View metadata, citation and similar papers at core.ac.uk

brought to you by CORE

provided by University of the Western Cape Research Repository

Borges, L. et al. (2013). Towards a new classification system for legumes: Progress report from the 6th International Legume Conference.
South African Journal of Botany, 89: 3-9
http://dx.doi.org/10.1016/j.sajb.2013.07.022

UNIVERSITY of the WESTERN CAPE

# Towards a new classification system for legumes: Progress report from the 6th International Legume Conference

The Legume PhylogenyWorking Group 1

This paper was compiled by L. Borges, A. Bruneau, D. Cardoso, M. Crisp, A. Delgado-Salinas, J.J. Doyle, A. Egan, P.S. Herendeen, C. Hughes, G. Kenicer, B. Klitgaard, E. Koenen, M. Lavin, G. Lewis, M. Luckow, B.Mackinder, V.Malécot, J.T. Miller, R.T. Pennington, L.P. de Queiroz, B. Schrire, M.F. Simon, K. Steele, B. Torke, J.J.Wieringa, M.F. Wojciechowski, who were equally responsible and listed here in alphabetical order only, with additional contributions from, S. Boatwright, M. de la Estrella, V. de Freitas Mansano, D.E. Prado, C. Stirton, M.Wink

## Abstract

Legume systematists have been making great progress in understanding evolutionary relationships within the Leguminosae (Fabaceae), the third largest family of flowering plants. As the phylogenetic picture has become clearer, so too has the need for a revised classification of the family. The organization of the family into three subfamilies and 42 tribes is outdated and evolutionarily misleading. The three traditionally recognized subfamilies, Caesalpinioideae, Mimosoideae, and Papilionoideae, do not adequately represent relationships within the family. The occasion of the Sixth International Legume Conference in Johannesburg, South Africa in January 2013, with its theme "Towards a new classification system for legumes," provided the impetus to move forward with developing a new classification. A draft classification, based on current phylogenetic results and a set of principles and guidelines, was prepared in advance of the conference as the basis for discussion. The principles, guidelines, and draft classification were presented and debated at the conference. The objectives of the discussion were to develop consensus on the principles that should guide the development of the classification, to discuss the draft classification's strengths and weaknesses and make proposals for its revision, and identify and prioritize phylogenetic deficiencies that must be resolved before the classification could be published. This paper describes the collaborative process by a large group of legume systematists, publishing under the name Legume Phylogeny Working Group, to develop a new phylogenetic classification system for the Leguminosae. The goals of this paper are to inform the broader legume community, and others, of the need for a revised classification, and spell out clearly what the alternatives and challenges are for a new classification system for the family.

University of the Western Cape Research Repository umesthrie@uwc.ac.za

**1. Legume phylogeny and classification**

The modern era of legume systematics began with the publication of *Advances in Legume Systematics* (Polhill and Raven, 1981). Roger Polhill and Peter Raven led a group of legume systematists in producing a major revision of the classification system for the Leguminosae. This was a landmark accomplishment in several respects. First, a taxonomic revision of a group the size of the Leguminosae (ca. 751 genera and 19,500 species; Lewis et al., 2005; LPWG, 2013), the third largest family of flowering plants, was a major undertaking. Second, and more significantly for the precedent that was set, the publication of *Advances* was a community effort that was initiated at the first International Legume Conference (Royal Botanic Gardens, Kew, 1978). The conference catalyzed research in many different aspects of legume biology as well as in systematics. *Advances in Legume Systematics*, *part 1* (Polhill and Raven, 1981) presented a comprehensive taxonomic revision of the family, and the genera, tribes and subfamilies outlined in this treatment have been studied in detail and tested through numerous subsequent phylogenetic analyses. Furthermore, "*Advances 1*" also incorporated non-Linnaean nomenclature in the classification system (e.g., *Peltophorum* group, *Dimorphandra* group) and that tradition has persisted with a substantial number of informal clade names in use today. Polhill (1994) updated the classification and in 2005 *Legumes of the World* (Lewis et al., 2005) provided a comprehensive account of the taxonomic changes and phylogenetic progress that occurred over nearly 25 years since publication of the first volume of *Advances*.

In 2010 the Legume Phylogeny Working Group (LPWG) was established to enhance progress in legume phylogenetics, and its first publication (LPWG, 2013) provided an overview of legume phylogeny and set an agenda for tackling the most significant challenges in legume phylogeny and classification. In parallel, the Global Legume Diversity Assessment (GLDA) group was created based on the idea that Leguminosae provide a proxy for overall angiosperm diversity. Its objective is to assess how rapidly we are losing plant species diversity by studying the legume family (Yahara et al., 2013). Current efforts to revisit and revise the classification system for legumes are being undertaken as a community project that was initiated for the Sixth International Legume Conference, held in Johannesburg, South Africa, in January, 2013. This paper describes the collaborative process by a large group of legume systematists, publishing under the name Legume Phylogeny Working Group, to develop a new phylogenetic classification system for the Leguminosae. The aims of this paper are to inform the broader legume community, and others, of the need for a revised classification and describe the potentially difficult choices that must be made. It has been clear since at least 1981 that the three traditionally recognized subfamilies, Caesalpinioideae, Mimosoideae, and Papilionoideae, do not adequately represent phylogenetic relationships within the family (Polhill et al., 1981) because the Mimosoideae and Papilionoideae are nested within a paraphyletic Caesalpinioideae (Fig. 1; Chappill, 1995; Käss and Wink, 1996; Doyle et al., 2000; Kajita et al., 2001; Bruneau et al., 2001, 2008; Herendeen et al., 2003a; Wojciechowski, 2003; Wojciechowski et al., 2004; Lewis et al., 2005). However, in 1981 the idea that only monophyletic groups should be named was only starting to be debated and thus there was little interest at that time in altering the traditional classification with three subfamilies. By the fourth International Legume Conference (2001, Canberra, Australia) it



