



On *Calliandra* and *Afrocalliandra* (Fabaceae-Caesalpinioideae)

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Abstract

The history of the genus *Calliandra* is reviewed, with particular reference to the two African species *C. gilbertii* and *C. redacta*. These species have been segregated as *Afrocalliandra*, based on proposed differences from a neotropical *Calliandra*. The stated differences are acalymmate, 7-celled (versus calymmate, 8-celled) polyads, presence (versus absence) of extrafloral nectaries, and presence (versus absence) of spines or thorns. A scrutiny of these claims shows that neither number of cells in the polyads, nor extrafloral nectaries, nor armature can be used to separate the two African species from the rest of the genus. The only remaining difference is the acalymmate polyads, a plesiomorphic state among mimosoids. On the contrary, a circumscription of *Calliandra* that includes also the two African species is, apart from being robustly supported by molecular data, also very strongly supported morphologically by 8-celled asymmetrical polyads with tail cells provided with viscin bodies (which are unique among legumes), by expanded stigmas with a wide area of polyad receptivity (which are unique among mimosoids), and by sagittate, petiolate and persistent cotyledons. A return to a circumscription of *Calliandra* that includes also the two African species is therefore proposed. *Calliandra* is subdivided into subg. *Calliandra*, with ca. 140 species in the Neotropics, and subg. *Afrocalliandra*, *comb. et stat. nov.*, with *C. gilbertii* in Somalia and Kenya, and *C. redacta* in South Africa.

Keywords: morphology, new combination, taxonomy

Introduction

The genus *Calliandra* Benth (1840: 138) comprised 18 species when established, all confined to the New World, but only four years later the number of species had risen to 60 (Benth 1844). Characters for *Calliandra* included bipinnate leaves, capitate inflorescences, numerous long-exserted stamens basally united into a tube and, in particular, pods with the valves elastically opening from the apex to the base.

Later, the genus was expanded to include also four Asian species, *Calliandra cynometroides* Beddome (1873: t. 317), *C. geminata* (Wight & Arnott 1834: 269) Benth (1875: 548), *C. griffithii* Benth (1875: 537), and *C. umbrosa* (Wallich 1830: t. 124) Benth (1875: 537), as well as several species from Madagascar, the first one *C. alternans* Benth (1875: 548). Two species from continental Africa were added by Thulin *et al.* (1981): *C. gilbertii* Thulin & Hude in Thulin *et al.* (1981: 27) from Kenya and Somalia, and *C. redacta* (Ross 1974: 231) Thulin & Hude in Thulin *et al.* (1981: 29) from South Africa.

Already Engler (1876) commented on the heterogeneity of the pollen in *Calliandra*, with some species having 8-celled and others 16-celled polyads. Guinet (1965) recognized these types as group I (circular 16-celled polyads) and group II (elongated 8-celled polyads). Within group I, Guinet further recognized IA for the species in Asia and Madagascar, and IB for the species in the Neotropics. Group II was restricted to species from the Neotropics.

When the pollen morphology of the two species from continental Africa was compared with other members of *Calliandra*, as well as with other mimosoids, it was obvious that the 8-celled polyads of these species are most similar to the neotropical species of group II, by having all cells in one plane, by having heteromorphic cells with the central ones much smaller, and by having a tail cell with a mucilage coating (Thulin *et al.* 1981). However, the two African species were found to differ from their neotropical counterparts by having the cells of the polyads free from each other (acalymmate polyad) and provided with proximal (internal) pores. Thulin *et al.* (1981) speculated that the calymmate condition found in the polyads of the neotropical species should be the derived state in relation to the acalymmate polyads in the African species. Niezgodna *et al.* (1983), without knowing about the existence of the two African species,

took a similar view and stated about the polyads in *Calliandra* that “the calymmate condition may have been recently derived from an acalymmate state characterizing most mimosoids”.

The pods of the two continental African species have elastically opening valves, just as in *Calliandra* in general. However, Thulin *et al.* (1981) pointed out that similar pods are found also in unrelated mimosoids, where they must have evolved in parallel. Further examples of mimosoids with elastically dehiscent pods were provided by Hernández & Guinet (1990), and according to Ringelberg *et al.* (2022), such pods have evolved at least six times independently across mimosoids.

