for 30 years floating in salt water (Perry & Dennis, 2003). This explains the species' pan-tropical distribution.

Long distance dispersal is presumed to account at least in part for the distribution of *Mezoneuron*. The distribution of *Mezoneuron*, spanning South East Asia, Africa, Madagascar, Australasia, and Hawaii is unique amongst the segregates of *Caesalpinia s.l.*: *Moullava* and *Pterolobium* are similarly spread between Asia and Africa, and *Guilandina* occurs pantropically, but only *Mezoneuron* also has endemic species on the islands of New Caledonia, and Hawaii (although at least two species of *Caesalpinia s.l.* are found in each of these areas). Reliable fossil evidence demonstrates the presence of the *Mezoneuron* fruit type in North America and Europe by the Middle Eocene ca. 45 Ma, although no extant species of the genus exist in these regions today. It is presumed that the lineage subsequently dispersed from these centres of origin into its present-day localities. Due to the fact that the position of the major continental land masses has not changed substantially since the Middle Eocene, the present-day distribution must be explained by long-distance dispersal, probably via the seasonally dry Tethys Seaway during the Tertiary period (the mechanism discussed to explain the dispersal of the family Leguminosae). Although some members of the Caesalpinia group, and by extension possibly including *Mezoneuron*, have seeds which possess the ability to survive long immersion in salt water, the potential for wind dispersal of whole fruits of *Mezoneuron* may have played a more significant dispersal role. The characteristic fruit of the genus, being flattened and bearing a sutural wing, is ideally adapted for airborne dispersal. Additionally, the indehiscent nature of the fruits suggests transportation of the entire fruit, rather than of the seeds individually, to be the intended dispersal mechanism. These winged fruits are well developed for dispersal by extreme meteorological events such as a hurricane, conferring a higher probability of successful arrival on a distant land mass.

In order to understand in more detail the routes and mechanisms by which *Mezoneuron* may have achieved its present-day distribution, time-calibrated molecular based phylogenetic analysis (Figure 6), and preliminary biogeographical analysis (not shown) have been carried out by the current author. For the time-calibrated analysis, the crown node age of *Mezoneuron* was set using the Eocene fossils dated to c. 45 Ma (Herendeen & Crane, 1992), and the age of the legume family to 70 Ma, according to the fossil evidence discussed earlier. The phylogeny shows the divergence of the *Mezoneuron* clade into two distinct lineages, one comprising the Asian, African, Madagascan and Hawaiian species, and the other with the New Caledonian and Australian species. The crown node of the former clade is dated to ca. 35 Ma, and within this, the Asian species appear to have arisen prior to those found in Africa and Madagascar. This suggests that Asia was the recipient of the initial dispersal of the group from the ancestral localities of North America and Europe, and that Africa was subsequently colonised by dispersal from Asia. The strong support of an Asian species, *M. andamanicum*, as sister to the African species within the same clade, is congruent with this hypothesis. Asia is the centre of diversity of *Mezoneuron*, containing more species (10) than any other single region, which supports the hypothesis of this region as the likely centre of origin of the genus: as noted by Nie et al. (2012), “The ancestral area for a taxon is usually expected to be correlated with high extant species richness”.

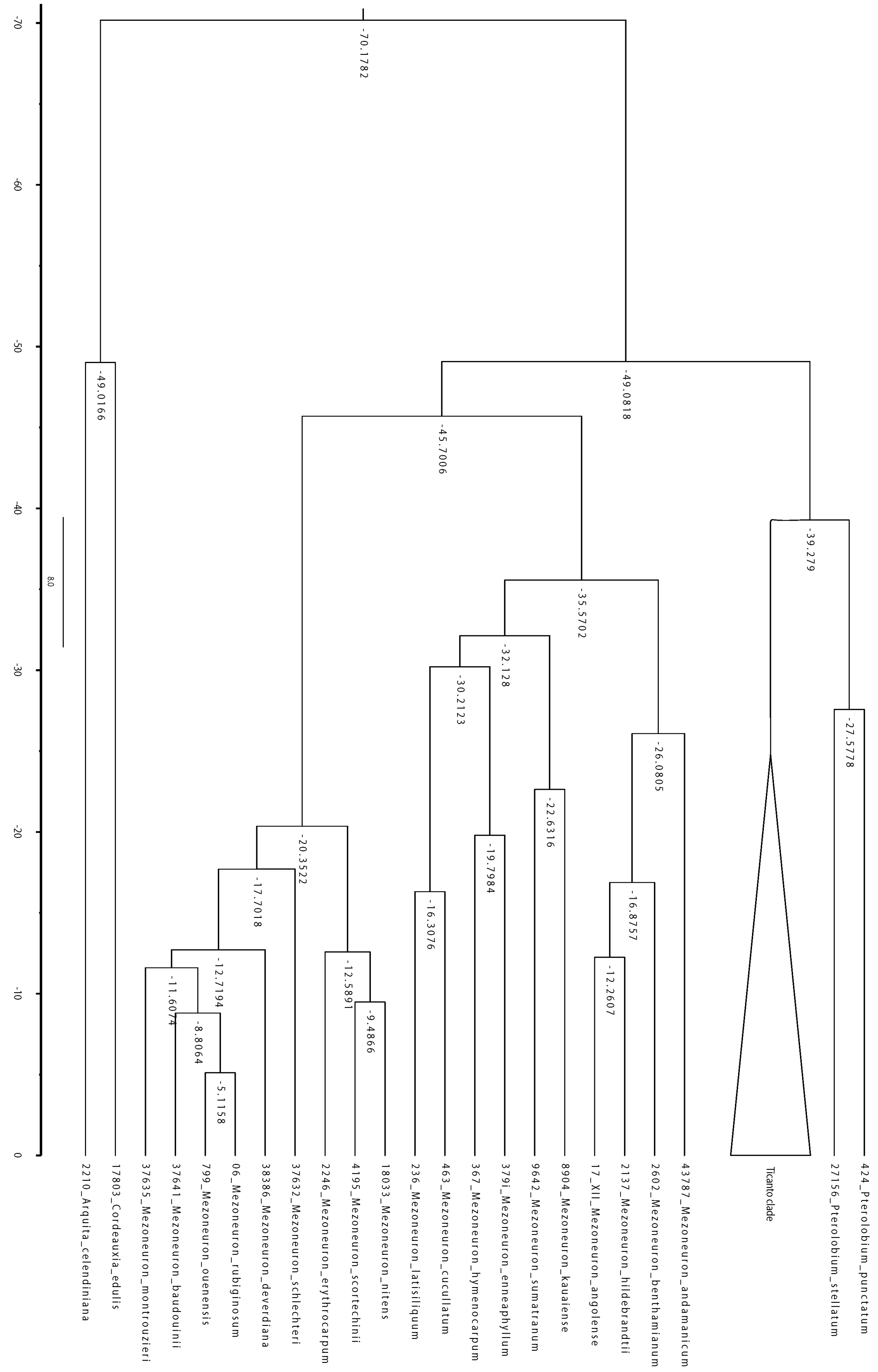


Figure 6. Time-calibrated phylogeny of *Mezoneuron*, based upon a concatenated analysis of *trn*L-F, *trn*D-T, *rps16*, *matK*, and *ITS*. Numbers at the nodes and on the lower axis denote millions of years.