http://repository.uwc.ac.za

was clearly understood that the traditional classification would not survive, but lack of phylogenetic resolution and support, as well as sparse sampling of genera, precluded formulation of a new subfamilial classification. Subsequent work has added new DNA sequence data for an increasing fraction of the genera (reviewed in LPWG, 2013), resulting in an enhanced phylogeny (Wojciechowski et al., 2004; Lavin et al., 2005; Bruneau et al., 2008; Simon et al., 2009; Cardoso et al., 2012; LPWG, 2013). Most importantly we now have much better, albeit still incomplete, generic sampling across critical parts of the tree, bringing the choices and dilemmas about how to generate a satisfactory new subfamilial and tribal classification into sharper focus.

Taxonomic classifications are used by a wide range of people, especially for a species-rich family like legumes that is very important both ecologically and economically. The traditional classification with three subfamilies is well known, universally familiar, and easy to teach, and provides a generally workable starting point for legume identification, even though there are exceptional taxa that do not fit the stereotypical characterizations of the three subfamilies, and even though caesalpinioids have been difficult to characterize other than based on plesiomorphic characters, or as non-mimosoids and non-papilionoids. Floras, field guides, and other popular literature are almost universally arranged according to the three subfamilies for ease of use, as are many herbarium collections. This means that the subfamilial rank is especially important in legumes. In contrast the numerous tribes recognized in the Leguminosae are rarely used in floras or other applications outside the legume systematics literature. Legume systematists have been reluctant to publish a new classification that would inevitably change in the near future as phylogenetic resolution improved. Deciding when to proceed with a new classification, even an interim one, has been a challenge (discussed in LPWG, 2013), but the occasion of the Sixth International Legume Conference in January 2013, with its theme "Towards a new classification system for legumes", provided the impetus to move forward.

Fig. 1 shows the non-monophyly of the Caesalpinioideae, illustrating why a new classification is needed, and the obvious consequences that the paraphyletic Caesalpinioideae will have on a new phylogenetic subfamily classification. This paper focuses mainly on subfamilies in discussing our progress toward developing a new phylogenetic Linnaean classification system. Many of the concerns and considerations discussed here apply equally to tribal level classification, but better sampled and resolved phylogenies are still required before a new tribal classification can be established.



http://repository.uwc.ac.za

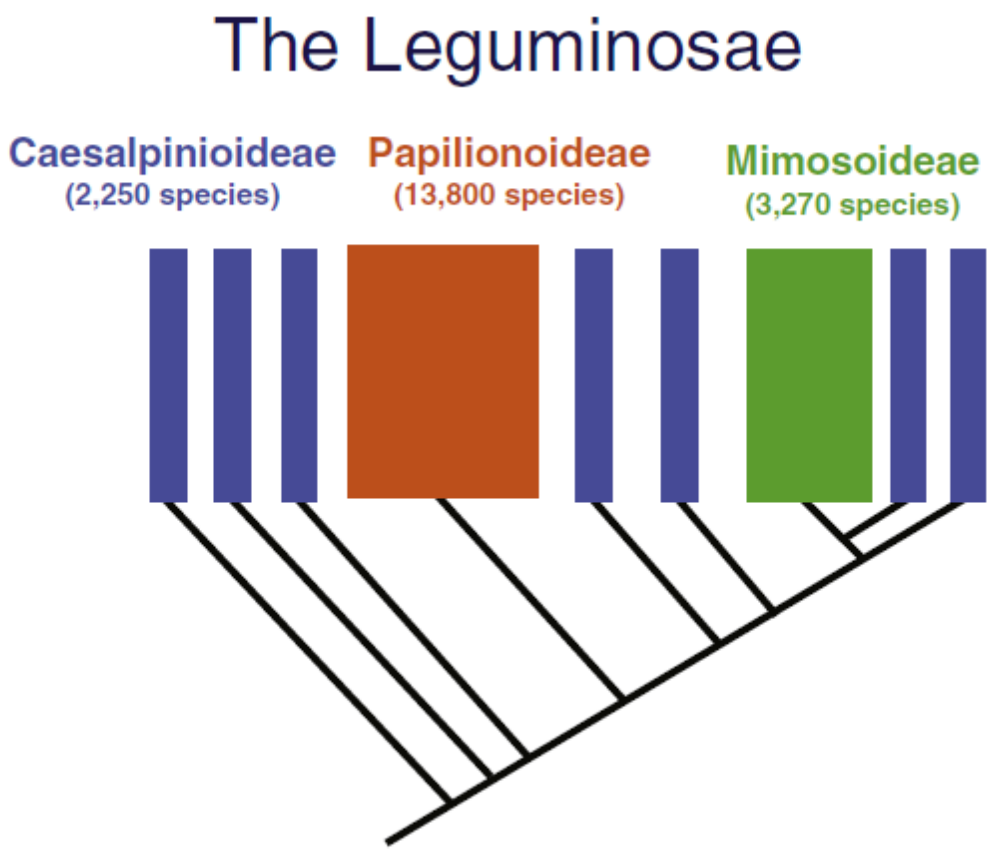


**Fig. 1.** Legume phylogeny overview illustrating paraphyletic subfamily Caesalpinioideae and nested placements of subfamilies Mimosoideae and Papilionoideae.