Segregates of *Calliandra*

Hernández (1986) segregated the species of Guinet’s group IB as the new genus *Zapoteca* Hernández (1986: 757) with about 25 species in tropical America, and provided new combinations for seven of them. The remaining neotropical species plus the two species from Africa, Guinet’s group II, formed *Calliandra* sensu stricto, whereas the species from Madagascar and India (Guinet’s group IA) were said to be in need of further critical study.

Besides the palynological differences between *Calliandra* and *Zapoteca*, Hernández (1986, 1989) also pointed to striking differences in, for example, the cotyledons (sagittate, petiolate, fleshy, and persistent in *Calliandra* versus ovate, sessile, foliaceous, and ephemeral in *Zapoteca*) and the shape and function of the stigmas (expanded, discoid or capitate with a wide area of polyad receptivity in *Calliandra*, versus cup-shaped with a narrow area of receptivity that can hold only a single polyad in *Zapoteca*).

Barneby (1998), in a monograph of *Calliandra*, included about 130 species in the genus, all from the Neotropics, whereas all Old World species were rejected, even though he did not place them in segregate genera at this point. Over the subsequent 15 years, the majority of the Old World species of *Calliandra* sensu Bentham (1875) have been placed in a series of segregate genera. *Viguieranthus* Villiers (2002: 271) was established for 18 species mainly on Madagascar, eight of them previously in *Calliandra* and ten newly described. For the Asian species, *C. geminata* was placed in synonymy of *Thailentadopsis nitida* (Vahl 1791: 103) Lewis & Schrire (2003: 492), and the new segregate genus *Sanjappa* Souza & Krishnaraj in Souza *et al.* (2016: 6) was established to accommodate the Indian *C. cynometroides* as *S. cynometroides* (Bedd.) Souza & Krishnaraj in Souza *et al.* (2016: 6). The two Asian species *C. griffithii* and *C. umbrosa*, treated as a single species with two subspecies by Paul (1979), are still unplaced outside *Calliandra*, as is an undescribed Asian species discussed by Ringelberg *et al.* (2022: 52).

The African species *Calliandra gilbertii* and *C. redacta* were generally accepted as transatlantically disjunct members of *Calliandra* until Barneby (1998) restricted the genus to the neotropical members only. The only reason given by Barneby (1998) for excluding these two “so-called calliandras in the Old World”, apart from their African origin, was that “their acalymmate pollen is discordant”.

Souza *et al.* (2013), based on both nuclear and plastid markers, made the first detailed phylogenetic study of *Calliandra* in a wide sense. The sampling included seven species of *Zapoteca*, six species of *Viguieranthus*, and two species of *Thailentadopsis* Kostermans (1977: 131). These three genera were all retrieved as well supported outside *Calliandra*. The 95 species sampled of *Calliandra*, including the two African species, formed a strongly supported clade within which was nested a sample of *Guinetia tehuantepecensis* Rico & Sousa in Rico Arce *et al.* (1999: 977).

Guinetia Rico & Sousa in Rico Arce *et al.* (1999: 977), a monotypic genus in Mexico, was said to differ from *Calliandra* by having pods initially dehiscent along one margin only. Otherwise, it agrees with *Calliandra* by having 8-celled polyads with a mucilaginous tail cell (“basal cell” with a “very reduced sticky appendage”), and by having sagittate, petiolate cotyledons (Rico Arce *et al.* 1999: Fig. 1L). The polyads of *Guinetia* are calymmate (Rico Arce *et al.* 1999) as in neotropical *Calliandra*. Given that it is deeply nested within *Calliandra* in their phylogeny, *Guinetia tehuantepecensis* was transferred to *Calliandra* by Souza *et al.* (2013), who regarded the deviating dehiscence of the pods in this species as a reversal.

Calliandra* versus *Afrocalliandra

Within *Calliandra*, the two African species formed a strongly supported clade sister to the rest of the genus in the study by Souza *et al.* (2013). The authors decided to handle this by placing the African species in the new genus *Afrocalliandra* Souza & Queiroz in Souza *et al.* (2013: 1213), as *A. gilbertii* (Thulin & Hilde) Souza & Queiroz in Souza *et al.* (2013: 1213) and *A. redacta* (J.H.Ross) Souza & Queiroz in Souza *et al.* (2013: 1213). Their main argument was the criterion of morphological diagnosability: “If we had chosen to include the species of the African clade in a more broadly circumscribed *Calliandra*, this would have rendered *Calliandra* to lack any clear-cut synapomorphy

and virtually lacking diagnostic characters with respect to *Zapoteca*, *Viguieranthus* and *Thailentadopsis*” (Souza *et al.* 2013: 1211). But what are the facts behind this statement?

