Further disintegration and redefinition of *Clerodendrum* (Lamiaceae): Implications for the understanding of the evolution of an intriguing breeding strategy

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Abstract The genus *Clerodendrum* s.l. is polyphyletic. Although recent studies have resulted in C. subg. Cyclonema and C. sect. *Konocalyxx* being removed to the resurrected genus *Rotheca*, and the unspecific genus *Huxleya* being sunk into *Clerodendrum*, it has been unclear whether *Clerodendrum* as currently circumscribed is monophyletic, particularly in relation to the American genera *Aegiphila*, *Amasonia*, and *Tetraclea*. This phylogenetic study employs four relatively fast-evolving chloroplast DNA regions, *trnT-L*, *trnL-F*, *trnD-T*, and *trnS-fM*, to clarify the generic boundaries of *Clerodendrum* and its relationship to allied genera. The results corroborate previous studies that there are three well-supported clades in the currently recognized *Clerodendrum*: an Asian clade, an African clade, and a Pantropical Coastal clade. The Asian clade and African clade are sister groups and together form a monophyletic group. However, the Pantropical Coastal clade is more closely related to the three American genera than it is to the other two *Clerodendrum* clades. In addition, a Caribbean species, *C. spinosum*, is found to be more closely related to the American genera than it is to any of the three major *Clerodendrum* groups. These results indicate that *Clerodendrum* as currently circumscribed is not monophyletic. We propose to separate the Pantropical Coastal clade and *C. spinosum* by reviving the genera *Volkameria* (including *Huxleya*) and *Ovieda*, respectively for these, and to restrict *Clerodendrum* to the Asian and African clades. Brief descriptions of the genera to be recognized are provided. All Neotropical ‘*Clerodendrum*’ taxa are referred to other genera, necessitating six new combinations, which are also provided, where required, for two other well-studied Old World *Volkameria* species; all names ever used in *Ovieda* are given their modern placings (two placed newly in synonymy). The study also sheds light on the evolution of an intriguing breeding strategy that avoids self-pollination or/and sexual interference. This strategy involves presentation of pollen and stigma in the centre of the flower in a sequential fashion by moving the filaments and style. It appears to have evolved in the common ancestor of *Clerodendrum*, *Volkameria*, *Ovieda*, *Amasonia*, *Tetraclea*, *Aegiphila* and *Kalalharia*, and still occurs in all of these taxa except *Aegiphila*, where it has been succeeded by a heterostylos system.

Keywords *Aegiphila*; breeding strategy; chloroplast DNA; *Clerodendrum*; *Huxleya*; *Ovieda*; phylogeny; *Volkameria*

### INTRODUCTION

The genus *Clerodendrum* L. as delimited by nineteenth-century botanists (Schauer, 1847; Briquet, 1895) is heterogeneous. However, this delimitation has been followed reasonably closely by subsequent authors, even though they recognized it to be problematic (Lam, 1919; Thomas, 1936; Moldenke, 1985; Verdourt, 1992). Cladistic analyses of morphological data (Cantino, 1992; Rimpler & al., 1992) provided preliminary evidence that *Clerodendrum* sensu lato (s.l.) was not monophyletic. But these analyses, primarily focused at subfamily or family level, included relatively few *Clerodendrum* s.l. species and did not provide good resolution of relationships within *Clerodendrum* s.l. or between the genus and other related ones. Phylogenetic studies based on chloroplast DNA (cpDNA) restriction site data (Steane & al., 1997) and nuclear ITS sequences (Steane & al., 1999), with extensive sampling within *Clerodendrum* s.l. and related genera, strongly suggested that *Clerodendrum* s.l. is polyphyletic. Subsequently, a number of species comprising the C. subg. *Cyclonema* (Hochst.) Gürke and C. sect. *Konocalyxx* (Thomas) Verdc. were removed to the resurrected genus *Rotheca* Raf. (Steane & Mabberley, 1998). In addition, the molecular studies divided *Clerodendrum* (sensu Steane & Mabberley, 1998) into three major clades that are in general associated with geographic distribution: an Asian clade, an African clade, and a Pantropical Coastal clade (Fig. 1A).