As indicated above, informal rank-free group names are also important in legume classification and are a feature of almost all published legume phylogeny papers since Polhill and Raven (1981). The Linnaean and rank-free (also referred to as non-Linnaean) classification systems need to be fully compatible, complementary and carefully integrated, and this is an ongoing effort by several LPWG members. For example, Wojciechowski (2013–this issue) proposes one possible way to formalize clade names and develop a non-Linnaean phylogenetic classification system for the family.

The conference in South Africa in 2013 presented an ideal opportunity for the legume systematics community to discuss a new classification. A draft classification compatible with established rules of nomenclature (McNeill et al., 2012) and based on a set of principles and guidelines (below) was prepared in advance of the conference as the basis for discussion. The efforts presented here focus on subfamilial and tribal levels; the classification does not address delimitation of genera, which is a future priority (cf. LPWG, 2013). The draft classification was presented on the first day of the conference and was debated in a discussion session on the last day. One of the goals of this paper is to explain why a new classification is needed and spell out clearly what the alternatives and implications are for a new subfamily classification system in the legumes.



http://repository.uwc.ac.za

## 2. Operating principles for developing a new classification

In initiating this group project we decided that it would be essential to set out a series of guidelines or principles to guide decision making in the development of the new classification. The international legume systematics community is diverse and many different perspectives are represented. Thus it was important to articulate our objective of a new phylogenetic classification and the criteria that would be employed to synthesize the many available phylogenies, arrive at a consensus, and translate this into a classification. We are not the first to undertake such a project. Consensus classifications have been published for a number of large taxonomic groups, such as grasses (Grass Phylogeny Working Group, 2001), composites (Funk et al., 2009), and fungi (Hibbett et al., 2007). Several papers have discussed principles for naming clades in phylogenetic classifications (e.g., Backlund and Bremer, 1998; Stevens, 2006; Humphreys and Linder, 2009) and for naming and prioritization to "promote economy of change" (Vences et al., 2013), providing useful pointers for the legume community as it moves forward with this project.

The following principles, guidelines, and logical consequences (collectively referred to as "Operating Principles" for this project) were developed to guide the process of developing the draft classification.

General principles:

1. The classification will be phylogenetically based and only monophyletic groups will be named.
2. In deciding which clades to name, preference will be given to groups that are recognizable by diagnostic morphological characters.
3. Not all clades will be named because within a Linnaean framework there are insufficient ranks to name all clades.
4. Widely used names will be retained whenever possible. Specific principles for legumes:
5. Legume classification has incorporated both Linnaean nomenclature and rank-free group or clade names since at least 1981 and we wish to continue that practice.
6. Legumes are monophyletic and should be treated as one family.

- Because the Caesalpinioideae is paraphyletic the number of subfamilies will increase.
- The monophyletic Mimosoideae and Papilionoideae should be retained as subfamilies for purposes of nomenclatural stability, although the former may need to be redefined.

Clearly these principles and guidelines are not fully compatible and consequently compromise is necessary in developing a new classification. The recognition of Papilionoideae and Mimosoideae constrains options for naming other major clades, and necessitates recognition of additional subfamilies to account for the paraphyletic Caesalpinioideae. A variety of other criteria have subsequently been suggested in developing the classification, including clade support and branch lengths. Some of the members of the working group have suggested that the principles be prioritized, but this would be a subjective decision and opinions would undoubtedly vary. While not explicitly



http://repository.uwc.ac.za

prioritized, these differences of opinion have entered into ongoing discussions following the conference. Nevertheless, one principle enjoys almost universal support, and that is the first one: only monophyletic groups will be named.

**3. Gathering the ingredients**

Preparing the draft classification required gathering the most recent information on legume diversity, nomenclature, and phylogeny. Available phylogenetic resources are extensive, especially when unpublished results from a number of laboratories throughout the world, as well as supermatrix analyses (see LPWG, 2013 for details) are taken into account. The phylogenetic trees presented in LPWG (2013) served as the primary resource for this project, and they were augmented by numerous other published studies cited in LPWG (2013) for details on resolution within particular clades. An updated list of currently recognized genera (Lewis et al., 2013 –this issue) was used to determine which genera had not yet been included in molecular phylogenies (Table 1 in LPWG, 2013) and to cross check against the phylogenies to be sure all genera are grouped correctly in the classification. A list of all validly published suprageneric names (subfamilies, tribes, subtribes) was compiled along with date of publication to determine the correct names for clades that are to be named in the new Linnaean classification. Many suprageneric names were obtained from a Web page maintained by James Reveal (Cornell University; http://www.plantsystematics.org/reveal/pbio/fam/allspgnames.html), with additions and corrections provided by project participants. Similarly, a list of informal clade names in use was compiled by G. Lewis, L. Queiroz, and M. Wojciechowski. A spreadsheet was used to compile the information on generic and suprageneric names, informal clade names, and clade composition. After compiling details on clade composition and relationships from the phylogenies and determining where resolution is relatively stable and consistent and where it is conflicting or inadequately supported we identified clades that could be named at the subfamilial and tribal levels, and then determined which of these groups already had published names available.