First, they again pointed to the acalymmate polyads in the African species versus the calymmate polyads in the rest of *Calliandra*. However, they also stated that the polyads in the African species are 7-celled versus 8-celled in the rest of *Calliandra*. This is made without any discussion and no mention of the fact that the polyads in the African species have previously always been described as 8-celled or normally 8-celled. Robbertse & Von Teichman (1979), who studied numerous polyads of *C. redacta* (as *Acacia redacta* J.H.Ross) found the polyads to be 7–10-celled with 8 cells as the most common state. Guinet & Hernández (1989) even reported occasional tetrads among the polyads of *C. gilbertii*. Uneven or deviating numbers of cells in polyads are not uncommon among mimosoids (Guinet & Grimes 1997), and in the case of *Calliandra*, the much smaller central cells (Thulin *et al.* 1981) may also be difficult to see.

Second, Souza *et al.* (2013) stated that the African species of *Calliandra* differ from the rest of the genus by the presence of extrafloral nectaries. However, this is mistaken. No extrafloral nectaries were recorded in the African species by Thulin *et al.* (1981), and according to Marazzi *et al.* (2019), extrafloral nectaries are lacking in both *Afrocalliandra* and *Calliandra*, as well as in their immediate sister genus (Ringelberg *et al.* 2022) *Acaciella* Britton & Rose (1928: 96).

Third, the African species have spines or thorns that are lacking in *Calliandra* according to Souza *et al.* (2013). The South African *C. redacta* indeed has stipules that are modified into thorns, but such stipules are also found in neotropical *Calliandra*, in a species endemic to Cuba, as is acknowledged by Souza *et al.* (2013: 1213) themselves. *Calliandra redacta* and the Cuban plant are both confined to arid habitats and the spinescent stipules in these two species have obviously evolved in parallel. In *C. gilbertii*, the second African species, the stipules are herbaceous, whereas the lateral branches become more or less spinescent at the ends, an apparent autapomorphy for this species. However, also in this case there is a neotropical parallel in *C. spinosa* Ducke (1959: 289), a species of the caatinga of northeastern Brazil with “terete long-shoots tapering at apex into a stout vulnerant thorn” (Barneby 1998: 95).

In summary, neither number of cells in the polyads, nor extrafloral nectaries, nor armature, the three morphological differences used by Souza *et al.* (2013) to distinguish *Afrocalliandra*, can be used to separate the two African species of *Calliandra* from the rest of the genus. The “criterion of morphological diagnosability” for *Afrocalliandra* as stated by Souza *et al.* (2013) therefore is not fulfilled. But what about their statement that a broadly circumscribed *Calliandra* that includes the African species would lack any clear-cut synapomorphy and virtually lack diagnostic characters?

First, the 8-celled asymmetrical polyads of such a widely circumscribed *Calliandra* are markedly different from the 16-celled radially symmetrical polyads of *Zapoteca*, *Viguieranthus*, *Sanjappa*, and *Thailentadopsis*. Furthermore, it is not only the number of cells that differs, but also that the polyads of *Calliandra* and *Afrocalliandra* share a distinctive asymmetrical, tear-shaped outline and the presence of a highly modified tail cell with an acuminate apex. This tail cell has a mucilage coating, a “viscin body” according to the terminology used by Greissl (2006). A polyad of a neotropical species of *Calliandra* was described and illustrated in remarkable detail by Mohl (1834), an illustration that was reproduced by Greissl (2006). These large 8-celled asymmetrical polyads were described as standing upright in the anthers with the sticky appendage at the end attaching to visitors of the flowers (Mohl 1834). The form and ontogeny of the polyads in *Calliandra*, and particularly the viscin body and its function, were further described and discussed by Greissl (2006), whereas Teppner & Stabentheiner (2007) provided details on the unique mode of anther opening and polyad presentation in the genus. *Calliandra* has a wide range of pollinators including members of Hymenoptera and Lepidoptera, hummingbirds, and bats. The viscin body can attach to surfaces of very different structure and plays a crucial role in the pollination process. Furthermore, after the transportation phase, during the contact between polyad and stigma, the polyad is laid down with its flat side on the stigmatic surface, with the viscin body acting as an articulation to allow the best possible contact between the polyad and the stigmatic exudate. The mucilage or viscin bodies of *Calliandra*, which are also found in the polyads of the two African species (Thulin *et al.* 1981: Fig. 3G), is apparently a feature that is unique among legumes, but analogous features are found among angiosperms in the pollinia of Orchidaceae and Apocynaceae (Greissl 2006).