A more recent study (Steane & al., 2004) which included three New World genera, *Aegiphila* Jacq., *Amasonia* L.f., and *Tetraclea* A.Gray, and a unspecific Australian genus *Huxleya* Ewart, put the delimitation of *Clerodendrum* (sensu Steane & Mabberley, 1998) into question again. *Huxleya* was found nested within the Pantropical Coastal clade and therefore was sunk into the genus *Clerodendrum* (Steane & al., 2004). The African and Asian clades were still recovered as sister groups and together formed a monophyletic group (Fig. 1B). The three New World genera, *Aegiphila*, *Amasonia*, and *Tetraclea*, each
represented by a single species in that study, formed a New World clade. However, the relationships among the New World clade, the Pantropical Coastal Clerodendrum, and the remaining Clerodendrum species (Asian + African), were unresolved (Steane & al., 2004; Fig. 1B), leaving the possibility that Clerodendrum (sensu Steane & al., 2004) as currently circumscribed is paraphyletic in relation to the clade of New World genera. In addition, the phylogenetic framework presented in those studies (Steane & al., 1997, 1999, 2004) is mainly based on cpDNA restriction site data and nuclear ITS sequences, with only a few chloroplast ndhF sequences. It is difficult to add more data to a restriction site dataset, due to the nature of this type of marker. For many Clerodendrum species the ITS region is difficult to sequence directly without cloning, possibly because of their being polyploids, which is indicated by the high chromosome number, \(2n = 46, 48, \text{or} 52\), of most species (see the Index to Plant Chromosome Numbers Database, http://mobot.mobot.org/W3T/Search/ipcn.html).

The major objectives of this paper are, therefore, to: (1) test the monophyly of Clerodendrum as currently circumscribed; (2) present a phylogenetic framework of Clerodendrum and its related genera based on cpDNA sequence data, to which additional sequence data may be added easily in future studies; and (3) use this phylogenetic framework to examine the evolution of morphological characters.

**MATERIALS AND METHODS**

Our sampling included 40 species of Clerodendrum (sensu Steane & al., 2004), representing the three major clades identified in previous studies, 13 species from six closely related genera (Aegiphila, Amasonia, Tetraclea, Kalaharia Baill., Oxera Labill., Faradaya F. Muell.), and three species from more distantly related genera in the Lamiaceae-Ajugoideae (Ajuga L., Teucrium L., Rotheca). Voucher information for these 56 samples is listed in Appendix 1.

Total genomic DNA was extracted from either silica-gel dried leaf tissue or herbarium specimens using the modified CTAB method (Doyle & Doyle, 1987). Four relatively fast-evolving non-coding cpDNA regions (Shaw & al., 2005) were chosen for sequencing. These were \(\text{trnD-trnT}\), \(\text{trnT-trnL}\), \(\text{trnL-trnF}\) (\(\text{trnL}\) intron and \(\text{trnL}-\text{F}\) intergenic spacer), and \(\text{trnS-trnF}\). PCR and sequencing primers with corresponding references are listed in Appendix 2. Procedures for PCR and sequencing are described in Yuan & Olmstead (2008). Sequences of the two outgroup species, *Verbena officinalis* L., *Aloysia virgata* (Ruiz & Pav.) Pers., are from Yuan & Olmstead (2008), while sequences of all other species were generated in this study and have been deposited in GenBank (\(\text{trnD-trnT}\): EU160617–EU160666, FJ951910–FJ951915; \(\text{trnT-trnL}\): FJ951916–FJ951970; \(\text{trnL-trnF}\): FJ951971–FJ952025; \(\text{trnL-trnF}\): FJ952026–FJ952081).

Sequence alignments were made manually using Se-Al v.2.0a11 (Rambaut, 1996) based on the similarity criterion (Simmons, 2004). The four cpDNA regions were combined as a single dataset for phylogenetic analyses because these regions are part of the haploid chloroplast genome and, therefore, share the same evolutionary history. Phylogenetically informative insertions/deletions (indels) were coded as binary characters using the simple gap coding method (Graham & al., 2000; Simmons & Ochoterena, 2000) and appended to the end.
of the dataset. Six poly-nucleotide or microsatellite regions (a microsatellite with “AT” repeats and a poly-T region in the trnD-trnF segment, two poly-T regions in the trnT-trnL segment, a poly-A region in the trnL-trnF segment, and a poly-C/T/G region in the trnF-M-trnS segment) have been excluded from analyses due to uncertainty of homology assessment. Both parsimony and Bayesian analyses were performed on the final dataset.