**4. The draft classification**

The draft classification was circulated at the Sixth International Legume Conference in Johannesburg for discussion, criticism, and improvement. The classification was presented on the first day of the conference and a discussion session on the last day of the conference was organized to focus on principles and conceptual issues and then on making decisions on aspects of the classification that require debate. The discussion session was also intended to decide which problem areas in the phylogeny must be resolved, and which need greater support, before publishing the classification. The draft classification included 15 subfamilies (Fig. 2A) and 57 tribes, with several areas of uncertainty that were left undecided in delimiting tribes. For the most part assembling the classification was a straightforward process, but there were a few areas in the phylogeny where inadequate resolution made it difficult to delimit taxa, or where the topology presented challenges. In some cases there were multiple options to recognize broader or



http://repository.uwc.ac.za

narrower subfamilies or tribes, and in these cases we tried to use the criterion of diagnosability to make decisions.

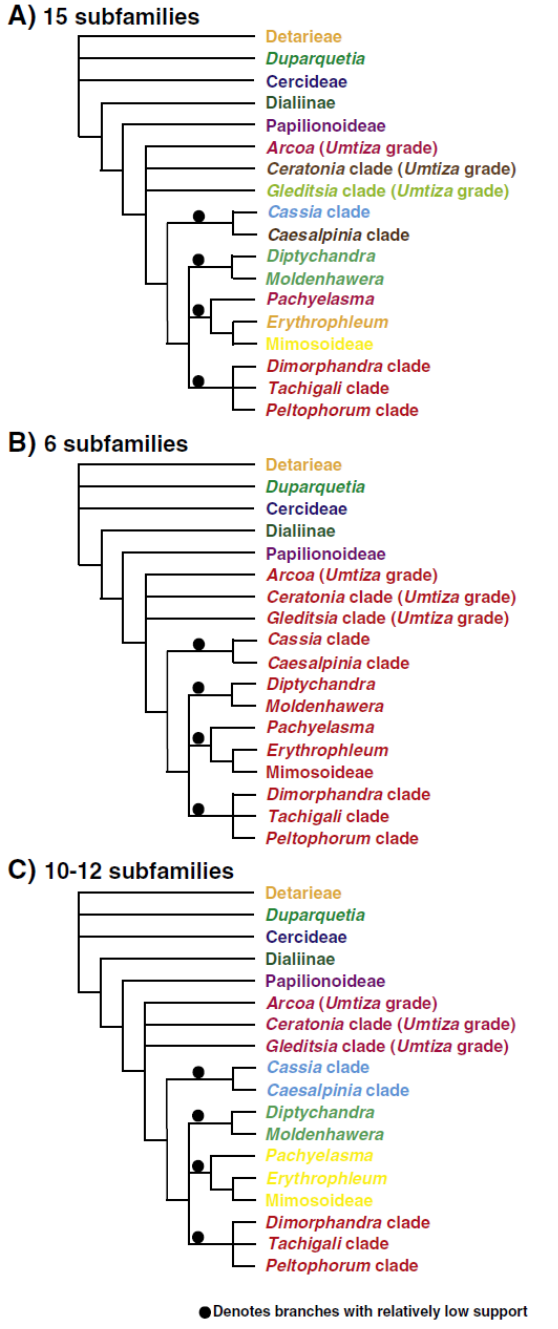


**Fig. 2.** Schematic overview phylogeny based on LPWG, 2013, Fig. 1 with subfamilies indicated using different colors. A. Draft classification presented to conference participants for discussion. B. Revised classification in which the number of subfamilies is reduced to six. C. Revised classification consisting of 10–12 subfamilies (exact number depends on how the *Umtiza* group and *Dimorphandra* group genera associated with mimosoids are eventually resolved).

There were several regions with a strongly imbalanced ("ladder-like") topology that made delimitation of subfamilies and tribes particularly challenging. As noted above, the recognition of Mimosoideae and Papilionoideae as subfamilies was preferred for purposes of stability. In developing the draft classification we initially gave preference to narrower taxon



http://repository.uwc.ac.za

delimitation for the tribes and subfamilies to facilitate diagnosability, and the number of resulting subfamilies and tribes was not considered at that stage. These preferences for stability and diagnosability, and the large number of subfamilies that follow as a consequence, were topics of discussion at the conference. It should be noted that for many of the newly delimited subfamilies and tribes there is a single published name for each group, but for others there either is no published name at the appropriate rank, or there are multiple names of equal priority. These nomenclatural matters will be addressed when the revised classification is published.

All discussion participants were in agreement that the new classification should include both Linnaean and non-Linnaean nomenclatures and that the two classification systems should be fully compatible and integrated. The discussion of the options for the Linnaean classification system that follows is with the explicit understanding that a non-Linnaean system, which was not included due to lack of time, will be added in the near future after discussion with legume systematists. The non-Linnaean system might be either a comprehensive treatment of the entire family, or a more targeted treatment that formalizes definitions of certain clade names (Wojciechowski, 2013–this issue).