The New Caledonian/ Australian clade arose c. 20 Ma, within which the origin of the New Caledonian subclade is dated to c. 17 Ma, whilst that of the Australian species is more recent at ca. 12 Ma. This demonstrates that the colonisation of New Caledonia appears to have occurred prior to that of Australia, with dispersal to Australia from the New Caledonian populations. The similarity between the species of the genus endemic to New Caledonia supports a recent diversification of this group, as does that between the species found in Australia. Morphological congruencies between these two geographically separated clades support their position as sister taxa. According to a preliminary biogeographical analysis by the present author using Lagrange software (Ree & Smith, 2008), the ancestor of the New Caledonian and Australian clade is likely to have been present in Australia and New Caledonia, or Asia and New Caledonia. New Caledonia has been separated from other land masses since the Late Cretaceous period (100.5–66 Ma) (Heads 2008), and is noted for its exceptional biodiversity, including extremely high levels of endemism: approximately 74% of the c. 3260 native plant species are endemic (Myers et al*.,* 2000; Jaffré et al*.,* 2001; IUCN, 2014). The endemic species of *Mezoneuron* in New Caledonia appear to have arisen within the last 20 million years, representing a recent colonisation in the context of the age of the islands, and in the context of the evolutionary history of the genus. The ability of *Mezoneuron* to adapt to the unusual environmental conditions of the islands, specifically the ultramafic substrates, reflects the probable genetic plasticity of the genus (a characteristic that also seems to be typical of *Caesalpinia s.l.* and the Caesalpinia group more broadly, which may give rise to the high levels of homoplasy found within these).

The biogeographical analysis of *Mezoneuron* that has been generated as part of the studies incorporating the papers here presented shows the likely route by which *Mezoneuron* achieved its current unusual, highly disjunct distribution. This provides new insights into the biogeographical and evolutionary history of *Caesalpinia s.l.*, including support for the probability of long-distance dispersal as a major mechanism within the group.

CONCLUSIONS AND FURTHER IMPLICATIONS OF THE WORK

The resolution of paraphyly is one of the primary aims of contemporary taxonomy, and is currently of particular importance in caesalpinioid legumes in light of the recent revelation of the extensive paraphyly of subfamily Caesalpinioideae (*sensu* traditional) and consequent reconfiguration of the family. Following demonstration of their paraphyly, the two large caesalpinioid genera *Bauhinia* and *Caesalpinia* have each been segregated into smaller genera; however, questions have persisted regarding the monophyly of the resultant genera, and their composition. The work presented herein makes significant progress towards resolving these questions. It describes one new genus from within *Phanera*, the largest generic segregate of *Bauhinia*, thus removing a degree of remaining paraphyly from this. It clarifies the species composition and nomenclature of the *Bauhinia* segregates *Phanera* and *Schnella*, and elucidates the geographical distributions of each of these. It provides novel distribution and morphology data for one species of the putative *Bauhinia* segregate, *Lasiobema.* It confirms the monophyly of *Mezoneuron*, a segregate of *Caesalpinia*, and illuminates the infraspecific relationships of the genus, demonstrating the existence of two morphologically and biogeographically distinct infrageneric clades. It explores the historical biogeography of *Mezoneuron* through time-calibrated phylogenetic analysis in the context of the fossil record. The study indicates the probable existence of further paraphyly within *Bauhinia s.l.* and *Caesalpinia s.l.*, and sets the groundwork for future analyses to resolve this.

The science of taxonomy is fundamental to human understanding of the life processes that occur on planet earth, and underpins a broad range of other disciplines, including conservation, ecology, medicine, and horticulture. Without the ability to accurately identify and classify living organisms, we cannot protect them from decline or extinction, understand their function as part of the ecosystem, or utilise them for human needs.

The work that is presented for this thesis represents significant progress in the taxonomy and classification of the family Leguminosae, one of the largest, most ecologically key, and economically important plant families in the world. In resolving genus-level circumscriptions and relationships in the family by circumscribing monophyletic groups, this work creates stable classifications in which taxon names are fixed, facilitating communication about the taxa. In authoritatively placing taxa within appropriate generic groupings it provides essential identification tools, as well as illuminating patterns of phylogenetic diversity, and enabling understanding of their relational roles; when we group species according to their relatedness, we are much better placed to interpret how they might function interchangeably, either in an ecological context or in the fulfilment of human needs (e.g. medicine, agriculture). At the level of species, this study has revised and defined species limits, including removing certain taxa to synonymy, and reconfiguring the rank of others. These taxonomic changes enable future users to accurately identify these taxa, and to correctly apply ecological investigations or conservation decisions to them.

Beyond these general benefits that arise from revisionary taxonomy, some more specific applications of this work are as follows:-

Regarding the resolution of paraphyly in the genera of interest, this study has erected hypotheses that can be tested through future research, to complete the generic level classification of these groups. Particularly important is the creation of the new genus *Cheniella* from *Bauhinia s.l./ Phanera*, which hypothesises the existence of further groups that will merit recognition as segregate genera following investigation using detailed molecular phylogenetic analyses.

The work has highlighted issues of species delimitation in situations of low morphological resolution, where factors such as homoplasy, cryptic speciation, or hybridisation may obscure taxonomic boundaries that are revealed by molecular phylogenetic analysis. The cases presented in this work define scenarios for further study with additional data, and also contribute to the philosophical discussion of these topics.

The interpretation of historical dispersal patterns and mechanisms, particularly in examples such as that presented here for *Mezoneuron* involving long-distance dispersal, can help us to understand how species in the present day may have the ability to adapt to climate change and other anthropogenic disturbances.

In general, pollination syndromes of plants are poorly understood and little studied, including in the genera here investigated. This study provides novel data and analysis of the possible pollination mechanisms of *Bauhinia s.l.*, which may have future applications in terms of interpreting plant-animal interactions. This may be particularly relevant in the context of potential responses of organisms to climate change or other environmental disturbances, and may be important for future conservation of these taxa.

There are several ways in which the work here presented is necessary for, and can contribute to, conservation. Conservation of taxa requires accurate knowledge of their identities; without the capacity to recognise species, we are unable to determine their conservation status or to recognise the need for conservation action to protect them. Defining taxonomic limits is therefore essential to conservation.

Conservation assessments are presented as part of this work for each species under study. For most species, these are provisional assessments based primarily upon herbarium specimen point data, although they are the most complete assessment possible given the existing data. It is anticipated that these will be used in several ways: to focus future targeted field collecting efforts; to inform conservation policy; to form the basis for full conservation assessments as further data becomes available. The conservation assessments provided in Paper 3 of the published works have already been used in this latter way, having been adapted by the Red List Authority of New Caledonia to produce formal assessments (as published in Paper 2). In doing so, they indicated that lack of information was a barrier to generating reliable assessments for two of the species, which were categorised as Data Deficient. This work has therefore served to indicate the need for further research to generate additional data for these species.