Parsimony analysis was conducted using PAUP* v.4.0b10 (Swofford, 2002). Heuristic searches were performed with 1000 random stepwise addition replicates and TBR branch swapping with the MULTREES option in effect. Nodal support was determined by bootstrap analyses (Felsenstein, 1985) of 500 replicates, each with 20 random stepwise addition replicates and TBR branch swapping with MULTREES on.

Bayesian analyses were conducted using MrBayes v.3.1.2 (Ronquist & Huelsenbeck, 2003). A mixed-model approach (Ronquist & Huelsenbeck, 2003) was employed to integrate the phylogenetically informative gaps as binary characters with nucleotide data. The final dataset was divided into two partitions, the “nucleotide” partition and “gap” partition. We used Akaike information criterion (AIC) implemented in Modeltest v.3.7 (Posada & Crandall, 1998) to determine the model of sequence evolution that best fits the “nucleotide” partition (GTR + G). The restriction site (binary) model in MrBayes v.3.1.2 (Ronquist & Huelsenbeck, 2003) was used for the “gap” partition, with ascertainment bias for gap characters incorporated (iset coding = informative). We performed two independent runs of 1,000,000 generations from a random starting tree using the default priors and four Markov chains (one cold and three heated chains), sampling one tree every 100 generations. Plots of log likelihood scores were used to determine stationarity and trees from the first 100,000 generations were discarded as burn-in.

■ RESULTS

The final dataset consisted of 44 scored gap characters and 4002 aligned nucleotides, of which 127 from the six poly-nucleotide or microsatellite regions were excluded due to uncertainty of homology assessment. One of the eight maximum parsimony trees resulting from parsimony analysis is shown in Fig. 2. The results are consistent with previous studies (Steane & al., 1997, 1999) in that Clerodendrum sensu Steane & al. (2004) is divided into three major clades: an African clade, an Asian clade, and a Pantropical Coastal clade. All three clades are strongly supported sister groups (100%/1.0, BB/PP), whereas the Pantropical Coastal Clerodendrum clade is sister to the New World clade (97%/1.0, BS/PP). Also consistent with previous studies (Steane & al., 2004), Kalaharia, a unispecific African genus, is recovered as sister group of the larger clade that includes all three Clerodendrum groups and the New World clade. The Oxera/Faraday clade is sister to the even more inclusive clade including Kalaharia (Fig. 2).

Within the Asian clade, relationships are fairly well resolved. One strongly supported monophyletic group, in particular, is worth mentioning. It consists of species (C. floribundum, C. indicum [type of Siphonanthus L.], C. minahassae, C. quadriloculare, C. tomentosum) that are characterized by an extremely long and narrow corolla tube (99%/1.0, BS/PP; Fig. 2), probably an adaptation to a particular type of pollinator. Within the African clade, however, relationships are poorly resolved but it is noticeable that one species, C. hildebrandtii, is strongly supported as sister to the rest of the African group (Fig. 2). Within the Pantropical Coastal clade, branches are short, indicating little sequence diversification between species. Within the New World clade, both Aegiphila and Amasonia are strongly supported monophyletic groups (Fig. 2). Tetraclea is resolved to be the sister lineage of Amasonia, but this relationship is only weakly supported (52%/0.49, BS/PP, these values are not shown in Fig. 2). Likewise, Clerodendrum spinosum is recovered as sister to the Amasonia/Tetraclea clade, but weakly supported (52%/0.78, BS/PP).

Bayesian analyses gave very similar results. The only difference between the Bayesian majority consensus tree and parsimony tree shown in Fig. 2 is on the relationship between Aegiphila anomala, A. alba, the A. hassleri + A. brachiata clade, and the A. elata + A. martinicensis clade, but neither the relationship suggested by parsimony analyses nor that indicated by Bayesian inference is well supported (BS < 50%, PP < 0.7).