## 5. Discussion and debate

Prior to the discussion on the last day of the conference it was clear that the process adopted for this project was successful, at least in terms of engaging a broad range of legume systematists in the discussion of a new classification system, although not in terms of reaching immediate consensus. Feedback from participants through the week was lively with many discussions as well as written annotations on the accompanying posters. During the conference it was apparent that the most significant criticism of the draft classification was the large number of proposed subfamilies (Fig. 2A). Interestingly, the number of proposed tribes was not criticized, even though the number increased from 42 in *Advances in Legume Systematics part 1* (Polhill and Raven, 1981) to 57 in the draft classification. Although there were suggestions that particular tribes were not warranted, these comments were based mostly on concern about poor resolution, relatively poor taxonomic sampling, or few characters, rather than as a concern that there were too many tribes.

The question about number of subfamilies stems from the desire that the classification should serve the needs of the broader community that uses the products of our taxonomic work, such as in floras, field guides, and in teaching. There was a concern expressed by a number of participants that a new classification consisting of 15 subfamilies would be dismissed by many people and instead they would continue using the traditional classification with its outdated groupings. It is difficult to satisfy the principle of naming only monophyletic groups while at the same time retaining the Mimosoideae as a subfamily and avoiding a proliferation of small subfamilies. The most obvious solution would be to recognize one or more, broader, more inclusive subfamilies, but this potential improvement could be countered by the concern that the broader subfamilies could be difficult to diagnose morphologically (although several participants noted that the traditional subfamilies are not



http://repository.uwc.ac.za

easily diagnosed, especially Caesalpinioideae). Thus it is evident that in creating a "user friendly" classification we must strike a balance between a "manageable" number of subfamilies and narrower subfamilies that can be more easily characterized and diagnosed.

Discussion participants were given several options to consider and debate:

7. Adopt the "Draft Classification" as presented, with corrections that were provided by conference attendees. This system included 15 subfamilies and 57 tribes.
8. Adopt a "Half Way" solution — keep the three traditional subfamilies for now and adopt the new tribes based on the Draft Classification (with corrections from attendees). Subfamilies would be revisited later when better resolution is obtained.
9. Adopt only a non-Linnaean Phylogenetic classification that names clades in a formal manner without the use of Linnaean ranks. The formal Linnaean classification would be abandoned because the topology makes the delimitation of a "reasonable number" of subfamilies and tribes too difficult.
10. Revise the draft classification such that the number of subfamilies is reduced.

The first three options were debated and all three were rejected. There was very little support for adopting the draft classification as presented with only minor corrections (Option 1). There was a greater level of support for the second option of a "Half Way" solution (adopt the new classification for tribes and revisit subfamilies at a later date), but the majority of the attendees were of the opinion that this would only defer difficult decisions. However, it was also clear from discussion that phylogenetic resolution and stability were not yet adequate to make tribal delimitation decisions in some regions of the phylogeny. Thus, the "Half Way" solution could not be implemented right away.

Discussion among conference participants explored alternative subfamily delimitation schemes that would yield a classification that requires fewer subfamilies. One possibility is a classification that would recognize six subfamilies (Fig. 2B): this involves recognition of a larger, strongly supported clade delimited by the most recent ancestor of *Arcoa* (*Umtiza* grade or clade) and *Peltophorum* (*Dimorphandra* group) as a single subfamily. This would merge all of tribe Caesalpinieae, the *Cassia* clade, and subfamily Mimosoideae into one subfamily, referred to informally here as the "combined Caesalpinioideae p.p.-Mimosoideae" subfamily. While the resulting smaller number of subfamilies was attractive to many participants, the primary criticism was that it would yield a morphologically heterogeneous subfamily (relative to traditional Mimosoideae, but not more heterogeneous than traditional Caesalpinioideae). Although we have not yet had an opportunity to evaluate thoroughly morphological diagnosability, it is worth noting that all bipinnate-leaved legumes would be included in the combined Caesalpinioideae p.p.-Mimosoideae subfamily, although some lineages within the clade have once pinnate leaves, and one large genus has phyllodes (which are derived from bipinnate leaves) (Champagne et al., 2007).



http://repository.uwc.ac.za

An alternative to the six subfamily classification would recognize 10–12 subfamilies (Fig. 2C). Although this scheme is consistent with the topology shown in Fig. 2, it is important to note that it depends on resolution that is not well supported and therefore could change. Thus it would be premature to adopt this classification at the present time. We note that this is not the case with the six subfamily option. While the 10–12 subfamilies scheme would allow the Mimosoideae to continue to be recognized, because the relationships in several regions are not stable, the number of subfamilies could increase in the future. The case of Dipsacales is relevant in this regard. The decision to keep apart from Caprifoliaceae the families Dipsacaceae and Valerianaceae before the phylogeny of the order was adequately resolved has necessitated the subsequent recognition of four more families (Backlund and Bremer, 1998; Pyck and Smets, 2004). Even now, the topology of this part of the Dipsacales tree is debated because of incongruence between datasets (Winkworth et al., 2008; Jacobs et al., 2011). Premature decisions can have disruptive consequences in the future, and we wish to avoid these situations as much as possible.

