

Original Article

Phylogeny and infrageneric classification of *Clerodendrum* (Lamiaceae)

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ABSTRACT

The infrageneric classification of the genus *Clerodendrum* (Lamiaceae) has been highly problematic due to different concepts and subdivisions being applied to the treatment of Asian, Australian, and African species. Earlier molecular phylogenetic studies based on Sanger sequencing and limited sampling have indicated that previous morphology-based infrageneric classifications are not congruent with the phylogeny due to morphological convergence in many lineages. Advances in high-throughput DNA sequencing provide more information allowing more robust phylogenetic reconstruction at larger scale. We present the first comprehensive phylogenetic study of *Clerodendrum* that includes representatives of all previously recognized infrageneric taxa and using targeted sequencing data obtained from the Angiosperms353 enrichment to resolve the phylogenetic relationships. In agreement with previous phylogenetic work, our phylogeny shows that Asian and Australian species form a sister clade to an African Clade. *Clerodendrum* is monophyletic with the exclusion of some tropical coastal species, including some Australian species, which fall within a clade containing *Volkameria* and New World genera. We recognize two subgenera: subgen. *Clerodendrum* for Asian and Australian species and the new subgen. *Afroclerodendrum* for African and Malagasy species. Our findings support an infrageneric classification of *Clerodendrum* with a total of 13 sections based on molecular phylogenetic evidence and morphology that clearly accommodate the Asian, remaining Australian, and African species. Of these, we propose three new sections: sect. *Albiflora*, sect. *Fortunata* and sect. *Megaflora* for clades presenting unique morphological characters. The sectional classification and taxonomic consequences are discussed.

Keywords: Africa; Angiosperms353; Asia; Australia; Madagascar; pendulous inflorescence; sect. *Albiflora*; sect. *Fortunata*; sect. *Megaflora*; taxonomy; *Volkameria*

INTRODUCTION

Clerodendrum L. is a genus in the mint family (Lamiaceae) comprising ~250 species distributed throughout Africa and Asia as far as Australia (Yuan *et al.* 2010, POWO 2023). In a few studies the genus has been referred to ‘*Clerodendron*’, the Greek spelling of the name (e.g. Adanson 1763, Gürke 1895). It is distinguishable from other genera by its almost radially symmetrical flower buds with almost equal corolla and stigma lobes as well as an accrescent, bright-coloured fruiting calyx and protandrous pollination syndrome (Steane and Mabblerley 1998, Harley *et al.* 2004, Yuan *et al.* 2010).

Clerodendrum has an economic value regarding its potential pharmaceutical properties (Lukhoba *et al.* 2006, Carović-Stanko *et al.* 2016) and popular horticultural species (e.g. *C. bungei* Steud., *C. nutans* Wall. ex Jack, *C. laevifolium* Blume, *C. paniculatum* L. and *C. trichotomum* Thunb.) much like several other genera in the Lamiaceae (e.g. *Coleus* Lour., *Hyptis* Jacq., *Plectranthus* L’Hér, *Salvia* L., *Scutellaria* L., *Stachys* L., *Teucrium* L., *Thymus* L., and *Vitex* L.). In several *Clerodendrum* species, many useful phytochemicals such as phenolic compounds, terpenes, flavonoids, and steroids have been isolated (Stenzel *et al.* 1988, Shrivastava and Patel 2007, Modi *et al.* 2010; Praveen *et al.* 2012; Khan *et al.* 2017, Somwong and

Suttisri 2018, Wang *et al.* 2018, Nguyen *et al.* 2020, Zhou *et al.* 2020). These are known to impart health benefits (e.g. anti-bacterial, anti-hypertensive) that appear to justify the commonplace use of several species as an ethnomedicine (Khare 2008, Neelima *et al.* 2011, Kar *et al.* 2014, Yadav *et al.* 2018).

The genus *Clerodendrum* was first described by Linnaeus (1753) in *Species Plantarum* based on the Indian species *C. infortunatum* L. in *Didynamia Angiospermia* group having two series of unequal stamens. Jaume Saint-Hilaire (1805) first placed *Clerodendrum* within the family Verbenaceae and this placement was adopted by many subsequent botanists, such as Miguel (1858), Clarke (1885), Benthams (1870, 1876), King and Gamble (1908), Lam (1919), Ridley (1923), Thomas (1936), Fletcher (1938), and Verdcourt (1992). *Clerodendrum* was transferred to the family Lamiaceae (Labiatae) under subfamily Viticoideae based on a cladistic analysis of morphological and anatomical evidence (Cantino *et al.* 1992), and this was confirmed by molecular phylogenetic analysis (Wagstaff and Olmstead 1997). The genus was then placed within the subfamily Ajugoideae based on subsequent molecular studies (Steane *et al.* 1997, Li *et al.* 2016, Zhao *et al.* 2021).

Previous subdivisions of *Clerodendrum* based on morphology are summarized in Table 1. The first major infrageneric classification of *Clerodendrum* was presented by Schauer (1847) who recognized two sections (sect. *Clerodendrum* Schauer (as sect. *Euclerodendrum*) and sect. *Siphonanthus* Schauer). Within sect. *Clerodendrum*, six unranked taxa were listed: *Axilliflora* Schauer, *Densiflora* Schauer, *Paniculata* Schauer, *Penduliflora* Schauer, *Racemiflora* Schauer (now treated as the genus *Rothea*), and *Squamata* Schauer. Here we consider Schauer's other taxa denoted by '§' to be unranked following Article 37.8 of the *International Code of Nomenclature for Algae, Fungi, and Plants* (Turland *et al.* 2018). Most species referred by Schauer (1847) are Asian with a few species from Africa (including some now recognized as *Volkameria* and *Ovieda*). Studying only African species, Gürke (1895) recognized sections: *Clerodendrum* (i.e. 'Euclerodendrum'), *Cornacchinia* (Savi) Briq. (= genus *Volkameria*), and *Cyclonema* (Hochst.) Gürke (= genus *Rothea*). But a global overview by Briquet (1895) recognized these and plus sections: sect. *Siphonanthus*, and sect. *Volkameria* (L.) Briq. retaining Schauer's (1847) unranked subdivisions under sect. *Clerodendrum*. Revising Malesian species (including *C. thomsoniae* that was introduced from Africa), Lam (1919) adopted Schauer's unranked taxa as subsections within sect. *Clerodendrum* (*Euclerodendrum*) but introduced the new section *Tridens* H.J.Lam. Thomas (1936) later study of African *Clerodendrum* raised Schauer's sections to subgeneric level (Table 1), while also introducing subgen. *Kalaharia* (Baill.) Thomas (= genus *Kalaharia* Baill.). However, Thomas (1936) did not include Latin diagnoses for his infrageneric taxa and hence these name are not validly published (Turland *et al.* 2018; Article 39.1). Recognizing Thomas's invalid names for African species, Moldenke (1985) adopted previous taxonomic views of Schauer (1847), Briquet (1895) and Lam (1919) in a broader treatment including Asian species. Although Moldenke raised Schauer's unranked subdivisions (= Lam's subsections) to section level, these names are invalid because their basionyms were not referenced (Turland *et al.* 2018; Article 41.5). In *Clerodendrum* in *Flora of Tropical East Africa*, Verdcourt's (1992)

treatment adopted a similar classification to Thomas (1936) and validating most of Thomas' taxa, but recognizing only four subgenera, and including 12 sections and three subsections within the largest taxon, subgen. *Clerodendrum* (Table 1). In their recent treatment of Malesian species, Wearn *et al.* (2019) instead adopted Lam's sections: sect. *Clerodendrum*, sect. *Siphonanthus*, and sect. *Tridens*.