■ DISCUSSION

Redefinition of Clerodendrum and revival of Volkameria and Ovieda. — Clerodendrum as currently circumscribed (Steane & Mabberley, 1998; Steane & al., 2004) is certainly not monophyletic (Fig. 2). In order to delimit Clerodendrum as a monophyletic group, either the New World clade should be incorporated in Clerodendrum or the Pantropical Coastal clade should be removed from Clerodendrum and raised to generic level. Renaming species will therefore be inevitable. We choose the second option here for two reasons: (1) Aegiphila, Amasonia, and Tetraclea, have ca. 120, 8, and 2 species, respectively, whereas the Pantropical Coastal clade comprises ca. 30 species. To minimize the number of name changes, it is more sensible to separate the Pantropical Coastal clade into a distinct genus, for which the earliest name is Volkameria L., in which a number of the germane names have already been published. (2) Retaining the generic distinction for Aegiphila, Amasonia, and Tetraclea while resurrecting Volkameria provides increased information about evolutionary relationships...
in the classification of this group. Besides separating the Pantropical Coastal clade as the revived genus *Volkameria, Clerodendrum spinosum* also needs to be removed from *Clerodendrum*. Its original name, *Ovieda spinosa* L., is revived for it. Therefore, the newly delimited *Clerodendrum* is restricted to the Asian and African clades. This is of no little historical interest in that molecular work has confirmed three of the four generic concepts used by Linnaeus for this group (see Taxonomy). It is also noteworthy that the long narrow corolla tube has evolved at least twice independently in the group: once in *Ovieda* and also in the common ancestor of the Asian clade comprising *C. indicum* (which was independently described

Fig. 2. One of eight most parsimonious trees. The Bayesian consensus tree is very similar to this in topology. Only bootstrap values (BS) and posterior probabilities (PP) greater than 80%/0.95 are shown along the branches to avoid being overcrowded. Branches that collapse in the strict consensus are marked by black dots. Geographic distributions are shown on the right. The long-corolla-tube clade is indicated by a thickened arrow.
in Ovieda at least three times; see below), *C. quadriloculare*, and others, as mentioned above.

Although it is difficult to find unique morphological synapomorphies to separate Clerodendrum, Volkameria, and Ovieda, no doubt a cardinal reason why a broad view of Clerodendrum has prevailed for so long, a combination of several characters, as listed in Table 1, can be readily used to distinguish the three genera.

**Phylogenetic position of *C. hildebrandtii*.** — Within the African clade, one species, *C. hildebrandtii*, is sister to the rest of the African group. This species is distinguished from other African species by its large corolla (few flowers in each inflorescence) and large cylindrical calyx. In fact, *C. hildebrandtii* is the sole member of Verdecourt’s (1992) *Cylindrocalyx* (Thomas) Verd. in his treatment of the genus in East Africa. However, approximately 20 species of Clerodendrum that are restricted to Madagascar closely resemble *C. hildebrandtii* in morphology. Unfortunately, we were unable to obtain any living material of these species or herbarium specimens of sufficient quality for DNA extraction. But we predict that this particular Madagascan group, together with *C. hildebrandtii*, will form a clade that is sister to the rest of the African clade. A future study with extensive sampling of this group will shed light on the evolution of this, perhaps the most beautiful, Clerodendrum group.

**Evolution of an intriguing breeding strategy.** — An interesting breeding strategy has been reported in some species of Clerodendrum sensu stricto (s.str.) and Volkameria (Corner, 1940; Primack & al., 1981; Reddy & Reddi, 1995). The stamens and the style are curled upwards tightly inside the flower bud. When the flower opens, the filaments and style start uncoiling. While the filaments project to the centre, the style continues to bend down towards the lower side of the flower. The flower is strongly protandrous and this is the functional male phase. After pollen has been released and the anthers wither, the filaments curl back sideways and the style with its receptive stigma projects back to the centre, taking the position occupied by the stamens in the male phase (see Fig. 3; also see illustration and a detailed description in Reddy & Reddi, 1995). This strategy was first noted by Corner (1940: 700). 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Fig. 3. Representative floral images of Clerodendrum s.str. and allied genera. A–B, Clerodendrum trichotomum Thunb. (photos by Y.-W. Yuan). A, flower at male phase. Note the stamens project to the centre, whereas the style bends down towards the lower side of the flower. B, flower at female phase. The filaments curl back sideways and the style with its receptive stigma projects back to the centre. C, Ovieda spinosa L. (photo courtesy of Jackeline Salazar). D, Volkameria inermis L. (photo courtesy of Forest & Kim Starr). E, Tetraclea coulteri A. Gray (photo courtesy of Burr Williams). The red and blue arrows indicate the flower at male and female phase, respectively. F, Amasonia campestris Moldenke (photo courtesy of Robin Foster). The red arrow indicates the flower at male phase. G–H, Aegiphila sp. (photos courtesy of Kevin Nixon, www.plant-systematics.org), showing the heterostylosus system. G, thrum flower; H, pin flower.
“Clerodendrum s.str. + Volkameria + Ovieda + Aegiphila + Amasonia + Tetraclea + Kalaharia” clade recovered by molecular data has never been recognized in traditional classification schemes. But, after finding that this complex breeding strategy is shared by these taxa, it becomes obvious that they are all closely related as indicated by DNA sequences.