In delimiting subfamilies, inadequate resolution and clade support present a challenge within the strongly supported clade delimited by the most recent ancestor of *Arcoa* and *Peltophorum*. In the six subfamily classification scheme this clade is recognized as a single subfamily. Although this clade as a whole is strongly supported, resolution within is inadequate or weakly supported in several critical areas. In addition to the *Umtiza* grade and the putative close relatives of mimosoids that present problems, the *Tachigali*/*Dimorphandra*/*Peltophorum* clade is also weakly supported. Improving resolution and support in the *Arcoa* to *Peltophorum* clade is the subject of active research and we hope that adequate improvement will be obtained in the near future.

The large number of proposed subfamilies in Fig. 2A is a consequence of the Mimosoideae and Papilionoideae being nested within the Caesalpinioideae, combined with the overall imbalanced topology along the backbone of the phylogeny. There are two regions that are the primary cause of subfamily proliferation. One is the "*Umtiza* grade," which is represented in Fig. 2A as consisting of three unresolved lineages. This group of seven genera (from tribes Cassieae, Detarieae, and Caesalpinieae) was previously referred to as the *Umtiza* clade based on a morphological and molecular analysis (Herendeen et al., 2003b), but in more recent analyses of caesalpinioid phylogeny (based on DNA sequence data only) the group is not supported as monophyletic (Bruneau et al., 2008; Manzanilla and Bruneau, 2012). Three subfamilies would be required to accommodate the three lineages of the *Umtiza* grade as shown in Fig. 2A. In the event that the group is supported as monophyletic in the future it would require one subfamily instead of three.

The other region to note is the clade that includes the Mimosoideae plus *Pachyelasma* and *Erythrophleum* of the *Dimorphandra* group (in some analyses *Diptychandra* and *Moldenhawera* are also included; Manzanilla and Bruneau, 2012). If the traditional Mimosoideae is to be maintained as a subfamily then additional subfamilies would be



http://repository.uwc.ac.za

required to accommodate the other lineages as shown in Fig. 2A. However, relationships in this region are not well supported and vary among recent publications (Bruneau et al., 2008; Simon et al., 2009; Manzanilla and Bruneau, 2012). In addition, species-level sampling in this area remains relatively poor and few characters have been found to support relationships. One proposed solution would be to expand the Mimosoideae to include several of these genera of the *Dimorphandra* group, but doing so would change the image for what constitutes the mimosoid legumes. This is particularly problematic because several of the other genera of the *Dimorphandra* clade, which groups with the *Tachigali* clade and *Peltophorum* clade, more closely resemble mimosoid legumes than do *Diptychandra*, *Moldenhawera*, *Pachyelasma*, and *Erythrophleum*. As a result diagnosability of this modestly expanded Mimosoideae would be particularly challenging. Furthermore, *Dimorphandra* itself is non-monophyletic and relationships among its segregates and these other genera are likely to change in more densely sampled phylogenies.

**6. Dealing with grades**

Naming options for paraphyletic groups were also addressed in the discussion. There was near-universal agreement that only monophyletic groups should be named as tribes and subfamilies (and other Linnaean taxonomic ranks, as well as non-Linnaean classification). Thus, for example, naming the three lineages of the paraphyletic *Umtiza* grade as one subfamily or treating the *Dimorphandra* group lineages subtending Mimosoideae as a subfamily were not viewed as acceptable. An alternative for dealing with these and other regions of problematic or inadequate resolution would be to exclude those taxa from the formal classification. For example, the lineages of the *Umtiza* grade could be called "*Umtiza* grade" in the classification but not named or included in a subfamily. Instead they would be noted as "currently unclassified at the subfamily rank." This approach may be most useful at the tribal level. There are a number of cases where there is a basal grade of genera that are not appropriate for inclusion in the tribe but may not merit recognition of multiple additional small tribes (e.g., basal genera within Millettioids, Phaseoloids, IR-lacking clade). Some of these challenging areas may be solved as future work yields greater phylogenetic resolution, much as many of the unresolved areas in the first version of the APG classification system (APG, 1998) were resolved in subsequent versions (APG II, 2003; APG III, 2009). However, it is inevitable that a number of these regions will remain problematic even after additional data are available. Thus it will be necessary to decide how to treat areas that would result in proliferation of higher taxa.

The discussion participants were asked to vote on several possible choices. In voting on the six subfamily classification approach approximately 50% voted in favor of accepting this system as shown in Fig. 2B. Most of the remaining participants supported moving forward with five of the six subfamilies, leaving the combined Caesalpinioideae p.p.-Mimosoideae clade unclassified pending further study.



http://repository.uwc.ac.za

## 7. How long do we wait?

Discussion participants also addressed the question how long do we wait before moving forward with a new classification? Given the taxonomic and morphological diversity of the family it should not be a surprise that developing a new classification that both reflects phylogeny and is useful to the broader community is complicated and time consuming. And because the family is so important and widely known we do not wish to cause more disruption than is necessary. Additionally, because this is explicitly a community-based effort, we must allow adequate time for legume systematists, especially those who were unable to attend the conference in South Africa, to engage in the discussion and work toward consensus. In addition, preparing other users of the classification for what undoubtedly will be viewed as a major change is an important consideration.