In the first molecular phylogenetic study by Steane *et al.* (1997), *Clerodendrum* was shown to be paraphyletic because certain species, previously placed in either subgen. *Cyclonema* or sect. *Konocalyx*, formed a distinct clade separated from the rest of *Clerodendrum* and the New World genera (Fig. 1A). These species were moved to the distinct genus *Rothea* Raf. by Steane and Mabberley (1998). Steane *et al.* (2004) transferred species referred to the genus *Huxleya* Ewart to *Clerodendrum*, as a clade of species being found in coastal habitats, while subgen. *Kalaharia* Baill. was treated as a distinct genus. In that study, the relationships between Asian (including two Australian species), African, and pantropical coastal *Clerodendrum* clades, together with a clade comprising New World genera, *Aegiphila* Jacq., *Amasonia* L.f., and *Tetraclea* A.Gray, were found to form a polytomy (Fig. 1B). The phylogenetic tree by Yuan *et al.* (2010) showed that *Clerodendrum* separated into two monophyletic clades (Fig. 1C): a core clade consisting of most species found in Asia with two of the 10 known Australian species (*sensu* Munir 1989), and African species, and including the type species of *Clerodendrum*. The second smaller clade comprised species predominantly found in coastal habitats, including the type species of *Volkameria*, and this clade is sister to the New World genera mentioned before. Accordingly, they recognized the 'coastal clade' as the genus *Volkameria*, which has been accepted by following studies (Leeratiwong and Chantaranothai 2003, 2010, 2014, Leeratiwong *et al.* 2011, Wearn and Mabberley 2011a, b, Li *et al.* 2016, Santos 2016, Xiang *et al.* 2018, Wearn *et al.* 2019, Sathaphorn *et al.* 2021, 2022). However, neither the two major clades nor subclades within different geographical clades were identified as infrageneric taxa. Previous morphology-based infrageneric classifications included Asian and African species in the same infrageneric taxa (Table 1), and Australian species were poorly represented in these studies. Morphological characters defining these taxa are homoplasious and do not reflect the actual relationships within the genus. Only Steane *et al.* (1997) attempted to relate existing infrageneric taxa to the phylogeny (Fig. 2) and showed that many relationships of these taxa were unresolved, and that sect. *Clerodendrum* and sect. *Macrocalyx* were non-monophyletic, being split across different Asian and African clades, respectively.

The studies by Steane *et al.* (1997, 2004) recorded that the previous morphology-based generic and infrageneric classifications were in conflict with the phylogeny using few plastid markers and nuclear ITS. Recently, high-throughput DNA sequencing (HTS) has been used to construct more robust and reliable phylogenetic analyses than those based on the Sanger sequencing of a few markers, using hundreds of genes or whole-genome sequences (Lemmon and Lemmon 2013, McKain *et al.* 2018, Soltis *et al.* 2018, Dodsworth *et al.* 2019). Within Lamiaceae, HTS has been used in whole-genome sequencing to retrieve the sequences within the plastome to study tribal

Table 1. Comparison of previous infrageneric classification within *Clerodendrum*. × indicates the presence of species from Asia or Africa. Remarks refer to the current taxonomic placement of the taxa.

| Authors | Infrageneric classification | | Species distribution | | Remarks | |
|----------------|-----------------------------|--|---|------|---------|--|
| | Subgenus | Section | Unranked/subsection | Asia | | Africa |
| Schauer (1847) | | sect. <i>Clerodendrum</i> (<i>Euclerodendrum</i>) | § <i>Axilliflora</i> Schauer [unranked] | × | × | 10 species have been moved to <i>Oviecta</i> and <i>Volkameria</i> (11 species remained in <i>Clerodendrum</i>). |
| | | | § <i>Penduliflora</i> Schauer [unranked] | × | | |
| | | | § <i>Racemiflora</i> Schauer [unranked] | | | |
| | | | § <i>Densiflora</i> Schauer [unranked] | × | | |
| | | | § <i>Paniculata</i> Schauer [unranked] | × | | |
| | | | § <i>Squamata</i> Schauer [unranked] | × | | |
| | | | | × | | |
| | | sect. <i>Siphonanthus</i> (L.) Schauer | | | | |
| | | sect. <i>Clerodendrum</i> (<i>Euclerodendrum</i>) | | | × | |
| | | sect. <i>Cornacchinia</i> (Savi) Briq. | | | | |
| Gürke (1895) | | sect. <i>Cyclonema</i> (Hochst.) Gürke | | | | Three species have been moved to <i>Rotheca</i> and <i>Volkameria</i> . = <i>Volkameria</i> = <i>Rotheca</i> = <i>Volkameria aculeata</i> |
| | | sect. <i>Volkameria</i> (L.) Briq. | | | × | |
| Briquet (1895) | | sect. <i>Clerodendrum</i> (<i>Euclerodendrum</i>) | § <i>Axilliflora</i> Schauer [unranked] | | × | Five species were moved to <i>Oviecta</i> and <i>Volkameria</i> . = <i>Rotheca</i> Including Australian <i>C. tracyanum</i> = <i>Rotheca</i> = <i>Volkameria</i> |
| | | | § <i>Penduliflora</i> Schauer [unranked] | × | | |
| | | | § <i>Racemiflora</i> Schauer [unranked] | | | |
| | | | § <i>Densiflora</i> Schauer [unranked] | × | | |
| | | | § <i>Paniculata</i> Schauer [unranked] | × | | |
| | | | § <i>Squamata</i> Schauer [unranked] | × | | |
| | | | | | | |
| | | sect. <i>Cyclonema</i> (Hochst.) Gürke | | | | |
| | | sect. <i>Cornacchinia</i> (Savi) Briq. | | | | |
| | | sect. <i>Siphonanthus</i> (L.) Schauer | | × | | |

Table 1. Continued

| Authors | Infrageneric classification | | Section | Unranked/subsection | Species distribution | | Remarks |
|---------------|-----------------------------|--|--|--|----------------------|--------|---|
| | Subgenus | | | | Asia | Africa | |
| Lam (1919) | | | sect. <i>Clerodendrum</i> (<i>Euclerodendrum</i>) | subsect. <i>Axilliflora</i> (Schauer) H.J.Lam | X | X | Including introduced species, <i>C. thomsoniae</i> from Africa and Australian <i>C. floribundum</i> . |
| | | | | subsect. <i>Densiflora</i> (Schauer) H.J.Lam | X | | |
| | | | | subsect. <i>Penduliflora</i> (Schauer) H.J.Lam | X | | |
| | | | | subsect. <i>Racemosa</i> (Schauer) H.J.Lam | | | = <i>Rotheca serrata</i> |
| | | | | subsect. <i>Paniculata</i> (Schauer) H.J.Lam | X | | |
| | | | | subsect. <i>Squamata</i> (Schauer) H.J.Lam | X | | |
| | | | sect. <i>Siphonanthus</i> (L.) Schauer | | X | | |
| | | | sect. <i>Tridens</i> H.J.Lam | | X | | |
| | | subgen. <i>Clerodendrum</i> (<i>Euclerodendrum</i>) | sec. <i>Cylindrocalyx</i> Thomas [nom. inval.] | | X | | All Thomas' taxa lack Latin diagnosis. |
| | | | sec. <i>Siphonocalyx</i> Thomas [nom. inval.] | subsect. <i>Phyllothyrsoides</i> Thomas [nom. inval.] | X | | |
| | | | subsect. <i>Thyrsoides</i> Thomas [nom. inval.] | X | | | |
| | | | subsect. <i>Cephalata</i> Thomas [nom. inval.] | X | | | |
| | | sect. <i>Eurycalyx</i> Thomas [nom. inval.] | | X | | | |
| Authors | | Infrageneric classification | | | Species distribution | | Remarks |
| Thomas (1936) | | Subgenus | Section | Unranked/subsection | Asia | Africa | |
| | | | sect. <i>Microcalyx</i> Thomas [nom. inval.] | subsect. <i>Paniculata</i> Thomas [nom. inval.] | X | | |
| | | | | subsect. <i>Pluricapitata</i> Thomas [nom. inval.] | X | | |
| | | | | subsect. <i>Corymbiflora</i> Thomas [nom. inval.] | X | | |
| | | | sect. <i>Odontocalyx</i> Thomas [nom. inval.] | | | | = <i>Volkameria</i> |