**TAXONOMY**

Genera recognized (see also Steane & Mabberley, 1998 for *Rotheca*) as a result of this work:

1. **Clerodendrum** L., Sp. Pl. 2: 637. 1753 – Type: *C. infortunatum* L.

   Trees, shrubs sometimes suckering, lianes or subherbeaceous perennials. Leaves simple (sometimes lobed), decussate or (rarely) whorled, never spiny. Inflorescences cymose, usually terminal. Flowers bisexual; calyx campanulate to tubular, variously lobed, often coloured, usually accrescent; corolla red to yellow, pink or white, with narrow tube, 5-lobed, the lobes usually unequal; stamens 4 or 5, didynamous, inserted within corolla tube, usually long-exserted; ovary imperfectly 4-locular, each locale with 1 ovule, style terminal, elongate, shortly 2-lobed. Fruit a drupe, often 4-sulcate or 4-lobed; endocarp tough, separating into 4 (or 2 pairs of) pyreens (sometimes only two maturing), each with one seed. Circa 150 species in tropical Old World with some species found as far south as Australia and as far north as China and Japan.


   Shrubs to 1.5 m, sometimes subherbeaceous; branches tuberculate. Leaves simple, decussate (occasionally some in spirals), coriaceous, margin toothed, teeth usually spiny, venation camptodromous, pinnate-rieticate, with conspicuous pronounced venation in relief on abaxial surface. Inflorescences corymbose, terminal. Flowers bisexual; calyx large, campanulate with 5 acute lobes, accrescent enclosing fruit, not brightly coloured; corolla white with long narrow tube, mouth 5-lobed; stamens 4, exerted; style solitary, as long as stamens; ovary globose. Fruit a drupe, globose to obovate, with 2 locules, each with one seed.

   One species, restricted to Hispaniola.


Notes. – Hitherto type material has not been designated (Jarvis, 2007: 716). Linnaeus cited Plumier (1703, as *Valdia*) but that shows insufficient detail to be the basis for his description. A much more detailed description, together with a plate that shows the inflorescence and leaf features that Linnaeus described in 1753 are shown in Burman’s 1760 work. Burman’s plate is based on a tracing of Pluimer’s drawing that was made by Claude Aubriet for Herman Boerhaave, and later prepared for publication by Burman. Burman sent proof copies to Linnaeus ahead of their publication, and it seems clear that Linnaeus must have received this one prior to 1753, hence its being appropriate as type material, even though published after Linnaeus’s own work (Jarvis, 2007: 151).