Knowledge of phylogenetic relationships, including at the genus level, can be used in conservation decision making with the aim of preservation of phylogenetic diversity rather than simply preservation of overall species diversity. This approach may be important in the light of evidence that phylogenetic diversity is lost at higher rates than species diversity (Buerki et al. 2015), and is addressed with initiatives such as EDGE, in which taxa that are deemed to be Evolutionarily Distinct and Globally Endangered can be prioritised for protection through conservation (Isaac et al. 2007).

A further potential application for the work presented in the current study is to provide the basis for ecosystem niche modelling. This is a method of predicting the occurrence of a species through interpretation of the environmental conditions in which they are found and of those in areas outside of the known distribution. Application of this method requires accurate delimitation of taxonomic boundaries, and detailed knowledge of the ecological preferences of the species, both of which are provided as part of the published works.

REFERENCES

Baker, J.G. 1879. *Bauhinia.* in: Hooker, J.D. The Flora of British India Vol. II, Sabiaceae to Cornaceae. L. Reeve & Co., London, U.K., pp. 275–285.

Bandyopadhyay, S., Ghoshal, P.P., & Pathak, M.K. 2012. Fifty new combinations in *Phanera* Lour. (Leguminosae: Caesalpinioideae) from Paleotropical Region. *Bangladesh Journal of Plant Taxonomy* 19: 55–61. http://dx.doi.org/10.3329/bjpt.v19i1.10942

Banks H., Forest F. & Lewis G. 2013. Palynological contribution to the systematics and taxonomy of *Bauhinia s.l.* (Leguminosae: Cercideae). *South African Journal of Botany* 89: 219–226. https://doi.org/10.1016/j.sajb.2013.07.028

Banks H., Forest F. & Lewis G. 2014. Evolution and diversity of pollen morphology in tribe Cercideae (Leguminosae). *Taxon* 63: 299–314. https://doi.org/10.12705/632.37

Bauhin, G. 1623. *Pinax Theatri Botanici.* Basel.

Baum, D.A. & Smith, S.D. 2013. Tree Thinking – An Introduction to Phylogenetic Biology. Roberts and Company Publishers, Inc., U.S.A. 476 pp.

Bentham, G. 1840. Contributions towards a flora of South America. Enumeration of plants collected by Mr. Schomburgk in British Guiana. *Journal of Botany (Hooker)* 2: 127–146.

Bentham, G. 1865. Leguminosae. *In*: Bentham, G. & Hooker, J.D. (Eds.) *Genera Plantarum* 1 (2). Londini: A. Black., pp. 434–600.

Bentham, G. & Hooker, J.D. 1862–1883. (eds.) *Genera Plantarum.* Londini: A. Black

Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K.L., Meier, R., Winkler, K., Ingram, K.K., Das, I. 2007. Cryptic species as a window on diversity and conservation. *Trends in Ecology and Evolution* **22:** 148–155.

Bortoluzzi, R.L.C.; Miotto, S.T.S. & Reis, A. 2006. *Leguminosas-Cesalpinioídeas - Tribos Cercideae, Detarieae: Bauhinia, Copaifera e Tamarindus.* In: Flora Ilustrada Catarinense. Herbário Barbosa Rodrigues, Itajaí. 96 pp.

Brickell, C. D., Crawley, M., Cullen, J., Frodin, D. G., Gardner, M., Grey-Wilson, C, Hillier, J., Knees, S., Lancaster, R., Mathew, B. F., Matthews, V. A., Miller, T., Noltie, H. F., Norton, S., Oakeley, H. J., Richards, J. & Woodhead, J. 2008. Do the views of users of taxonomic output count for anything? *Taxon* 57: 1047–1048.

Britton, N.L., Rose, J.N., 1930. (Rosales), Krameriacae, Caesalpiniaceae. *North American Flora* 23, 301–342.

Brummit, R.K. 2002. How to chop up a tree. *Taxon* 51: 31–41.

Brummitt, R.K. 2008. Evolution in taxonomic perspective. *Taxon* 57(4): 1049–1050.

Brummitt, R.K. & Sosef, M.S.M. 1998. Paraphyletic Taxa Are Inherent in Linnaean Classification. A Reply to Freudenstein. *Taxon* 47(2): 411–412.

Bruneau, A., Herendeen, P.S., Klitgaard, B.B., Lewis, G.P., 2001. Phylogenetic relationships in the Caesalpinioideae (Leguminosae) as inferred from chloroplast trnL intron sequences. *Systematic Botany* 26, 487–514.

Bruneau, A., Mercure, M., Lewis, G.P., Herendeen, P.S., 2008. Phylogenetic patterns and diversification in the Caesalpinioid legumes. *Botany* 86, 697–718.

Buerki, S., Callmander, M.W., Bachman, S., Moat, J., Labat, J.-N., Forest, F. 2015. Incorporating evolutionary history into conservation planning in biodiversity hotspots. *Philosophical Transactions of the Royal Society B – Biological Sciences* 370: 20140014. DOI: 10.1098/rstb.2014.0014

Calvillo-Canadell, L., Cevallos-Ferriz, S.R.S.: *Bauhcis moranii* gen. et sp. nov. (Cercideae, Caesalpinioideae), an Oligocene plant from Tepexi de Rodríguez, Puebla, Mexico, with leaf architecture similar to Bauhinia and Cercis. *Rev Palaeobot Palynol* 2002, 122: 171–184.

Cantino, P.D. & de Quieroz, K. 2010. *Phylocode* version 4c. Available at: https://www.ohio.edu/phylocode/preface.html (accessed 25 January 2017)

Chatan, W. 2013. A new species of *Bauhinia* L. (Caesalpinioideae, Leguminosae) from Nakhon Phanom Province, Thailand. *PhytoKeys* 26: 1–5.

Chen, T.C. (1988) *Bauhinia*. Flora Republicae Popularis Sinicae 39, Leguminosae 1:145–203. Science Press, Beijing.

Clark, R. P. 2015. *Lasiobema flavum* (Leguminosae: Caesalpinioideae), a new record for the Flora of Thailand. *Thai Forest Bulletin (Botany)* 43: 70–73.

Clark, R. & Gagnon, E. 2015. A revision of *Mezoneuron* (Leguminosae – Caesalpinioideae) in New Caledonia, with perspectives on vegetation, geology and conservation. *Phytotaxa* 207(1): 68–92.
DOI: http://dx.doi.org/10.11646/phytotaxa.207.1.3

Clark, R.P. 2016. A Taxonomic Revision of *Mezoneuron* (Leguminosae: Caesalpinioideae: Caesalpinieae). *Phytotaxa* 274(1): 1–72.
DOI: http://dx.doi.org/10.11646/phytotaxa.274.1.1

Clark, R.P., Mackinder, B.A., Banks, H. 2017. *Cheniella* gen. nov. (Leguminosae: Cercidoideae) from S. China, IndoChina and Malesia. *European Journal of Taxonomy* 360: 1–37. https://doi.org/10.5852/ejt.2017.360

Cronquist, A. 1987. A Botanical Critique of Cladism. *Botanical Review* 53(1): 1–52.

Cronquist, A. 1988. The Evolution and Classification of Flowering Plants. New York Botanical Garden, New York. 555 pp.

Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection*. John Murray, London. 502 pp.

Davis, C.C., Bell, C.D., Mathews, S., Donoghue, M.J. 2002a. Laurasian migration explains Gondwanan disjunctions: Evidence from Malpighiaceae. *Proceedings of the National Academy of Sciences* 99(10): 6833–6837.

Davis, C.C., Fritsch, P.W., Li, J., Donoghue, M.J. 2002b. Phylogeny and Biogeography of *Cercis* (Fabaceae): Evidence from Nuclear Ribosomal ITS and Chloroplast *ndhF* Sequence Data. *Systematic Botany* 27(2): 289–302.

de Candolle, A.P. 1825. *Mémoires sur la famille des légumineuses*. A. Belin, Paris. 525 pp.

de Jussieu, A.L. 1789. *Genera Plantarum*. Herissant et Theophilum Barrois, Paris. 498 pp.

de Quieroz, L.P. 2006. New species and combinations in *Phanera* Lour. (Caesalpinioideae: Cercideae) from the caatinga biome. *Neodiversity* 1: 1–6.

de Wit, H.C. 1956. A revision of Malaysian Bauhinieae. *Reinwardtia* 3: 381–539.

Dezhao, C., Chen, T., Zhang, D., Larsen, K., & Larsen, S.S. (eds.) 2010. *Flora of China 10, Fabaceae*. Science Press, Beijing & Missouri Botanical Garden Press, St Louis, pp. 6–21.

Dietrich, D.N.F. 1840. *Synopsis Plantarum*. Vimariae. https://doi.org/10.5962/bhl.title.168

Donoghue, M.J. 2008. A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Sciences* 105 (Suppl. 1): 11549–11555. www.pnas.org_cgi_doi_10.1073_pnas.0801962105

Drummond, A.J., Suchard, M.A., Xie, D., Rambaut, A. 2012. Bayesian phylogenetics with BEAUti and BEAST 1.7. *Molecular Biology and Evolution* 29: 1969–1973.

Eichler, A.W. 1883. *Syllabus der Vorlesungen uber Specielle und Medicinisch-Pharmaceutische Botanik.* Leipzig.

Engler, A. & Prantl, K. 1887–1915. *Die naturlichen pflanzenfamilien.* Leipzig. 23 vols.

Estrella, M., Forest, F., Wieringa, J.J., Fougere-Danezan, M., Bruneau, A. 2017. Insights on the evolutionary origin of Detarioideae, a clade of ecologically dominant tropical African trees. *New Phytologist* 214: 1722–1735.

Gagnon, E., Hughes, C.E., Lewis, G.P., Bruneau, A. 2015. A new cryptic species in a new cryptic genus in the *Caesalpinia* group (Leguminosae) from the seasonally dry inter-Andean valleys of South America. *Taxon* 64(3): 468–490

Gagnon, E., Bruneau, A., Hughes, C.E., de Quieroz, L.P., Lewis, G.P. 2016. A new generic system for the pantropical Caesalpinia group (Leguminosae). *PhytoKeys* 71: 1–160 (2016) doi: 10.3897/phytokeys.71.9203

Gagnon, E., Lewis, G.P., Solange Sotuyo, J., Hughes, C.E. & Bruneau, A. 2013. A molecular phylogeny of *Caesalpinia sensu lato*: Increased sampling reveals new insights and more genera than expected. South *African Journal of Botany* 89: 111–127. http://dx.doi.org/10.1016/j.sajb.2013.07.027

George, A.S. 2014. The case against the transfer of *Dryandra* to *Banksia* (Proteaceae) 1. *Annals of the Missouri Botanical Garden* 100, 32–49. doi:10.3417/2012086

Givnish, T.J. & Renner, S.S. 2004. Tropical intercontinental disjunctions: Gondwana breakup, immigration from the boreotropics, and transoceanic dispersal. *International Journal of Plant Sciences* 165: (4 Suppl.): S1–S6.

Gunn, C.R. & Dennis, J.V. 1999. World Guide to Tropical Drift Seeds and Fruits. Kreiger Publishing Company, Malabar, Florida. 240 pp.

Hao G., Zhang D.X., Zhang M.Y., Guo L.X. & Li S.J. 2003. Phylogenetics of *Bauhinia* subgenus *Phanera* (Leguminosae: Caesalpinioideae) based on ITS sequences of nuclear ribosomal DNA. *Botanical Bulletin of Academia Sinica* 44: 223–228.

Hattink, T.A. 1974. A Revision of Malesian *Caesalpinia*, including *Mezoneuron* (Leguminosae-Caesalpiniaceae). *Reinwardtia* 9 (1): 1–69.

Heads, M. 2008. Panbiogeography of New Caledonia, south-west Pacific: basal angiosperms on basement terranes, ultramafic endemics inherited from volcanic island arcs and old taxa endemic to young islands. *Journal of Biogeography* 35: 2153–2175. http://dx.doi.org/10.1111/j.1365-2699.2008.01977.

Herendeen, P.S. & Crane, P.R. 1992. Early Caesalpinioid Fruits from the Palaeogene of Southern England. In: Herendeen, P.S. & Dilcher, D.L. (eds.) Advances in Legume Systematics. Part 4: The Fossil Record. Royal Botanic Gardens, Kew, Richmond, U.K. pp. 57–68.

Herendeen, P.S., Lewis, G.P. & Bruneau, A. 2003. Floral morphology in caesalpinioid legumes: Testing the monophyly of the "*Umtiza*" clade. *International Journal of Plant Sciences* 164: S393–S407. https://doi.org/10.1086/376881

Hennig, W. 1966. *Phylogenetic Systematics*. University of Illinois Press: Urbana, Illinois, U.S

Hörandl, E. 2006. Paraphyletic versus monophyletic taxa - Evolutionary versus cladistic classifications. *Taxon* 55: 564–570.

Hou, D. 1996. *Caesalpinia.* In: Hou, D., Larsen, K., Larsen, S.S., Laferriere, J.E. & Duyfjes, B.E.E. (eds.). *Flora Malesiana*. Series 1, 12(2). Leiden University, Leiden. pp. 535–555.

Hou, D., Larsen, K., & Larsen, S.S. 1996. Caesalpiniaceae. In: Hou, D., Larsen, S.S., Laferriere, J.E., & Duyfjes, B.E.E. (eds.) *Flora Malesiana*. Series 1, 12(2). Leiden University, Leiden, pp. 442–535.

Humphries, C.J. & Huxley, R. 2007. Carl Linnaeus. In: Huxley, R. (ed.) 2007. *The Great Naturalists:* 133–139. The Natural History Museum, London.

Hutchinson, J. 1973. *The families of flowering plants* (3rd Edition). Oxford University Press (2nd Edition 1959; 1st Edition 1926, 1934)

Huxley, R. 2007. John Ray. In: Huxley, R. (ed.) 2007. *The Great Naturalists*. The Natural History Museum, London. pp. 92-97.

Isnard, S. & Feild, T.S. 2015. The evolution of angiosperm lianescence: A perspective from xylem structure-function. In: *Ecology of Lianas.* Wiley Blackwell, Oxford, U.K., pp. 221–238.