Fortunately, progress is coming rapidly in legume systematics and it seems clear that the legume phylogeny is stabilizing (see LPWG, 2013 for details). Thus we are hopeful that many of the regions of poor resolution will be improved in the near future. Our goal is to publish a new classification within the next 12–24 months. In thinking about the process for presenting a new classification we are reminded that the Angiosperm Phylogeny Group currently has its third version of a classification system for angiosperms (APG III, 2009). We do not need to wait until the phylogeny is fully resolved and stable before presenting a new classification. Progress towards phylogenetic classifications can indeed be incremental providing one keeps the larger phylogenetic picture in mind and makes no decisions that have unintended complications when the phylogeny becomes better resolved. The more immediate challenge is gathering the information from the many published (and in press) phylogenies and reconciling those areas that are not resolved consistently. Preparation of the LPWG (2013) review paper and preparing the draft classification and discussing it and the challenges we faced at the International Legume Conference in Johannesburg have provided an excellent start toward achieving this important goal.

## Acknowledgments

We express our sincere thanks to Ben-Erik Van Wyk, Annah Moteetee, Stephen Boatwright, Marianne le Roux and Helen Long for organizing the International Legume Conference and their assistance in facilitating the classification discussion during the conference. We also thank two anonymous reviewers for their useful comments and suggestions.



http://repository.uwc.ac.za

**References**


APG, 1998. An ordinal classification for the families of flowering plants. Annals of the Missouri Botanical Garden 85, 531–553.

APG II, 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Botanical Journal of the Linnean Society 141, 399–436.

APG III, 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Botanical Journal of the Linnean Society 161, 105–121.

Backlund, A., Bremer, K., 1998. To be or not to be — principles of classification and monotypic plant families. Taxon 47, 391–401.

Bruneau, A., Forest, F., 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.

Cardoso, D., de Queiroz, Pennington, R.T., de Lima, H.C., Fonty, E., Wojciechowski, M.F., Lavin, M., 2012. Revisiting the phylogeny of papilionoid legumes: new insights from comprehensively sampled early-branching lineages. American Journal of Botany 99, 1991–2013.

Champagne, C.E.M., Goliber, T.E., Wojciechowski, M.F., Mei, R.W., Townsley, B.T., Wang, K., Paz, M.M., Geeta, R., Sinha, N.R., 2007. Compound leaf development and evolution in the legumes. The Plant Cell 19, 3369–3378.

Chappill, J.A., 1995. Cladistic analysis of the Leguminosae: the development of an explicit hypothesis. In: Crisp, M.D., Doyle, J.J. (Eds.), Advances in Legume Systematics 7. Royal Botanic Garden, Kew, pp. 1–9.

Doyle, J.J., Chappill, J.A., Bailey, C.D., Kajita, T., 2000. Towards a comprehensive phylogeny of legumes: evidence from *rbcL* sequences and non-molecular data. In: Herendeen, P.S., Bruneau, A. (Eds.), Advances in Legume Systematics 9. Royal Botanic Gardens, Kew, pp. 1–20.

Funk, V.A., Susanna, A., Stuessy, T.F., Bayer, R.J. (Eds.), 2009. Systematics, Evolution, and Biogeography of Compositae. International Association for Plant Taxonomy.

Grass Phylogeny Working Group, 2001. Phylogeny and subfamilial classification of the grasses (Poaceae). Annals of the Missouri Botanical Garden 88, 373–457.

Herendeen, P.S., Bruneau, A., Lewis, G.P., 2003a. Phylogenetic relationships in the caesalpinioid legumes: a preliminary analysis based on morphological and molecular data. In: Bruneau, A., Klitgaard, B.B. (Eds.), Advances in Legume Systematics 10. Royal Botanic Gardens, Kew, pp. 37–62.

Herendeen, P.S., Lewis, G.P., Bruneau, A., 2003b. Floral morphology in caesalpinioid legumes: testing the monophyly of the "Umtiza" clade. International Journal of Plant Sciences 164, S393–S407.

Hibbett, D.S., Binder, M., Bischoff, J.F., Blackwell, M., Cannon, P.F., Eriksson, O.E., Huhndorf, S., James, T., Kirk, P.M., Lücking, R., Lumbsch, H.T., Lutzoni, F., Matheny, P.B., McLaughlin, D.J., Powell, M.J., Redhead, S., Schoch, C.L., Spatafora, J.W., Stalpers,




http://repository.uwc.ac.za

J.A., Vilgalys, R., Aime, M.C., Aptroot, A., Bauer, R., Begerow, D., Benny, G.L., Castlebury, L.A., Crous, P.W., Dai, Y.-C., Gams, W., Geiser, D.M., Griffith, G.W., Gueidan, C., Hawksworth, D.L., Hestmark, G., Hosaka, K., Humber, R.A., Hyde, K.D., Ironside, J.E., Kõljalg, U., Kurtzman, C.P., Larsson, K.-H., Lichtwardt, R., Longcore, J., Miadlikowska, J., Miller, A., Moncalvo, J.-M., Mozley-Standridge, S., Oberwinkler, F., Parmasto, E., Reeb, V., Rogers, J.D., Roux, C., Ryvarden, L., Sampaio, J.P., Schüßler, A., Sugiyama, J., Thorn, R.G., Tibell, L., Untereiner, W.A., Walker, C., Wang, Z., Weir, A., Weiss, M., White, M.M., Winka, K., Yao, Y.-J., Zhang, N., 2007. A higher-level phylogenetic classification of the fungi. Mycological Research 111, 509–547.