Table 1. Continued

| Authors | Infrageneric classification | | Unranked/subsection | Species distribution | | Remarks |
|----------------------------------|---|--|---|----------------------|--------|---------------------|
| | Subgenus | Section | | Asia | Africa | |
| | | sect. <i>Konocalyx</i> Thomas [nom. inval.] | | | | = <i>Rotheca</i> |
| | | sect. <i>Stenocalyx</i> Thomas [nom. inval.] | | | × | |
| | | sect. <i>Oxycalyx</i> Thomas [nom. inval.] | subsect. <i>Acuminata</i> Thomas [nom. inval.] | | × | |
| | | | subsect. <i>Apiculata</i> Thomas [nom. inval.] | | × | |
| | | | subsect. <i>Obtusata</i> Thomas [nom. inval.] | | × | |
| | | sect. <i>Macrocalyx</i> Thomas [nom. inval.] | subsect. <i>Laxiflora</i> Thomas [nom. inval.] | | × | |
| | | | subsect. <i>Spicata</i> Thomas [nom. inval.] | | × | |
| | | | subsect. <i>Capitata</i> Thomas [nom. inval.] | | × | |
| | subgen. <i>Cyclonema</i> (Hochst.) Gürke | sect. <i>Pleurocymosa</i> Thomas [nom. inval.] | | | | = <i>Rotheca</i> |
| | | sect. <i>Oligocymosa</i> Thomas [nom. inval.] | | | | |
| | | sect. <i>Chaunocymosa</i> Thomas [nom. inval.] | | | | |
| | | sect. <i>Stacheocymosa</i> Thomas [nom. inval.] | | | | |
| | subgen. <i>Kalaharia</i> (Baill.) Thomas [nom. inval.] | | | | | = <i>Kalaharia</i> |
| | subgen. <i>Cornacchinia</i> (Savi) Briq. | | | | | = <i>Volkameria</i> |
| | subgen. <i>Volkameria</i> (L.) Briq. | | | | | = <i>Volkameria</i> |
| Moldenke (1985) | subgen. <i>Cyclonema</i> (Hochst.) Gürke | sect. <i>Pleurocymosa</i> Thomas [nom. inval.] | | | | = <i>Rotheca</i> |
| | | sect. <i>Oligocymosa</i> Thomas [nom. inval.] | | | | |
| | | sect. <i>Chaunocymosa</i> Thomas [nom. inval.] | | | | |
| | | sect. <i>Stacheocymosa</i> Thomas [nom. inval.] | | | | |

Table 1. Continued

| Authors | Infrageneric classification | Section | Species distribution | | Remarks |
|--------------------|---|---|----------------------|-------------|---------------------|
| | | | Unranked/subsection | Asia Africa | |
| | Subgenus | | | | |
| | subgen. <i>Tridens</i> H.J.Lam [nom. inval.] | | | × | |
| | subgen. <i>Cornacchinia</i> (Savi) Briq. | sect. <i>Konocalyx</i> Thomas [nom. inval.] | | | = <i>Volkameria</i> |
| | subgen. <i>Volkameria</i> (L.) Briq. | | | | = <i>Volkameria</i> |
| | subgen. <i>Clerodendrum</i> | | | | |
| | | sect. <i>Clerodendrum</i> [nom. inval.] | | × | |
| | | sect. <i>Axilliflora</i> Schauer [nom. inval.] | | | |
| | | sect. <i>Penduliflora</i> Schauer [nom. inval.] | | × | |
| | | sect. <i>Densiflora</i> Schauer [nom. inval.] | | × | |
| | | sect. <i>Paniculata</i> Schauer [nom. illegit.] | | × | |
| | | sect. <i>Squamata</i> Schauer [nom. inval.] | | × | |
| | | sect. <i>Racemiflora</i> Schauer [nom. inval.] | | | = <i>Rothea</i> |
| | | sect. <i>Stenocalyx</i> Thomas [nom. inval.] | | | |
| | | sect. <i>Oxycalyx</i> Thomas [nom. inval.] | | × | |
| | | sect. <i>Obtusata</i> Thomas [nom. inval.] | | × | |
| | | | | | |
| | | subsect. <i>Acuminata</i> Thomas [nom. inval.] | | × | |
| | | subsect. <i>Apiculata</i> Thomas [nom. inval.] | | × | |
| Authors | Infrageneric classification | | Species distribution | | Remarks |
| | Subgenus | | Asia Africa | | |
| | | Section | | | |
| | | sect. <i>Macrocalyx</i> Thomas [nom. inval.] | | × | |
| | | | | | |
| | | subsect. <i>Capitata</i> Thomas [nom. inval.] | | × | |
| | | subsect. <i>Spicata</i> Thomas [nom. inval.] | | × | |
| | | subsect. <i>Spicata</i> Thomas [nom. inval.] | | × | |
| Moldenke (1985) | | Unranked/subsection | | | |
| | | subsect. <i>Capitata</i> Thomas [nom. inval.] | | × | |
| | | subsect. <i>Spicata</i> Thomas [nom. inval.] | | × | |
| | | subsect. <i>Spicata</i> Thomas [nom. inval.] | | × | |

Table 1. Continued

| Authors | Infrageneric classification | | Species distribution | | Remarks |
|---------------------|---|--|---|------|----------------------|
| | Subgenus | Section | Unranked/subsection | Asia | |
| | | sect. <i>Cylindrocalyx</i> Thomas [nom. inval.] | subsect. <i>Laxiflora</i> Thomas [nom. inval.] | | × |
| | | sect. <i>Siphonocalyx</i> Thomas [nom. inval.] | subsect. <i>Cephalata</i> Thomas [nom. inval.] | | × |
| | | | subsect. <i>Phyllotrysoides</i> Thomas [nom. inval.] | | × |
| | | | subsect. <i>Thyrsoidea</i> Thomas [nom. inval.] | | × |
| | | sect. <i>Eurycalyx</i> Thomas [nom. inval.] | | | × |
| | | sect. <i>Microcalyx</i> Thomas [nom. inval.] | subsect. <i>Paniculata</i> Thomas [nom. inval.] | | × |
| | | | subsect. <i>Corymbiflora</i> Thomas [nom. inval.] | | × |
| | | | subsect. <i>Pluricapitata</i> Thomas [nom. inval.] | | × |
| | | | | | = <i>Volkameria</i> |
| | subgen. <i>Siphonanthus</i> (L.) Schauer [nom. inval.] | sect. <i>Odontocalyx</i> Thomas [nom. inval.] | | × | |
| Verdcourt (1992) | subgen. <i>Clerodendrum</i> | sect. <i>Clerodendrum</i> . | | × | Cultivated in Africa |
| | | sect. <i>Densiflora</i> (Schauer) Verdcourt | | × | Cultivated in Africa |
| | | sect. <i>Oxycalyx</i> Verdcourt | subsect. <i>Oxycalyx</i> Verdcourt | | × |
| | | | subsect. <i>Apiculata</i> Verdcourt | | × |
| | | | subsect. <i>Fallix</i> Verdcourt | × | Cultivated in Africa |
| | | sect. <i>Macrocalyx</i> Verdcourt | | | × |
| | | sect. <i>Capitata</i> Verdcourt | | | × |
| | | sect. <i>Cylindrocalyx</i> Verdcourt | | | × |

Table 1. Continued

| Authors | Infrageneric classification | | Unranked/subsection | Species distribution | | Remarks |
|---------|---|---|---------------------|----------------------|--------|---------------------|
| | Subgenus | Section | | Asia | Africa | |
| | | sect. <i>Siphonocalyx</i> Verdcourt | | × | | |
| | | sect. <i>Eurycalyx</i> Verdcourt | | × | | |
| | | sect. <i>Microcalyx</i> Verdcourt | | × | | |
| | | sect. <i>Odontocalyx</i> Verdcourt | | | | = <i>Volkameria</i> |
| | | sect. <i>Cornacchinia</i> (Savi) Briq. | | | | = <i>Volkameria</i> |
| | | sect. <i>Konocalyx</i> Verdcourt | | | | = <i>Rothea</i> |
| | subgen. <i>Cyclonema</i> (Hochst.) Gürke | sect. <i>Cyclonema</i> Verdcourt | | | | = <i>Rothea</i> |
| | | sect. <i>Stachyocymosa</i> Verdcourt | | | | = <i>Rothea</i> |
| | subgen. <i>Kalaharia</i> (Baill.) Thomas [nom. inval.] | sect. <i>Clerodendrum</i> | | × | | = <i>Kalaharia</i> |
| | | sect. <i>Siphonanthus</i> (L.) Schauer | | × | | |
| | | sect. <i>Tridens</i> H.J.Lam | | × | | |