Isaac, N.J.B., Turvey, S.T., Collen, B., Waterman, C., Baillie, J.E.M. 2007. Mammals on the EDGE: Conservation Priorities Based on Threat and Phylogeny. PLoS ONE 2(3): e296. doi:10.1371/journal.pone.0000296

IUCN. 2014. *The IUCN red list of threatened species*, version 2014.3. IUCN Red List Unit, Cambridge U.K. Available at: http://www.iucnredlist.org/

Jaffré, T., Morat, P., Veillon, J.-M., Rigault, F. & Dagostini, G. 2001. Composition and Characterisation of the Native Flora of New Caledonia. Documents Scientifiques et Techniques, II4. Institut de Recherche pour le Developpement, Noumea. Available at: http://www.ird.nc/images/Jaffr%E9%20et%20al,%202001-flore%20nc.pdf.

Korthals, P.W. 1839–42. Verhandelingen over de natuurlijke geschiedenis der Nederlandsche overzeesche bezittingen. Leiden: In commissie bij. S. en J. Luchtmans en C.C. van der Hoek. p. 84.

Larsen, K., Larsen, S.S., & Vidal, J. 1980. Légumineuses–Césalpinioïdées. In: Aubréville, A., & Leroy, J.-F. (eds.), *Flore du Cambodge du Laos et du Viêtnam.* Muséum National d'Histoire Naturelle, Paris, pp. 1–227.

Larsen, K., Larsen, S.S., & Vidal, J. 1984. Leguminosae-Caesalpinioideae. In: Smitinand, T., & Larsen, K. (eds.). *Flora of Thailand.* The Forest Herbarium, Royal Forest Department, Bangkok, 129 pp.

Larsen, K. & Larsen, S.S. 1997. *Bauhinia sirindhorniae* sp. nov. (Leguminosae-Caesalpinioideae) a remarkable new species from Thailand. *Nordic Journal of Botany* 17(2): 113–118.

Lau C.P., Saunders R.M.K. & Ramsden L. 2009. Floral biology, breeding systems and population genetic structure of three climbing *Bauhinia* species (Leguminosae: Caesalpinioideae) in Hong Kong, China. *Journal of Tropical Ecology* 25: 147–159. https://doi.org/10.1017/S0266467408005762

Lavin, M., Herendeen, P.S., Wojciechowski, M.F. 2005. Evolutionary Rates Analysis of Leguminosae Implicates a Rapid Diversification of Lineages during the Tertiary. *Systematic Biology* 54(4): 575–594.

Lawrence, G.H.M. 1951. *Taxonomy of Vascular Plants.* The Macmillan Company, New York. 823 pp.

The Legume Phylogeny Working Group (LPWG) 2017. A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. *Taxon* 66(1): 44–77.

Lewis, G.P. 1987. *Legumes of Bahia.* Royal Botanic Gardens, Kew, Richmond, U.K. 369 pp.

Lewis, G.P. 1998. *Caesalpinia, A Revision of the Poinianella-Erythrostemon Group*. Royal Botanic Gardens, Kew, Richmond, U.K. 233 pp.

Lewis, G.P. 2005. Tribe Caesalpinieae. In: Lewis, G., Schrire, B., Mackinder, B., Lock, M. (eds.) *Legumes of the World*. Kew Royal Botanic Gardens, Kew, Richmond, U.K. 127–159.

Lewis, G., & Forest, F. 2005. Cercideae. In: Lewis, G., Schrire, B., Mackinder, B., & Lock, M. (eds.) *Legumes of the World*: 57–67. Royal Botanic Gardens, Kew, Richmond, U.K.

Lewis, G.P. & Schrire, B. 1995. A reappraisal of the Caesalpinia group (Caesalpinioideae: Caesalpinieae) using phylogenetic analysis. In: Crisp, M.D., Doyle, J.J. (eds.), Advances in legume systematics, part 7: phylogeny. Royal Botanic Gardens, Kew, Richmond, U.K., pp. 41–52.

Linnaeus, C. 1735. *Systema Naturae.* Lugduni Batavorum: Apud Theodorum Haak, ex Typographia Joannis Wilhelmi de Groot.

Linnaeus, C. 1753. *Decandria Monogynia.* Species Plantarum. Vol. 1. Laurentius Salvius, Stockholm, pp. 373–397.

Lock, J.M. 1989. *Legumes of Africa, A Check-list*. Royal Botanic Gardens, Kew, Richmond, U.K. 619 pp.

Lock, J.M. & Ford, C.S. 2004. *Legumes of Malesia, A Check-list.* Royal Botanic Gardens, Kew, Richmond, U.K. 295 pp.

Mackinder, B.A., Clark, R. 2014. A synopsis of the Asian and Australasian genus *Phanera* Lour. (Cercideae: Caesalpinioideae: Leguminosae) including 19 new combinations. *Phytotaxa* 166 (1): 049–68.

Magallon, S., Gomez-Acevedo, S., Sanchez-Reyes, L.L., Hernandez-Hernandez, T. 2015. A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytologist* 207: 437–453.

Manzanilla, V., Bruneau, A. 2012. Phylogeny reconstruction in the Caesalpinieae grade (Leguminosae) based on duplicated copies of the sucrose synthase gene and plastid markers. *Molecular Phylogenetics and Evolution* 65: 149–162. doi: 10.1016/j.ympev.2012.05.035

McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, P.S., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prudhomme van Reine, W.F., Smith, G.F., Wiersema, J.H. 2012. *International Code of Nomenclature for algae, fungi, and plants (Melbourne Code).* Koeltz Botanical Books, Germany. 240 pp.

Meng, H.H., Jacques, F.M., Su, T., Huang, Y.J., Zhang, S.T., Ma, H.J., & Zhou, Z.K. 2014. New Biogeographic insight into *Bauhinia s.l.* (Leguminosae): integration from fossil records and molecular analyses. *BMC evolutionary biology* 14 (1): 181. http://dx.doi.org/10.1186/s12862-014-0181-4

Miller, M.A., Pfeiffer, W., and Schwartz, T. 2010. *Creating the CIPRES Science Gateway for inference of large phylogenetic trees*. In: Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, L.A. pp. 1–8.

Milne, R.I., 2006. Northern hemisphere plant disjunctions: a window on tertiaryland bridges and climate change? *Annals of Botany* (Oxford) 98: 465–472.

Morley, R.J. 2000. *Origin and Evolution of Tropical Rainforests.* John Wiley & Sons, p. 378.

Morley, R.J. 2003. Interplate dispersal routes for megathermal angiosperms. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 5–20.

Murray, D.R. (ed.). 2012. *Seed Dispersal.* Academic Press, Sydney. p. 62.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J. 2000. Biodiverisity hotspots for conservation priorities. *Nature* 403: 853–858.

Nie, Z-L., Sun, H., Manchester, S.R., Meng, Y., Luke, Q., Wen, J. 2012. Evolution of the intercontinental disjunctions in six continents in the Ampelopsis clade of the grape family (Vitaceae). *BMC Evolutionary Biology* 12:17

Nordal, I. & Stedje, B. 2005. Paraphyletic taxa should be accepted. *Taxon* 54(1): 5–8.