Humphreys, A.M., Linder, H.P., 2009. Concept versus data in delimitation of plant genera. Taxon 58, 1054–1074.

Jacobs, B., Geuten, K., Pyck, N., Huysmans, S., Jansen, S., Smets, E., 2011. Unraveling the phylogeny of *Heptacodium* and *Zabelia* (Caprifoliaceae): an interdisciplinary approach. Systematic Botany 36, 231–252.

Kajita, T., Ohashi, H., Tateishi, Y., Bailey, C.D., Doyle, J.J., 2001. *rbcL* and legume phylogeny, with particular reference to Phaseoleae, Millettieae, and allies. Systematic Botany 26, 515–536.

Käss, E., Wink, M., 1996. Molecular evolution of the Leguminosae: phylogeny of the three subfamilies based on rbcL-sequences. Biochemical Systematics and Ecology 24, 365–378.

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, 575–594.

Lewis, G.P., Schrire, B.D., Mackinder, B., Lock, M. (Eds.), 2005. Legumes of the World. Royal Botanic Gardens, Kew.

Lewis, G.P., Schrire, B.D., Mackinder, B.A., Rico, L., Clark, R., 2013. A linear sequence of legume genera set in a phylogenetic context — a tool for collections management and taxon sampling. South African Journal of Botany 89, 76–84 (this issue).

LPWG [Legume Phylogeny Working Group], 2013. Legume phylogeny and classification in the 21st century: progress, prospects and lessons for other species-rich clades. Taxon 62, 217–248.

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.

McNeill, J., Turland, N.J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herenden, P.S., Knapp, S., Marhold, K., Prado, J., Prud'homme Van Reine, W.K., Smith, G.F., Wiersema, J.H., Turland, N.J. (Eds.), 2012. International Code of Nomenclature for algae, fungi, and plants. Adopted by the Eighteenth International Botanical Congress, Melbourne, July 2011. Regnum Vegetabile 154. A.R.G. Gantner Verlag, Ruggell.

Polhill, R.M., 1994. Classification of the Leguminosae and complete synopsis of legume genera. In: Bisby, F.A., Buckingham, J., Harborne, J.B. (Eds.), Phytochemical Dictionary of the Leguminosae. Chapman & Hall, Cambridge, pp. xxxv–lvii.



http://repository.uwc.ac.za

Polhill, R.M., Raven, P.H. (Eds.), 1981. Advances in Legume Systematics 1. Royal Botanic Gardens, Kew.

Polhill, R.M., Raven, P.H., Stirton, C.H., 1981. Evolution and systematics of the Leguminosae. In: Polhill, R.M., Raven, P.H. (Eds.), Advances in Legume Systematics 1. Royal Botanic Gardens, Kew, pp. 1–26.

Pyck, N., Smets, E., 2004. On the systematic position of *Triplostegia* (Dipsacales): a combined molecular and morphological approach. Belgian Journal of Botany 137, 125–139.

Simon, M.F., Grether, R., De Queiroz, L.P., Skemae, C., Pennington, R.T., Hughes, C.E., 2009. Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. Proceedings of the National Academy of Sciences of the United States of America 106 (48), 20359–20364.

Stevens, P.F., 2006. An end to all things? — plants and their names. Australian Systematic Botany 19, 115–133.

Vences, M., Guayasamin, J.M., Miralles, A., de la Riva, I., 2013. To name or not to name: criteria to promote economy of change in Linnaean classification schemes. Zootaxa 3636, 201–244.

Winkworth, R.C., Bell, C.D., Donoghue, M.J., 2008. Mitochondrial sequence data and Dipsacales phylogeny: mixed models, partitioned Bayesian analyses, and model selection. Molecular Phylogenetics and Evolution 46, 830–843.

Wojciechowski, M.F., 2003. Reconstructing the phylogeny of legumes (Leguminosae): an early 21st century perspective. In: Klitgaard, B.B., Bruneau, A. (Eds.), Advances in Legume Systematics 10. Royal Botanic Gardens, Kew, pp. 5–35.

Wojciechowski, M.F., 2013. Towards a new classification of Leguminosae: incorporating non-Linnean phylogenetic nomenclature. South African Journal of Botany 89, 85–93 (this issue).

Wojciechowski, M.F., Lavin, M., Sanderson, M.J., 2004. A phylogeny of the legumes (Leguminosae) based on analysis of the plastid *matK* gene sequences resolves many well-supported subclades within the family. American Journal of Botany 91, 1846–1862.

Yahara, T., Javadi, F., Onoda, Y., de Queiroz, L.P., Faith, D.P., Prado, D.E., Akasaka, M., Kadoya, T., Ishihama, F., Davies, S., Ferry Slik, J.W., Yi, T., Ma, K., Bin, C., Darnaedi, D., Pennington,

R.T., Tuda, M., Shimada, M., Ito, M., Egan, A.N., Buerki, S., Raes, N., Kajita, T., Mimura, M., , Nkonki, T., 2013. Global legume diversity assessments: concepts, key indicators, and strategies. Taxon 62, 249–266.



http://repository.uwc.ac.za