Wearn *et al.* (2019)

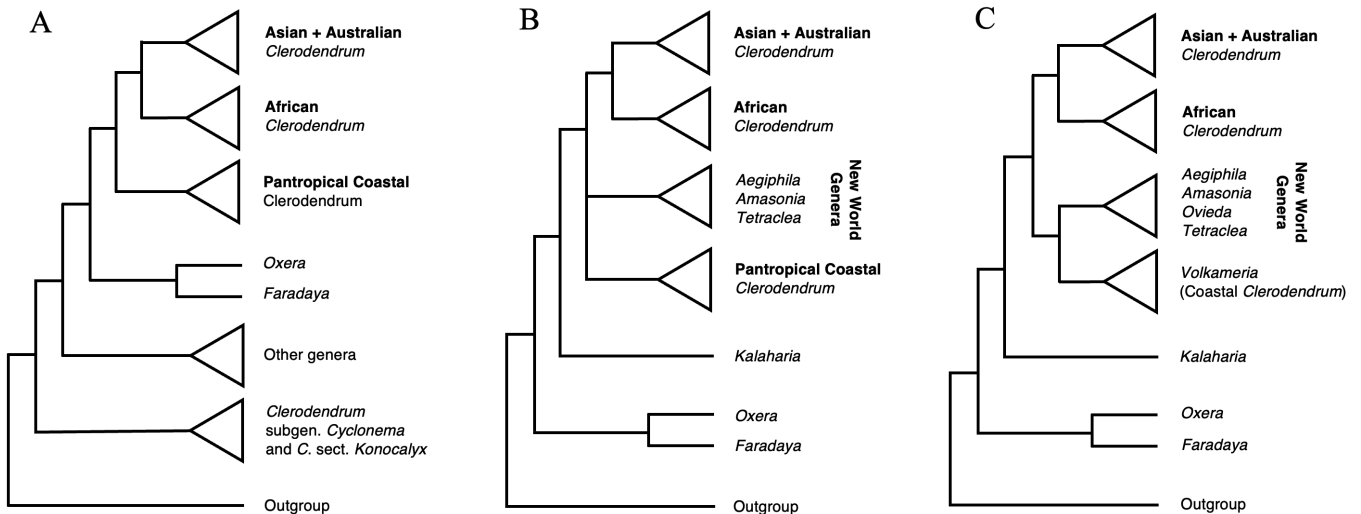


Figure 1. Summarized phylogenies of *Clerodendrum* and related genera from previous studies. A, Result from Steane *et al.* (1997, 1999), showing non-monophyly of *Clerodendrum s.l.*; B, result from Steane *et al.* (2004), showing unresolved relationships within *Clerodendrum* and new world genera clade; and C, result from Yuan *et al.* (2010), showing the monophyly of *Clerodendrum*, which is restricted to Asia, Australia, and Africa (*Clerodendrum s.str.*).

classification (Zhao *et al.* 2021). Target sequencing has emerged to reduce the cost and the computational effort by using baits (probes) to capture hundreds of targeted single-copy nuclear loci. In Lamiaceae, use of this technology resulted in the well-resolved taxonomic relationships within the genus *Salvia* (Lara-Cabrera *et al.* 2021). The universal Angiosperms353 probe kit (Johnson *et al.* 2019) is designed to work across all angiosperm families and has been widely applied to provide phylogenetic insights regarding classification and evolution of various of plant groups, for example, Orders Commelinales (Zuntini *et al.* 2021) and Cornales (Thomas *et al.* 2021), Families Araliaceae (Shee *et al.* 2020), Cunoniaceae (Pillon *et al.* 2021), Cyperaceae (Larridon *et al.* 2021), Gesneriaceae (Ogutcen *et al.* 2021), and Ochnaceae (Shah *et al.* 2021a, b). This target enrichment probe captures and amplifies up to 353 low-copy nuclear genes. This provides a reliable framework for the further investigation of understudied and taxonomically difficult groups and to improve the resolution in the phylogeny.

There is no subsequent phylogenetic work concerning infrageneric delimitation covering both Asian and African clades including unplaced Australian species recognized by Munir (1989) that lack phylogenetic information. In addition, we found that some Australian *Clerodendrum* exhibit morphological characters resembling those of *Volkameria*. Since we designed the target enrichment probe captures to study phylogenetic relationships within the genus, these relationships can be used to apply a taxonomy that recognizes monophyletic taxa at the generic, or subgeneric, sectional levels. This study aims to (i) resolve the phylogenetic relationships within Asian, Australian and African *Clerodendrum* assisted by targeted sequence capture; (ii) revise previously published, morphology-based, infrageneric classifications of *Clerodendrum* with an emphasis on Asian species, where there is more conflict in existing infrageneric accounts; and (iii) assess the phylogenetic position of selected Australian species, e.g. *C. floribundum* R.Br., *C. longiflorum* Decne, *C. parvulum* L.S.Sm., and *C. tatei* (F.Muell.) Munir.

MATERIALS AND METHODS

Taxon sampling

Sampling for the phylogenetic tree was influenced by an examination of all *Clerodendrum* species seen at AAU, BCU, BK, BKF, BM, CMUB, E, K, KEP, KLU, L, P, PSU, QBG, and SING herbaria (Thiers 2023) and an examination of type specimens on Global Plants on JSTOR (<https://plants.jstor.org/>). A total of 88 samples comprising nine outgroups and 79 accessions of *Clerodendrum*, were sampled from herbarium specimens or freshly collected silica-dried leaf materials (Supporting Information, Table S1). This study brought phylogenetic information of *Clerodendrum* up to ~102 species, ~41% of all species in the genus including species covered in the previous molecular phylogenetic works (Steane *et al.* 1997, 1999, 2004, Yuan *et al.* 2010). Asian and Australian species were selected to include representatives of all previous infrageneric ranks by Schauer (1847), Lam (1919), Munir (1989), and Wearn *et al.* (2019), while all African infrageneric ranks based on Thomas (1936) and Verdcourt (1992) were covered with the exception of the monotypic invalidly published section *Stenocalyx* (Thomas 1936) as represented by *C. eupatorioides* Baker (Supporting Information, Table S1). Verdcourt identified the type of this name as *Eremomastax speciosa* (Hochst.) Cufod. in the family Acanthaceae {Cameroon, Mann 1295 [K (K000029078!)]}. The outgroups were selected based on previous molecular studies (e.g. Yuan *et al.* 2010, Zhao *et al.* 2021), consisting of representatives of the following genera: *Aegiphila*, *Amasonia*, *Caryopteris* Bunge, *Oxera* Labill., *Hymenopyramis* Wall. Ex Griff., *Kalaharia*, *Rothea*, *Tetraclea*, and *Volkameria*.

DNA extraction, library preparation, and sequencing

Molecular laboratory work in this study was carried out at the Jodrell Laboratory at the Royal Botanic Gardens, Kew (Richmond, Surrey, UK), following Baker *et al.* (2022). Genomic DNA was extracted from leaf tissue using a modified cetyl-tri-methylammonium bromide approach, with