Note: *Ovieda* Spreng. (1824) = *Lapeirousia* Poir. (Iridaceae). For *Clerodendrum* s.l., Baillon (1891) resurrected *Ovieda* L., which had been made a synonym of *Clerodendrum* by authors from the 1820s onwards, so his action was inadmissible, though *Ovieda* as the name for *Clerodendrum* s.l. (including *Volkameria*) gained some currency in American publications (*Ovieda aculeata* (L.) Baill., Hist. Pl. 11: 95. 1891 non *O. aculeata* Klatt (1864 = *Lapeirousia aculeata* (de la Roche) Ker, Iridaceae) = *Volkameria aculeata* L.; *O. bracteosa* (Kostel.) Baill., l.c. (*C. bracteosum* Kostel., [type:icon]: Rheed., Hort. Malab. 4: t. 29. 1683 = *Rotheca serrata* (L.) Steane & Mabb. [syn. nov.]); *O. fragrans* (Willd.) Hitchcock (= *C. chinosec* (Osbeck) Mabb.); *O. inermis* Burm. f. (= *C. indicum* (L.) Kuntze); *O. infortunata* (L.) Baill., l.c. (= *C. infortunatum* L.); *O. mitis* L. (= *C. indicum* (L.) Kuntze); *O. ovalifolia* A. Juss. (*C. ovalifolia* (A. Juss.) Bakh. [type: India, Pondichéry, *Commerson* s.n. in Hb. Juss. (microfiche 347/19-P-JUSS)] = *V. inermis* L. [syn. nov.]); *O. trichotoma* (Thunb.) Baill., l.c. (= *C. trichotomyum* Thunb.); *O. verticillata* Roxb. ex D. Don [nom. in synon.] = *C. indicum* (L.) Kuntze).

*Additions to Index kewensis and other standard lists.


Shrubs, sometimes subherbeaceous, lianes, rarely small trees; branches ± tetragonal, usually ash-grey, nodes swollen. Leaves decussate (to ternate), subglabrous,with entire margin, never spiny, venation arcuate-reticulate. Inflorescences axillary to supra-axillary cymes. Flowers usually fragrant; calyx campanulate, only rarely accrescent, margin with 5 broadly triangular small teeth; corolla hypocrateriform, white, sometimes pink or purple, lobes unequal; stamens 4 (or 5), didynamous, inserted within corolla tube, exerted; ovary cylindrical; stigma shortly bifid. Fruits generally globose to obovoid, becoming black or brown and separating into 4 corky pyreens, each with 1 seed.

Approximately 25–30 species, pantropical but with apparently only one species in Asia (*V. inermis* L.).

Notes. – Pending a critical review of *Volkameria* taxon of Madagascar, where they appear to be numerous (Moldenke, 1956), the germane species are not transferred from *Clerodendrum* here, though one at least already has a name in

2. **V. aculeata** L. = *C. aculeatum* (L.) Schdl. Tropical America.


### LITERATURE CITED


Cantino, P.D. 1997. The biology and systematics of *Oxera* and *Faradaya,* and to Kevin Nixon, Jackeline Salazar, Burr Williams, Robin Foster, Forest & Kim Starr for permission to use their floral images. We also thank James Wearn (Royal Botanic Gardens Kew) for help in preparing a generic description of *Ovieda* and its typification, and thank Phil Garnock-Jones and an anonymous reviewer for helpful comments on the manuscript. Funding for this research was provided by a McIntire-Stennis Formula Fund to DJM and a NSF Grant (DEB 0542493) to RGO.

We would like to thank all the people who provided plant material; these include Shixiao Luo, Scot Zona, Rogier de Kok, Jun Wen, John Tan, and Robert Jansen. Thanks are also due to the directors/curators of the following herbaria for the loan of herbarium specimens and permission to take tissue samples: MAPR (Gary Brecken), MO (Jim Solomon), L (Erik Smets), and US (Jun Wen, Vicki Funk).

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Appendix 1. Plant material used in this study. Each entry consists of: taxon name, country in which it was collected, year of collection, collector with collection number, and herbarium (accession number when available) where voucher was deposited.


Appendix 2. Primers used for PCR and sequencing; the ones that were specifically designed for this study are marked by an asterisk (*).

trnL-F: c, d, e, f (Taberlet & al., 1991); trnS-M: trnS1UAG & trnM1ACU (Shaw & al., 2005), psbZ2F(V) (Yuan & Olmstead, 2008), psbZR(C)* (5′-CATCATTATTAGTACTCGTA-3'); trnT-F: trnT1AC-245 & trnT2ACG-R (Shaw & al., 2005), trnD-D2EdT* (5′-AATCGTGAACTGC GGTCCTCC-3'), trnD-D2EdT* (5′-CTACCGAATTGACTGCGTA-3'); trnL-F (Taberlet & al., 1991), RCl3er* (5′-ACCATAGGAAACCCATATT-3').