Nores, M.J., Simpson, B.B., Hick, P., Anton, A.M., Fortunato, R.H. 2012. The phylogenetic relationships of four monospecific caesalpinioids (Leguminosae) endemic to southern South America. *Taxon* 61(4): 790–802.

Pennington, R.T., Cronk, Q.C.B., Richardson, J.A. 2004. Introduction and synthesis: plant phylogeny and the origin of the major biomes. *Philosophical Transactions of the Royal Society B – Biological Sciences* 359: 1455–1464.

Perry, E. & Dennis, J.V. 2003. *Sea-Beans from the Tropics.* Kreiger Publishing Company, Malabar, Florida. 217 pp.

Pillon, Y., Hopkins, H.F.C., Munzinger, J., Amir, H., Chase, M.W. 2009. Cryptic species, gene recombination and hybridization in the genus *Spiraeanthemum* (Cunoniaceae) from New Caledonia. *Botanical Journal of the Linnean Society*, 2009, 161, 137–152.

Polhill, R.M. & Vidal, J.E. 1981. Caesalpinieae. In: Polhill, R.M. & Raven, P.H. (eds.) *Advances in Legume Systematics* 1: 81–95. Royal Botanic Gardens, Kew, Richmond, U.K.

Raven, P. H. & Axelrod, D.I. 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanic Garden* 61: 539–657.

Ray, J. 1682. *New Method of Plants*. Henrici Faithorne & Joannis Kersey, London. 166 pp.

Ree, R.H. & Smith, S.A. 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology* 57: 4–14.

Renner, S.S. 2004. Plant Dispersal across the Tropical Atlantic by Wind and Sea Currents. *International Journal of Plant Sciences* 165 (No. S4): S23–S33.

Rensch, B. 1954. *Neure Probleme der Abstammungslehre: Die transpezifische Evolution*, ed. 2. Stuttgart: Ferdinand Enke.

Rensch, B. 1959. *Evolution Above the Species Level.* New York: Columbia University Press.

Ronquist, F., Teslenko, M., Van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. 2012. MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542. http://dx.doi.org/10.1093/sysbio/sys029

Schmitz, A. 1973. Contribution palynologique à la taxonomie des *Bauhineae* (*Caesalpiniaceae*). *Bulletin du Jardin Botanique National de Belgique* 43(3–4): 377.

Schmitz, A. 1977. Nouvelle Contribution à la Taxonomie1 des *Bauhinieae* (*Caesalpiniaceae*). *Bulletin de la Société Royale de Botanique de Belgique* 110: 13.

Scott-Ram, N.R. 1990. *Transformed Cladistics, Taxonomy and Evolution.* Cambridge University Press, Cambridge

Schrire, B.D., Lewis, G.P., Lavin, M. 2005. Biogeography of the Leguminosae. In: Lewis, G., Schrire, B., Mackinder, B., & Lock, M. (eds.), *Legumes of the World*: 21–54. Royal Botanic Gardens, Kew, Richmond, U.K.

Scotland, R. W., Olmstead, R.G., Bennett, J.R. 2003. Phylogeny Reconstruction: The Role of Morphology. *Systematic Biology* 52(4): 539–548.

Simpson, G.G. 1961. *Principles of Animal Taxonomy.* Colombia University Press, New York. 539 pp.

Simpson, B.B., Larkin, L.L. & Weeks, A. 2003. Progress towards resolving the relationships of the *Caesalpinia* group (Caesalpinieae, Caesalpinioideae, Leguminosae). In: Klitgaard, B.B. & Bruneau, A. (eds.) *Advances in Legumes Systematics Part 10, Higher Level Systematics.* Royal Botanic Gardens, Kew, Richmond, U.K. pp. 123–148.

Simpson, B.B. & Miao, B.-M. 1997. The circumscription of *Hoffmannseggia* (Fabaceae, Caesalpinioideae, Caesalpinieae) and its allies using morphological and cpDNA restriction site data. *Plant Systematics and Evolution* 205: 157–178.

Singh, G. 2010. Plant Systematics: An Integrated Approach (3rd Edition). Science Publishers, New Hampshire, U.S.A. 742 pp.

Sinou, C., Forest, F., Lewis, G.P., & Bruneau, A. 2009. The genus *Bauhinia s.l.* (Leguminosae): a phylogeny based on the plastid trnL-trnF region. *Botany* 87: 947–960.

Sivarajan, V.V. 1991. Edited by Robson, N.K.B. Introduction to the Principles of Plant Taxonomy, 2nd Edition. Cambridge University Press, Cambridge, U.K. 292 pp.

Sosef, M.S.M. 1997. Hierarchical Models, Reticulate Evolution and the Inevitability of Paraphyletic Supraspecific Taxa. *Taxon* 46(1): 75–85.

Sotuyo, S., Delgado-Salinas, A., Chase, M.W., Lewis, G.P., Oyama, K. 2007. Cryptic speciation in the *Caesalpinia hintonii* complex (Leguminosae: Caesalpinioideae) in a seasonally dry Mexican forest. *Annals of Botany* 100: 1307–1314.

Stamatakis, A. 2014. RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. Bioinformatics 10.1093/bioinformatics/btu033 http://bioinformatics.oxfordjournals.org/content/early/2014/01/21/bioinformatics.btu033.abstract

Steussy, T.F. 2009. Plant Taxonomy: The Systematic Evaluation of Comparative Data, 2nd Edition. Colombia University Press, New York. 539 pp.

Steussy, T. & Hörandl, E. 2014. Evolutionary Systematics and Paraphyly: Introduction. *Annals of the Missouri Botanical Garden* 100(1–2): 2–5. http://dx.doi.org/10.3417/2012083

Takhtajan, A. 1958. *Origin of Angiospermous Plants.* American Institute of Biological Sciences [translation of Russian edition of 1954]

Takhtajan, A. 2009. Flowering Plants. Springer. 871 pp.

Taubert, P. 1891. Caesalpinioideae-Bauhinieae (Leguminosae). In: Engler, A. & Prantl, K. *Die naturlichen pflanzenfamilien*. Leipzig, Germany. Vol. 3, pp 146–153.

Theophrastus (translated) 1916. *Enquiry into plants and minor works on odours and weather signs.* William Heinemann, London. 499 pp.

Thiv, M., van der Niet, T., Rutschmann, F., Thulin, M., Brune, T., Linder, H.P. 2011. Old – New world and trans-African disjunctions of *Thamnosma* (Rutaceae): intercontinental long-distance dispersal and local differentiation in the succulent biome. *American Journal of Botany* 98(1): 76–87.

Thomas, D.C., Chatrou, L.W., Stull, G.W., Johnson, D.M., Harris, D.J., Thongpairoj, U., Saunders, R.M.K. 2015. The historical origins of palaeotropical intercontinental disjunctions in the pantropical flowering plant family Annonaceae. *Perspectives in Plant Ecology, Evolution and Systematics* 17: 1–16. http://dx.doi.org/10.1016/j.ppees.2014.11.001

Thorne, R.F. 1973. Floristic relationships between tropical Africa and tropical America. In*:* Meggers, B.J., Ayensu, E.S., Duckworth, W.D. (eds*.) Tropical forest ecosystems in Africa and South America: a comparative review*. Smithsonian Institution, Washington, D.C. pp. 27–47.