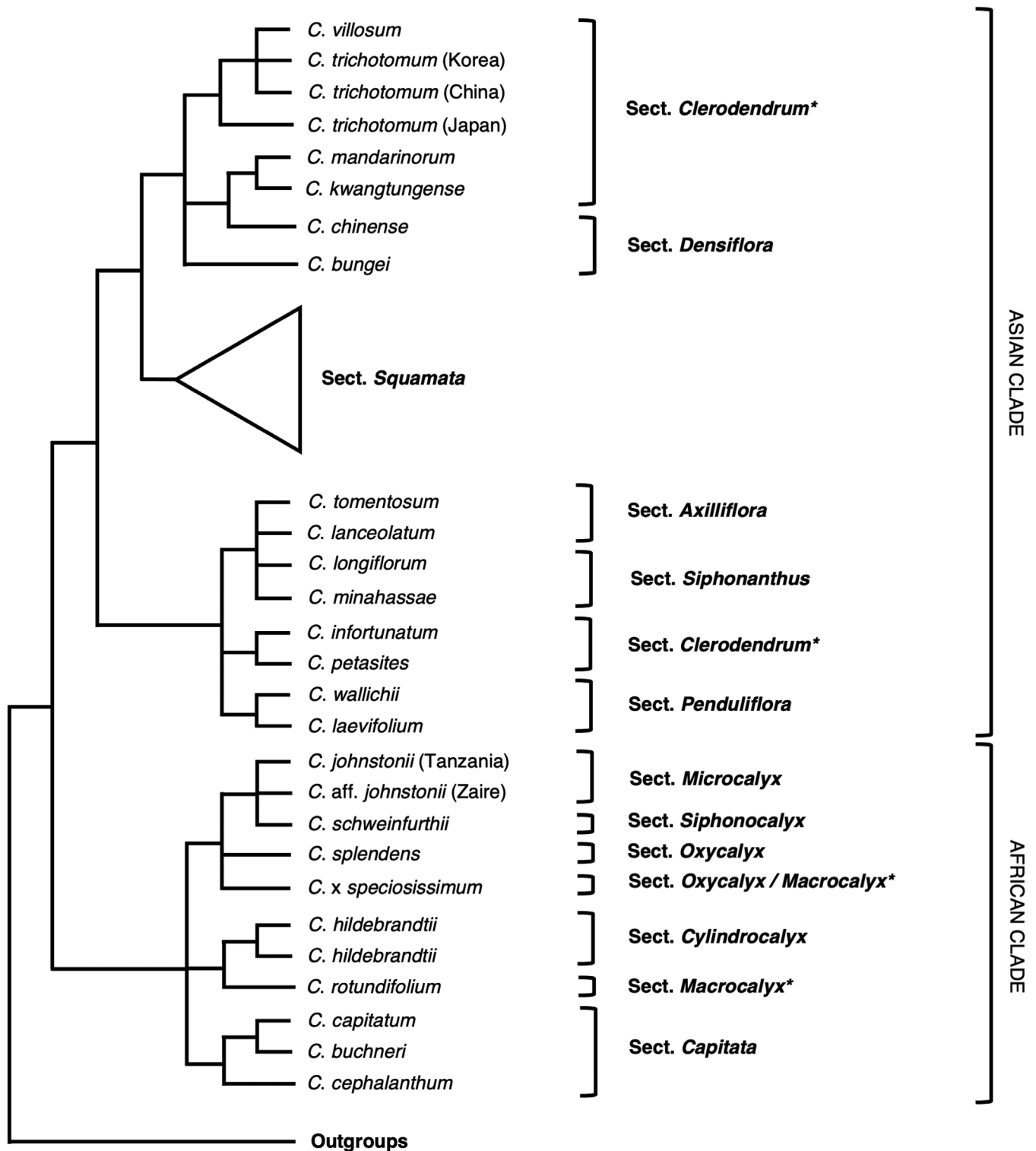


Figure 2. An overview of infrageneric classification modified from Steane *et al.* (1997) based on plastid markers, illustrating the paraphyly of the sect. *Clerodendrum* and unresolved sectional delimitation. Asterisks indicate the non-monophyletic group.

chloroform:isoamyl alcohol (SEVAG) and precipitation in isopropanol at -20°C , modified from Doyle and Doyle (1987). The extracted DNA were purified with Agencourt AMPure XP Bead Clean-up (Beckman Coulter, Indianapolis, IN, USA) following the manufacturer's protocol. All cleaned extracts were quantified with a Quantus Fluorometer

(Promega, Madison, WI, USA) and run on a 1% agarose gel to check the average fragment size. DNA extracts with an average size > 350 bp were sonicated using a Covaris M220 Focus-ultrasonicator (Covaris, Woburn, MA, USA) following the manufacturer's protocol to obtain an average fragment size of 350 bp. Dual-index libraries for Illumina sequencing were

Table 2. Comparison of the alignments and variable sites before and after trimming between exons and supercontigs datasets.

| | Exons dataset | | Supercontigs dataset | |
|-------------------------------|---------------|---------|----------------------|---------|
| | Untrimmed | Trimmed | Untrimmed | Trimmed |
| Average alignment length (bp) | 988 | 772 | 4844 | 2081 |
| Total alignment length (bp) | 332 897 | 260 052 | 1 632 518 | 701 267 |
| Average variable sites (bp) | 428 | 383 | 2219 | 1523 |
| Total variable sites (bp) | 144 309 | 128 959 | 747 960 | 513 097 |
| Proportion of variable sites | 0.43 | 0.50 | 0.46 | 0.73 |

prepared using NEBNext Ultra II DNA Library Prep Kit and the NEBNext Multiplex Oligos for Illumina (Primers 1 and 2; New England Biolabs, Ipswich, MA, USA) following the manufacturer's protocol, using half of recommended volumes. Approximately 200 ng (or a minimum of 50 ng) of the fragmented DNA were processed to the end-preparation reaction. Following the adapter ligation and size-selection, the DNA fragments were amplified using eight cycles of PCR. The libraries were quantified using Quantus Fluorometer and fragment size was checked with the Agilent Technologies 4200 TapeStation System (Santa Clara, CA, USA) using standard D1000 Screen Tapes. The final library size including the adapters was *c.* 500 bp on average. For targeted enrichment of nuclear loci, samples with similar library concentrations and fragment sizes were pooled at equimolar amounts and hybridized with the Angiosperms353 probe (Johnson *et al.* 2019) following Arbor Bioscience's protocol (Ann Arbor, MI, USA). The hybridization was performed for 24 h at 65°C, followed by 12 cycles of PCR. Final products were assessed on TapeStation to check the fragment size and were pooled equimolarly for the sequencing. Sequencing of library pools was performed on an Illumina HiSeqX instrument (San Diego, CA, USA) at Macrogen (Seoul, South Korea) producing 2 × 150 bp paired-end reads.

Phylogenetic analyses

The raw sequence reads were trimmed to remove adapter sequences and portions of low quality with Trimmomatic v.0.36 (Bolger *et al.* 2014) using the following setting LEADING: 20 TRAILING: 20 SLIDINGWINDOW: 4:20 MINLEN: 36. The HybPiper pipeline v.1.31 (Johnson *et al.* 2016) was implemented using the Angiosperms353 target loci amino acid, available at <http://github.com/mossmatters/Angiosperms353>. Mapped reads were assembled into contigs with SPAdes v.3.13.1 (Bankevich *et al.* 2012) and the retrieve_sequences.py script from the HybPiper suite using the.DNA flag to produce outputs of a single sequence per gene, which is selected using lengths, similarity, and coverage. We also removed loci presenting in < 70% of all samples. HybPiper recovered additional 'splash zone' (Dodsworth *et al.* 2019), which include non-coding intronic or flanking regions that were combined with exons to form supercontigs retrieved from intronerate.py script (Johnson *et al.* 2016). AMAS (Borowiec 2016) was used to produce summary statistics for each exon and supercontig regions and the number of potentially variable sites (Supporting Information, Table S2). Gene matrices were individually aligned using MAFFT v.7.305b in auto mode (Katoh *et al.* 2002) with default algorithm and

-maxiter 1000. To examine the impact of missing sites in the alignments, we analysed untrimmed alignments and trimmed alignments using Phyutility (Smith and Dunn 2008) to remove sites with > 30% gaps.

For the concatenated approach, a phylogenetic tree was generated using maximum likelihood analysis with the concatenated supermatrix of exon and supercontig alignments using IQTREE v.2.0 (Nguyen *et al.* 2015) with 1000 ultrafast bootstraps using the '-B' option. The data were treated as a single partition and the optimal model was selected automatically by the program. Trees were visualized using FigTree v.1.4.4 (<https://github.com/rambaut/figtree/releases>). For the multi-species coalescent approach (MSC), individual maximum likelihood gene trees were constructed from the alignment exons and supercontig regions with IQTREE v.2.0 (Nguyen *et al.* 2015) with 1000 ultrafast bootstraps using the '-B' option. Internal branches with bootstrap support values < 10% were collapsed with 'nw_ed' in Newick utility v.1.6 (Junier and Zdobnov 2010), and long branches were removed by TreeShrink v.1.3.3 (Mai and Mirarab 2018) to avoid poor support in the subsequent species tree analysis. Species trees were inferred from the gene trees using ASTRAL-III v.5.6.3 (Zhang *et al.* 2018) with the '-t 2' option providing annotation outputs for quartet support values to allow visualization of the main topology, and first and second alternative topologies as pie charts. A consensus topology of all the datasets was constructed in Rstudio v.3.6.3 (R Core Team 2020) using the following packages: ape (Paradis and Schliep 2018), ggimage (Yu 2019a), ggtree (Yu *et al.* 2017), treeio (Yu 2019b), and their dependencies.