Second, as pointed out by Hernández (1986, 1989), the stigmas in *Calliandra* are expanded, discoid or capitate with a wide area of polyad receptivity, and this also applies to the two African species (Thulin *et al.* 1981). In contrast, the species of *Zapoteca* have cup-shaped stigmas with a very narrow area of receptivity that can hold only a single polyad. Narrow cup-shaped stigmas were found in all other mimosoids studied (Hernández 1986), whereas the expanded stigma in *Calliandra* apparently is a unique synapomorphy for this genus, including the African species.

Third, Hernández (1986, 1989) pointed out that the cotyledons of *Calliandra* are sagittate, petiolate, fleshy, and persistent compared to the elliptic to ovate, sessile, foliaceous, and ephemeral cotyledons in *Zapoteca*. The cotyledons of 31 species of *Calliandra*, all of them neotropical, were studied by Hernández (1986). However, the cotyledons

of the two African species are also sagittate and petiolate, and closely match those of their neotropical counterparts (Robbertse & Von Teichman 1979: 12, Fig. 1B; Thulin *et al.* 1981: 30, Fig. 2B). Sagittate and petiolate cotyledons are found also in other mimosoids, such as in the unrelated monotypic *Calliandropsis* Hernández & Guinet (1990: 609) in Mexico, but information on cotyledons is lacking for many genera, which makes comparisons difficult. Nevertheless, it is clear that neotropical and African *Calliandra* share the same type of cotyledons.

Following Souza *et al.* (2013), the Legume Phylogeny Working Group (LPWG 2017) published a phylogenetic study based on plastid *matK* sequences focusing on the whole Fabaceae family. The two African species together were again resolved as sister to the neotropical members of *Calliandra*, just as in Souza *et al.* (2013). The same result was obtained in the much more detailed study by Ferm *et al.* (2021), focusing on “the ingoid clade” and based on both nuclear and plastid regions. In this analysis, the grouping with *Calliandra* and *Afrocalliandra* together was retrieved with strong support, and the African and neotropical clades were both strongly supported as well. Using a DNA sequence dataset that is an order of magnitude larger, Ringelberg *et al.* (2022) confirmed the sister group relationship between *Calliandra* and *Afrocalliandra*. There is thus no doubt that these two lineages together form a very robustly supported clade.

Conclusion

In conclusion, rather than lacking any clear-cut synapomorphy and diagnostic characters as stated by Souza *et al.* (2013), a broadly circumscribed *Calliandra*, including the two African species, is not only robustly supported by molecular data, but is also very strongly supported morphologically by 8-celled asymmetrical polyads with tail cells provided with viscin bodies (which are unique among legumes), by expanded stigmas with a wide area of polyad receptivity (which are unique among mimosoids), and by sagittate, petiolate and persistent cotyledons. In the taxonomy proposed by Souza *et al.* (2013), this strongly supported group is left without a name, whereas a grouping of the two African species, which can be recognized only by having acalymmate polyads, a plesiomorphic state among mimosoids, is given generic rank. Using the same criterion as Souza *et al.* (2013), i.e., morphological diagnosability, it is here instead proposed to return to a circumscription of *Calliandra* that includes the two African species. Following the suggestion by Guinet & Hernández (1989), *Calliandra* is here divided into two subgenera, with the two African species in *Calliandra* subg. *Afrocalliandra*.

Nomenclature and taxonomy

Calliandra Benth (1840: 138), *nom. cons.*

Type:—*Calliandra houstoniana* (Miller 1768: *Mimosa* no. 16) Standley (1922: 386), *typ. cons.*

Calliandra subg. *Calliandra*

Ca. 140 species in the Neotropics, subdivided into six sections according to Souza *et al.* (2013).

Calliandra subg. *Afrocalliandra* (Souza & Queiroz) Thulin, *comb. et stat. nov.*

≡ *Afrocalliandra* Souza & Queiroz in Souza *et al.* (2013: 1213).

Type:—*Calliandra redacta* (Ross 1974: 231) Thulin & Hunde (1981: 29).

Two species in continental Africa, *Calliandra gilbertii* in Somalia and Kenya, and *C. redacta* in South Africa.

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