Tiffney, B.H. 1985. The Eocene North Atlantic land bridge: its importance in tertiary and modern phytogeography of the northern hemisphere. *Journal of the Arnold Arboretum* 66: 243–273.

Toledo-Aceves, T. 2015. Above- and belowground competition between lianas and trees. In: Schnitzer, A., Bongers, F., Burnham, R.J., Putz, F.E. *Ecology of Lianas.* Wiley Blackwell, Oxford, U.K. pp. 149–163

Tournefort, J.P. 1700. *Institutiones rei herbariæ.* E Typographia Regia, Paris. 54 pp.

Trethowan, L., Clark, R.P., Mackinder, B.A. 2015. A synopsis of the neotropical genus *Schnella* (Cercideae: Caesalpinioideae: Leguminosae) including 12 new combinations. *Phytotaxa* 204(4): 237–252.

Turner, I.M. 2016. Species names attributed to Bentham & Hooker's Genera Plantarum. *Annales Botanici Fennici*, 53(5–6): 285–337.

Verdcourt, B. 1979. *A Manual of New Guinea Legumes.* Office of Forests, Division of Botany, Lae, Papua New Guinea. 645 pp.

Vaz A.M.S. da F. 2010. New combinations in *Phanera* (Leguminosae; Cercideae) from Brazil. *Rodriguésia* 61 (Suppl.): S33–S40.

Vidal, J.E. & Thol, S.H. 1976. Révision des Caesalpinia Asiatiques. Bulletin du Muséum National d'Histoire Naturelle. Sér. 3, Botanique, pp. 69–136.

Wang, Q., Song, Z., Chen, Y., Shen, S., Li, Z. 2014. Leaves and fruits of *Bauhinia* (Leguminosae, Caesalpinioideae, Cercideae) from the Oligocene Ningming Formation of Guangxi, South China and their biogeographic implications. *BMC Evolutionary Biology* 14: 1471–2148.

Wen, J. & Ickert-Bond, S.M. 2009. Evolution of the Madrean–Tethyan disjunctions and the North and South American amphitropical disjunctions in plants. *Journal of Systematics and Evolution* 47(5): 331–348. doi: 10.1111/j.1759-6831.2009.00054.x

Wolfe, J.A. 1975. Some aspects of plant geography of the northern hemisphere during the late Cretaceous and Tertiary. *Annals of the Missouri Botanical Garden* 62: 264–279.

Wunderlin R.P. 1976. Enumeration and typification of genera in tribe Cercideae. *Rhodora* 78: 750–760.

Wunderlin R.P. 1979. Consideration of *Barklya* and the subtribes of the Cercideae (Caesalpinioideae: Fabaceae). *Phytologia* 44: 325–327.

Wunderlin R.P., Larsen K. & Larsen S.S. 1981. Cercideae. In: Polhill R.M. & Raven P.H. (eds) *Advances in Legume Systematics*, *Part 1*. Royal Botanic Gardens, Kew., Richmond, U.K., pp. 107–116.

Wunderlin, R.P. 1983. Revision of the arborescent *Bauhinias* (Fabaceae: Caesalpinioideae: Cercideae) native to Middle America. *Annals of the Missouri Botanic Garden* 70(1): 95–127. doi:10.2307/2399009.

Wunderlin R.P., Larsen K. & Larsen S.S. 1987. Reorganization of the Cercideae (Fabaceae: Caesalpinioideae). *Biologiske Skrifter* 28: 1–40.

Wunderlin, R.P. & Eilers, R.M. 2009. Revision of *Bauhinia* subgenus *Phanera* section *Schnella* (Cercideae: Caesalpinioideae: Fabaceae). *Journal of the Botanical Research Institute of Texas* 3: 619–628.

Wunderlin, R.P. 2010a. Reorganization of the Cercideae (Fabaceae: Caesalpinoideae). *Phytoneuron* 48: 1–5.

Wunderlin, R.P. 2010b. New Combinations in *Schnella* (Fabaceae: Caesalpinioideae: Cercideae). *Phytoneuron* 49: 1–5.

Wunderlin, R.P. 2011. New combination in *Phanera* (Fabaceae). *Phytoneuron* 19: 1–2.

Yakovlev, G.P. 1972. A contribution to the system of the order Fabales Nakai (Leguminales Jones). *Botaniceskij Zurnal. Moscow and Leningrad* 57: 585–594.

Zhang D.X. & Chen T.C. 1992. Systematics and Biogeography of *Bauhinia* L. (Leguminosae) II. Cladistic Analysis of Ser. *Corymbosae*. *Acta Botanica Austro Sinica* 8: 31–35.

APPENDIX 1. The Published Work

The Version of Record of the published works have been removed from the electronic version of the thesis for copyright reasons. The metadata and links to the published versions are given on the page below.

1. Clark, R.P., Mackinder, B.A., Banks, H. 2017. *Cheniella* gen. nov. (Leguminosae: Cercidoideae) from S. China, IndoChina and Malesia. *European Journal of Taxonomy* 360: 1–37. https://doi.org/10.5852/ejt.2017.360 https://europeanjournaloftaxonomy.eu/index.php/ejt/article/view/485

Links functional 23.08.2019

2. Clark, R.P. 2016. A Taxonomic Revision of *Mezoneuron* (Leguminosae: Caesalpinioideae: Caesalpinieae). *Phytotaxa* 274(1): 1–72. http://www.mapress.com/j/pt/

http://dx.doi.org/10.11646/phytotaxa.274.1.1

Links functional 23.08.2019

3. Clark, R. & Gagnon, E. 2015. A revision of *Mezoneuron* (Leguminosae – Caesalpinioideae) in New Caledonia, with perspectives on vegetation, geology and conservation. *Phytotaxa* 207(1): 68–92. https://biotaxa.org/Phytotaxa/article/view/phytotaxa.207.1.3

http://dx.doi.org/10.11646/phytotaxa.207.1.3

Links functional 23.08.2019

4. Clark, R.P. 2015. *Lasiobema flavum* (Leguminosae: Caesalpinioideae), a new record for the Flora of Thailand. *Thai Forest Bulletin (Botany)* 43: 70–73. https://www.tci-thaijo.org/index.php/ThaiForestBulletin/article/view/44210
Link functional 23.08.2019

5. Trethowan, L., Clark, R.P., Mackinder, B.A. 2015. A synopsis of the neotropical genus *Schnella* (Cercideae: Caesalpinioideae: Leguminosae) including 12 new combinations. *Phytotaxa* 204(4): 237–252.
https://biotaxa.org/Phytotaxa/article/view/phytotaxa.204.4.1
http://dx.doi.org/10.11646/phytotaxa.204.4.1
Links functional 23.08.2019

6. Mackinder, B.A., Clark, R. 2014. A synopsis of the Asian and Australasian genus *Phanera* Lour. (Cercideae: Caesalpinioideae: Leguminosae) including 19 new combinations. *Phytotaxa* 166 (1): 49–68.
https://biotaxa.org/Phytotaxa/article/view/phytotaxa.166.1.3
http://dx.doi.org/10.11646/phytotaxa.166.1.3
Links functional 23.08.2019

APPENDIX 2. Co-authors’ Statements of Candidate Contribution

Royal Botanic Garden Edinburgh
20A Inverleith Row
Edinburgh
EH3 5LR
United Kingdom

26.04.2017

To Whom it may Concern,

As co-author of the listed paper, I hereby endorse the following statement of contribution to the paper by Ruth Clark.