Raw sequence data of all samples included in this study, accession number ERS11630409 to ERS11630496 (Supporting Information, Table S1), are available from European Nucleotide Archive under the Bioproject number PRJEB51682: <https://www.ncbi.nlm.nih.gov/>.

RESULTS

Data quality and topological impact

The capture success of the Angiosperms353 probe kit for *Clerodendrum* and closely related genera of Lamiaceae was high. The number of recovered loci ranged from 217 to 347 loci per taxon (average 333 loci) or 61–98% of the on-target exons (average 94%), summarized in Table 2; Supporting Information, Fig. S1. After filtering low recovery loci from 353 targeted exons, a total of 337 loci for the alignment were retained. The exons dataset had an alignment range between 216 and 3849 bp (mean 988 bp) before trimming and 117 to 3438 (mean 772

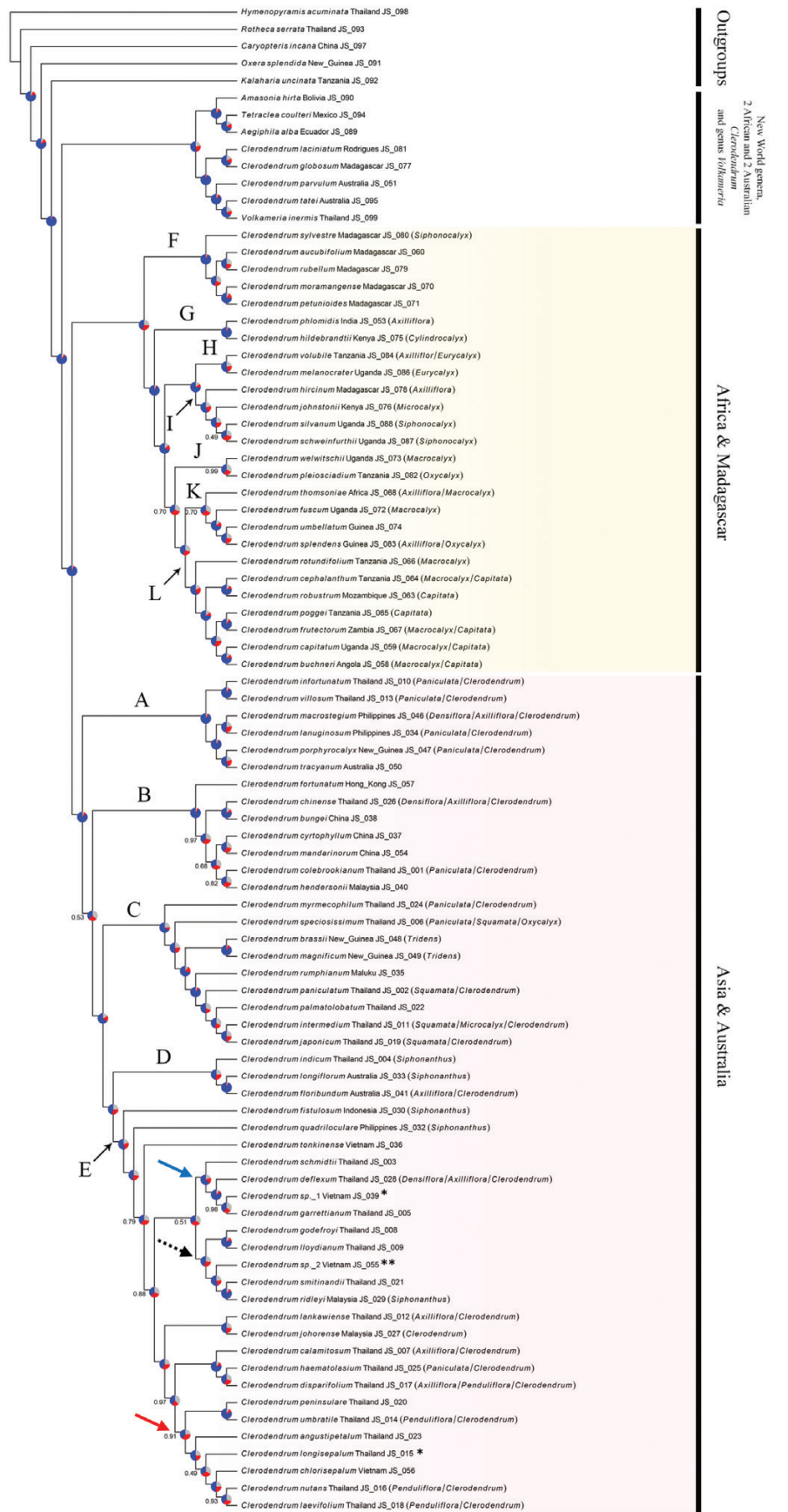


Figure 3. Phylogenetic reconstruction of the genus *Clerodendrum* based on multi-species coalescent approach using the trimmed supercontigs dataset. Labels A–L are well-supported clades with a congruently morphological grouping. Numbers of branches represent local posterior probabilities (LPPs) and branches without number indicate full support. Pie chart nodes correspond to quartet support. Brackets after species names indicate previous sections or subsections of that species (see Table 1). Smooth arrows and dashed arrows in Clade E refer to pendulous and upright inflorescence’s groups, respectively. Single and double asterisks in Clade E indicate species having an upright and a pendulous inflorescence, respectively.

bp) after trimming (Supporting Information, Table S3A, S4A). For the supercontigs dataset, before trimming alignment length was between 1039 and 21 164 bp (mean 4844 bp) and between 521 and 7489 bp (mean 2081 bp) after trimming (Supporting Information, Table S3B, S4B). In total, untrimmed exons and untrimmed supercontigs had a total alignment of 332 897 and 1 632 518 bp, respectively, while trimmed exons and trimmed supercontigs are 260 052 and 701 267 bp, respectively. Overall, the retrieved data from supercontigs dataset was much higher than the exons dataset according to the alignment length as well as number of potentially variable sites summarized in Table 2. In the exons dataset, the alignment length obtained from the untrimmed dataset had a higher number of base pairs than the trimmed dataset; however, the relative number of variable sites in the trimmed dataset was higher than the untrimmed dataset (0.50 vs. 0.43). Similarly, in the supercontigs dataset, the relative number of variable sites from the trimmed dataset was almost double that of the untrimmed dataset (0.73 vs. 0.46).

The species trees in this study were produced from the trimmed datasets due to the higher proportions of variable sites for both exons and supercontigs (Table 2). The trees inferred from the MSC approach based on the supercontigs dataset was shown in Figure 3 and the tree based on the exon dataset was provided in Supporting Information, Figure S2. These two datasets recovered a similar topology, although demonstrated conflict between sister clades observed at shallower levels on the trees. Species positions inferred from the concatenated approach based on supercontigs datasets compared to exons datasets also had some minor differences (Supporting Information, Figs S3, S4). Overall, sections and species members in each section were similar except for conflict between some species placements as discussed next.

The MSC obtained from the supercontigs dataset represented the most robust topology (Fig. 3) because it provided the highest support at nodes for which quartet support was usually > 80%, and because support was higher compared to the exon datasets (Supporting Information, Fig. S1) or concatenated approach. For these reasons, we used this tree to describe our overall interpretation of phylogenetic relationships in *Clerodendrum* in the following section.

Phylogenetic relationships

Species of *Clerodendrum*, with the exception of two Australian species and two species from Madagascar and Mauritius (Rodrigues Island), were found in one clade with full support (1 LPP, Fig. 3). The four exceptions were recovered in a sister clade to the *Clerodendrum* clade, along with *Volkameria* (*V. inermis* L.) and the New World genera: *Amasonia* (*A. hirta* Benth.), *Tetraclea* (*T. coulteri* A.Gray), and *Aegiphila* (*A. abla* Moldenke).

Clerodendrum was composed of two fully supported sister clades (1 LPP), one consisting of all African and Malagasy species and the Indian *C. phlomidis* L.f. (hereafter referred to as the African and Malagasy Clade), the other comprising all other Asian and Australian species sampled (hereafter referred to as the Asian and Australian Clade). Within the Asian and Australian Clade, there were five well-supported clades recovered with high support and organized in a grade (Fig. 3, Clades A–E). Clade A (containing the type species of the genus, *C. infortunatum*) was

sister to the rest of Asian clades (0.53 LPP). Clade E was the largest of the five and consisted of approximately half of the sampled Asian species. Australian species within the *Clerodendrum* clade were not recovered in the same clade. *Clerodendrum tracyanum* (F.Muell.) Benth. in Clade A, *C. floribundum*, and *C. longiflorum* in Clade D.

Conflicting topologies were observed in the placement of Clade A relative to Clade B in the MSC analyses obtained from different datasets (Fig. 3; Supporting Information, Fig. S2), but neither scenario is well-supported. However, in the maximum likelihood analyses, Clade A was recovered as sister to B with maximum support in both exon and supercontig datasets (Supporting Information, Figs S3, S4). Some species positions obtained from supercontigs dataset such as *C. fortunatum* L. (Clade B) and *C. tonkinense* Dop (Clade E) were found in different positions in comparison between the maximum likelihood analysis (Supporting Information, Fig. S4) and the MSC approach (Fig. 3, Clades B & E, respectively).

Seven distinct clades could be identified in the African and Malagasy Clade (Fig. 3, Clades F–L). Clade F, including all endemic Malagasy species (except *C. hircinum* Schauer found in Clade I), was recovered as the earliest divergent lineage in the African and Malagasy Clade. Clade G included *C. hildebrandtii* Vatke and the only Asian species, *C. phlomidis*. Clade H and Clade I are sister groups with full support (1 LPP). The clade comprising Clades H and I is sister to a clade (0.7 LPP) including Clade J (0.99 LPP), Clade K (0.7 LPP) and Clade L (1 LPP). In the MSC approach, *C. pleiosciadium* Gürke was sister to *C. welwitschii* Gürke in Clade J using the supercontigs dataset (Fig. 3), but, based on the exons dataset, *C. pleiosciadium* was found within Clade K forming the sister relationship to the rest members of Clade K (0.66 LPP) (Supporting Information, Fig. S2).

DISCUSSION

Phylogenetic reconstruction

Phylogenetic analyses using the universal Angiosperms353 probe (Johnson *et al.* 2019) provided a robust hypothesis of phylogenetic relationships of Asian, Australian, and African *Clerodendrum*, and permitted a re-evaluation of the infrageneric classification of *Clerodendrum*. The species tree from our study (Fig. 3) reveals that species of *Clerodendrum* fall into three main clades that are: (i) the New World genera and *Volkameria* Clade, (ii) the Asian and Australian Clade, and (iii) the African and Malagasy Clade. The Asian and Australian Clade is sister to the African and Malagasy Clade as shown in previous studies (Steane *et al.* 1997, 1999, 2004, Yuan *et al.* 2010).

The Australian species, *C. parvulum* (Fig. 10A), *C. tatei* (Fig. 10D) and Mauritius species, *C. laciniatum* Balf.f. (Fig. 10B, C), and *C. globosum* Moldenke (Fig. 10E), form a clade with *Volkameria inermis* and form a fully supported sister group to the New World genera. These *Clerodendrum* species exhibit small leaves, axillary inflorescences, and a non-acrescent calyx (Fig. 10C), which are likely to belong to genus *Volkameria* as defined by Yuan *et al.* (2010). This finding is congruent with the previous report by Steane *et al.* (2004) that *C. tatei* has morphological similarities and growth form with *V. aculeata* L. (= *Huxleya linifolia* Ewart & B.Rees). Therefore, these

Table 3. Comparison of diagnosed characters of Asian and Australian sections of the subgenus *Clerodendrum*.

| Characters | Sect. <i>Albiflora</i> | Sect. <i>Clerodendrum</i> | Sect. <i>Densiflora</i> | Sect. <i>Fortunata</i> | Sect. <i>Siphonanthus</i> | Sect. <i>Tridens</i> |
|------------------------|--|---|--|---|---|---|
| Habit | Shrub or tree, 0.4–10 m tall | Shrub, 1–3 m tall | Shrub to small tree, 1–6 m tall | Shrub, 1–1.5 m tall | Shrub, 1–3 m tall | Shrub, 1–2.5 m tall |
| Stem indumentum | Glabrous to pubescent or pilose | Covering villose hairs | Glabrous to pubescent | Densely pubescent | Glabrous | Usually glabrous to pubescent; nodes with a band of hairs |
| Leaf indumentum | Glabrous or pubescent or pilose | Pubescent on both sides | Pubescent on both sides, lower surface bearing sessile glands at leaf base | Glabrous on upper surface with pubescent on veins; pubescent on lower surface | Upper surface glabrous, lower surface glabrous to glabrescent | Pubescent on both sides lower surface with peltate glandular scales |
| Inflorescence position | Terminal | Terminal | Terminal | Axillary | Terminal or axillary | Terminal |
| Inflorescence type | Upright or pendulous | Upright | Upright | Upright | Upright | Upright |
| Inflorescence shape | Spike-like to pyramidal | Spike-like to pyramidal | Rounded, somewhat corymbose | Spike-like to pyramidal | Spike-like to pyramidal | Spike-like to pyramidal |
| Cymes | Lax to condensed | Lax | Condensed | Lax | Lax | Condensed |
| Calyx shape | Campanulate or urceolate | Campanulate | Campanulate | Campanulate | Campanulate | Campanulate |
| Calyx tube length | 0.5–6 mm | 2–4 mm long | 1.5–8 mm long | 0.8–1 mm long | 2–7 mm | 1–5 mm |
| Calyx lobe length | 2–18 mm, shorter or longer than tube length | 2.5–13 mm, longer or equal to calyx tube length | 0.8–12 mm, mostly shorter or equal to calyx tube length | 9–12 mm, much longer than tube | 3.5–8 mm, longer or equal to tube length | 3–15 mm, longer than tube |
| Calyx lobe shape | Usually triangular, spreading | Usually broadly ovate | Narrowly triangular | Ovate-triangular | Broadly triangular | Triangular |
| Corolla colour | White to creamy-white, rarely pale-yellow | White to creamy-white with or without pink blotches at centre | White to creamy-white or pink | White to creamy-white | White to creamy-white | Red, rarely yellow or orange |
| Corolla tube length | 0.8–3(–3.2) cm (3.4–4 cm long in <i>C. smitinandii</i> , 7–8 cm long in <i>C. quadriloculare</i>) | 7–25 mm | 7–28 mm | 9–12 mm | 3–10 cm | 12–22 mm |