Clark, R., Mackinder, B.A., Banks, H. *Cheniella* gen. nov. (Cercideae, Caesalpinioideae, Leguminosae) from S. China, IndoChina and Malesia Accepted by the European Journal of Taxonomy 18.01.2017. [69 pp. as preliminary PDF).

I (Ruth Clark) was involved from the outset in the discussions that developed the concept of the new genus. In producing the paper I:

- wrote the taxon descriptions and key to the species
- produced the comparative table of morphological characters
- proposed the new subspecies, and other taxonomic changes
- generated the preliminary conservation assessments
- wrote the discussion
- created the maps
- worked with the botanical artist to create the composite illustration
- organised and carried out a field trip, which resulted in the collection of specimens and field data
- presented the paper at an international conference
- served as lead author in corresponding with the journal, and addressing the reviewers' comments

Yours Faithfully,

Barbara Mackinder

Dr Barbara Mackinder

Royal Botanic Gardens, Kew
Kew Green,
Richmond
Surrey
TW9 3AE

15.12.2017

To Whom it may Concern,

As **co-author of the listed paper, I hereby endorse the following statement of contribution to the paper by Ruth Clark.**

Clark, R., Mackinder, B.A., Banks, H. *Cheniella* gen. nov. (Cercideae, Caesalpinioideae, Leguminosae) from S. China, IndoChina and Malesia. *European Journal of Taxonomy* 360: 1-37.

I (Ruth Clark) was involved from the outset in the discussions that developed the concept of the new genus. In producing the paper, I:

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- proposed the new subspecies, and other taxonomic changes
- generated the preliminary conservation assessments
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- created the maps
- worked with the botanical artist to create the composite illustration
- organised and carried out a field trip, which resulted in the collection of specimens and field data
- presented the paper at an international conference
- served as lead author in corresponding with the journal, and addressing the reviewers' comments

Yours Faithfully,

Dr Hannah Banks

The 26th of April 2017

To Whom it may Concern,

As **co-author of the listed paper, I hereby endorse the following statement of contribution to the paper by Ruth Clark.**

Clark, R. & Gagnon, E. (2015) A revision of *Mezoneuron* (Leguminosae – Caesalpinioideae) in New Caledonia, with perspectives on vegetation, geology and conservation. *Phytotaxa* 207(1): 68-92.

I declare that Ruth Clark was the lead author in this research, in which she:

- organised and headed the field work that provided much of the data on which the paper was based;
- carried out the taxonomic studies, implemented the taxonomic changes, wrote the taxon descriptions and the key to species;
- mapped the species occurrence data by geo-referencing herbarium specimens
- generated the preliminary conservation assessments;
- wrote the text;
- worked with the botanical artist to create the composite illustration;
- listed the exsiccatae (specimen details);

My own contribution to the paper consisted of:

- providing the phylogenetic tree featured in the publication;
- providing critical commentary and revisions of the manuscript.

Yours Faithfully,

Dr Edeline Gagnon

45 Everett Road
Withington
Manchester
M203EA

26.04.2017

To Whom it may Concern,

As co-author of the listed paper, I hereby endorse the following statement of contribution to the paper by Ruth Clark.

Trethowan, L., Clark, R.P., Mackinder, B.A. (2015) A synopsis of the neotropical genus *Schnella* (Cercideae : Caesalpinioideae: Leguminosae) including 12 new combinations. *Phytotaxa* 204(4): 237-252.

The project Legumes of the World Online was initiated in 2006 by the legume team at Kew, then comprising five individuals, to translate the book Legumes of the World into online format. As part of the development of this resource, a CSYS ('Sandwich Year') student was employed for one year to work exclusively on the pages of the website concerned with the tribe Cercideae, with the aim of expanding and improving these pages as a pilot on which to base the development of the rest of the site. The Cercideae were selected as the study group for being probably the earliest diverging lineage of legumes, with therefore a pivotal role in understanding the evolution of the rest of the family, as well as being a group with a long and complex taxonomic history, including many important recent changes. One of the reinstated genera arising from these changes was *Schnella.*

I (Ruth Clark) took the lead in training the student (L. Trethowan), as his line manager, in the essential taxonomic and nomenclatural skills required to carry out the work on which this paper was based, as well as giving guidance in the fundamental skills of scientific writing, and contributing to his grounding in knowledge of the legume family. These inputs enabled the student to fulfil the role of lead author on this paper.

My direct contributions to the paper in addition to the above were:
- Co-wrote the introductory text.
- Worked with the lead author to resolve nomenclatural problems.
- Advised with the production of the distribution map.
- Commented on and revised the manuscript throughout.
- Acted as the corresponding author, liaising with the journal during the full editorial and publication process.

Yours Faithfully,

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26.04.2017

To Whom it may Concern,

As co-author of the listed paper, I hereby endorse the following statement of contribution to the paper by Ruth Clark.

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- Advised with the production of the distribution map.
- Commented on and revised the manuscript throughout.
- Acted as the corresponding author, liaising with the journal during the full editorial and publication process.

Yours Faithfully,

Barbara Mackinder

Dr Barbara Mackinder

Royal Botanic Garden Edinburgh
20A lnverleith Row
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26.04.2017

To Whom it may Concern,

As co-author of the listed paper, I hereby endorse the following statement of contribution to the paper by Ruth Clark.

Mackinder, B.A., Ruth Clark (2014) A synopsis of the Asian and Australasian genus *Phanera* Lour. (Cercideae: Caesalpinioideae : Leguminosae) including 19 new combinations. *Phytotaxa* 166 (1): 49-68.

This paper arose through a long-term collaborative interest in the genus *Bauhinia sensu lato* between myself (Ruth Clark) and Dr Barbara Mackinder. The many taxonomic changes implemented within *Bauhinia s.l.* in the last decade or so, by which it has been extensively subdivided, made it of great taxonomic and curatorial interest. As the then primary curator of the Leguminosae collections at Kew, my interest stemmed both from a research perspective, and also from the wish to create a complete list of the taxa and synonymy in *Phanera,* one of the major segregate genera of *Bauhinia s.l.,* as a tool by which the herbarium collections could be systematically rearranged to accurately reflect the latest classification.

My contributions to the manuscript were:

- Co-wrote the paper.
- Reviewed early drafts of the introductory text, and suggested improvements.
- Checked and verified the nomenclature.
- Established the full distribution range of the taxa by utilising the herbarium collections, online collections, and literature.
- Provided comments and revisions on successive drafts of the manuscript.

Yours Faithfully,

Barbara Mackinder

Dr Barbara Mackinder