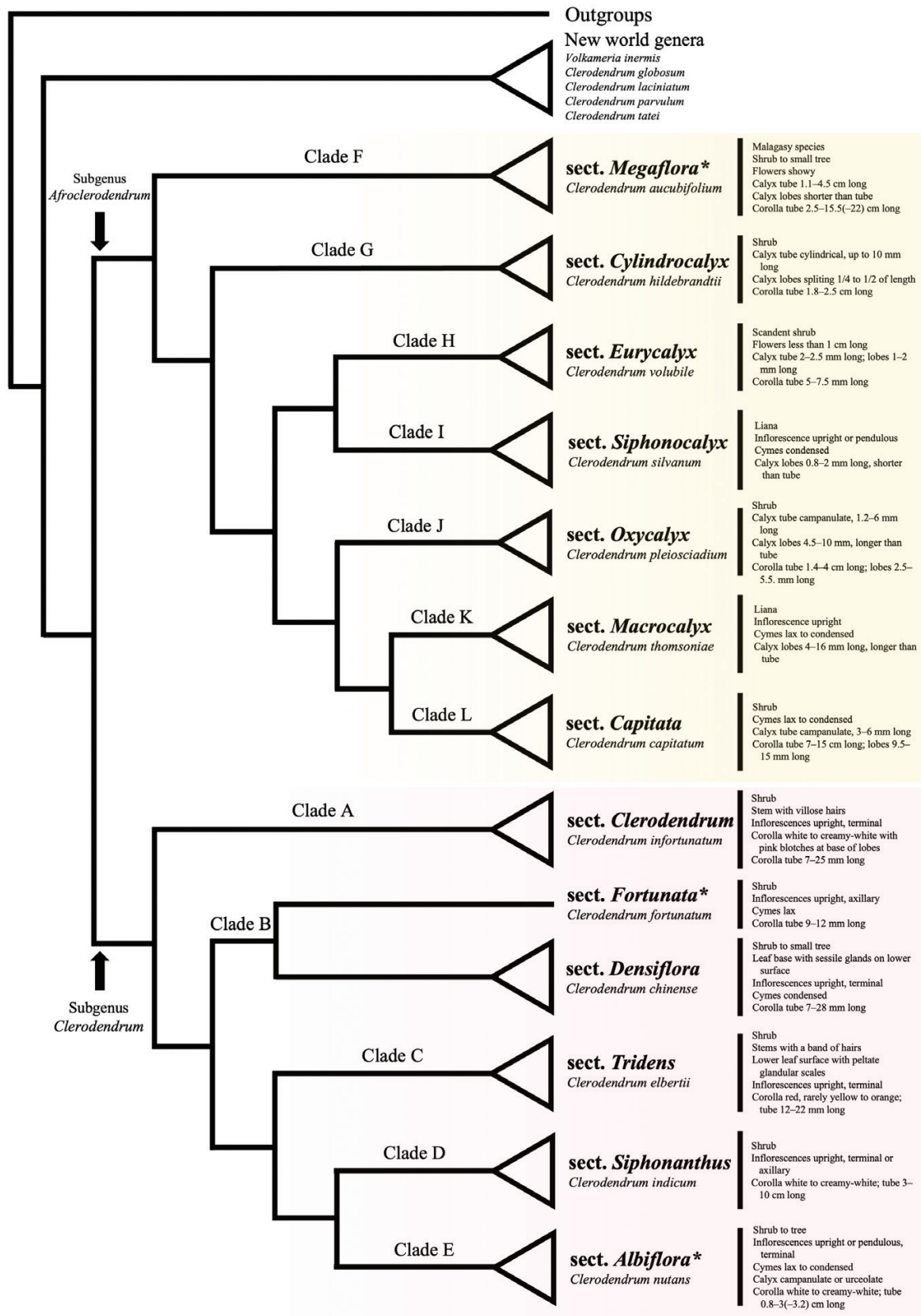


Figure 4. An overview of the infrageneric classification from our findings with main morphological diagnoses of each section. The type of each section is indicated below the section name. Asterisks represent the new sections from this study.

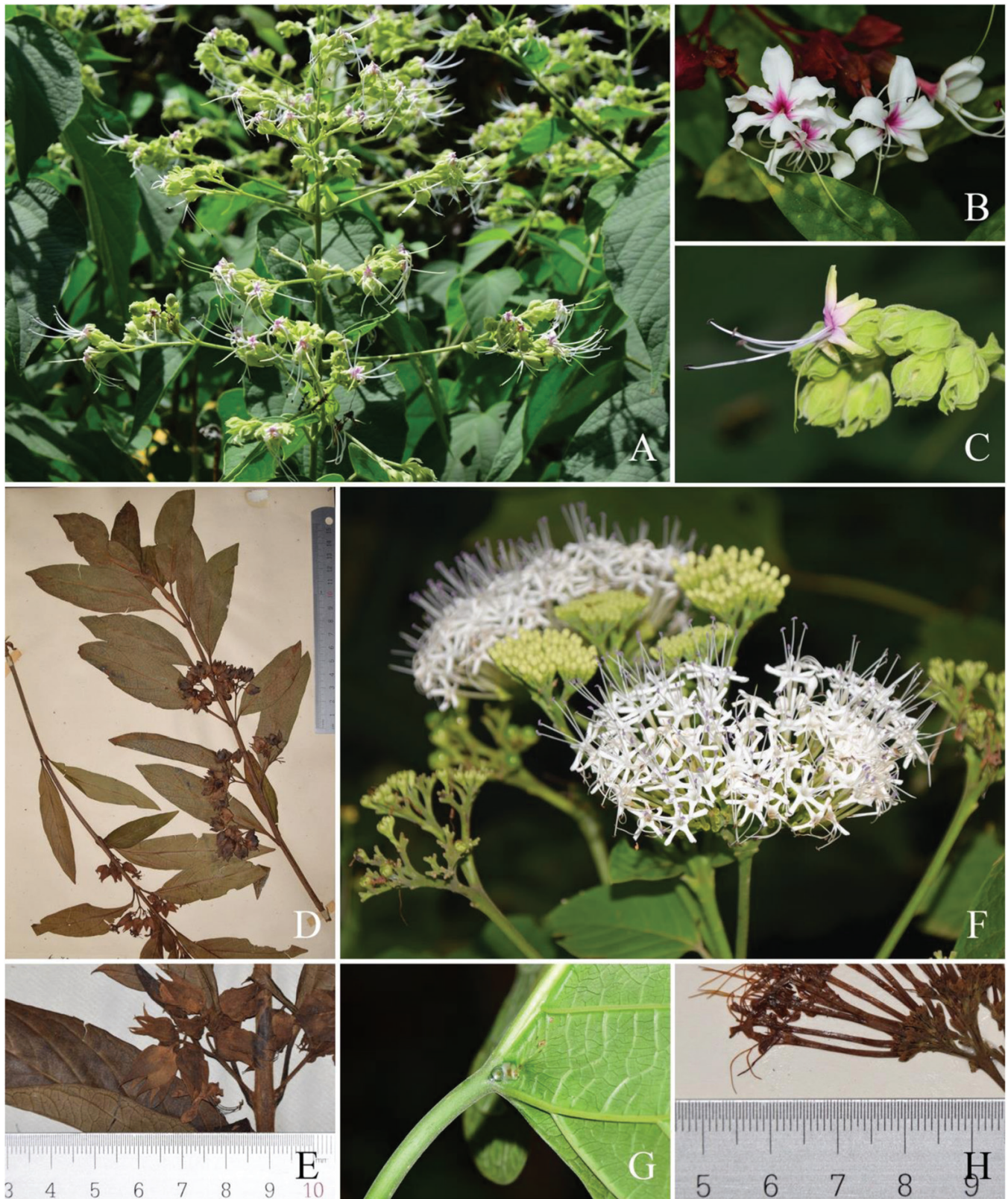


Figure 5. Selected diagnostic characters of sect. *Clerodendrum* (A–C), sect. *Fortunatum* (D–E) and sect. *Densiflora* (F–H). A and C, The lax inflorescence and flower of *C. villosum*. B, Flowers of *C. infortunatum*. D and E, Flowering branch and inflorescence of *C. fortunatum*. F and H, Condensed inflorescence and calyx of *C. colebrookianum*. G, Sessile glands of *C. colebrookianum*. Photos by J. Sathaphorn (A, C–H) and C. Leeratiwong (B). Specimens: D–E [Wilford 157 (K)]; and H [Suddee *et al.* 939 (K)].



Figure 6. Selected diagnostic characters of sect. *Tridens* (A–D) and sect. *Siphonanthus* (E, F). A, Inflorescence of *C. paniculatum*. B, C, Flowers of *C. intermedium* and *C. japonicum*, respectively. D, Deeply lobed leaves of *C. palmatolobatum*. E, Axillary inflorescences of *C. indicum*. F, Flower of *C. indicum*. All photos by J. Sattaphorn.

Clerodendrum species should be transferred to the genus *Volkameria* based on the phylogenetic placement and morphological affinities.

The recognized clades (Clades A–L) within *Clerodendrum* are considered together with the morphological characters that might diagnose these clades. Most well-supported clades

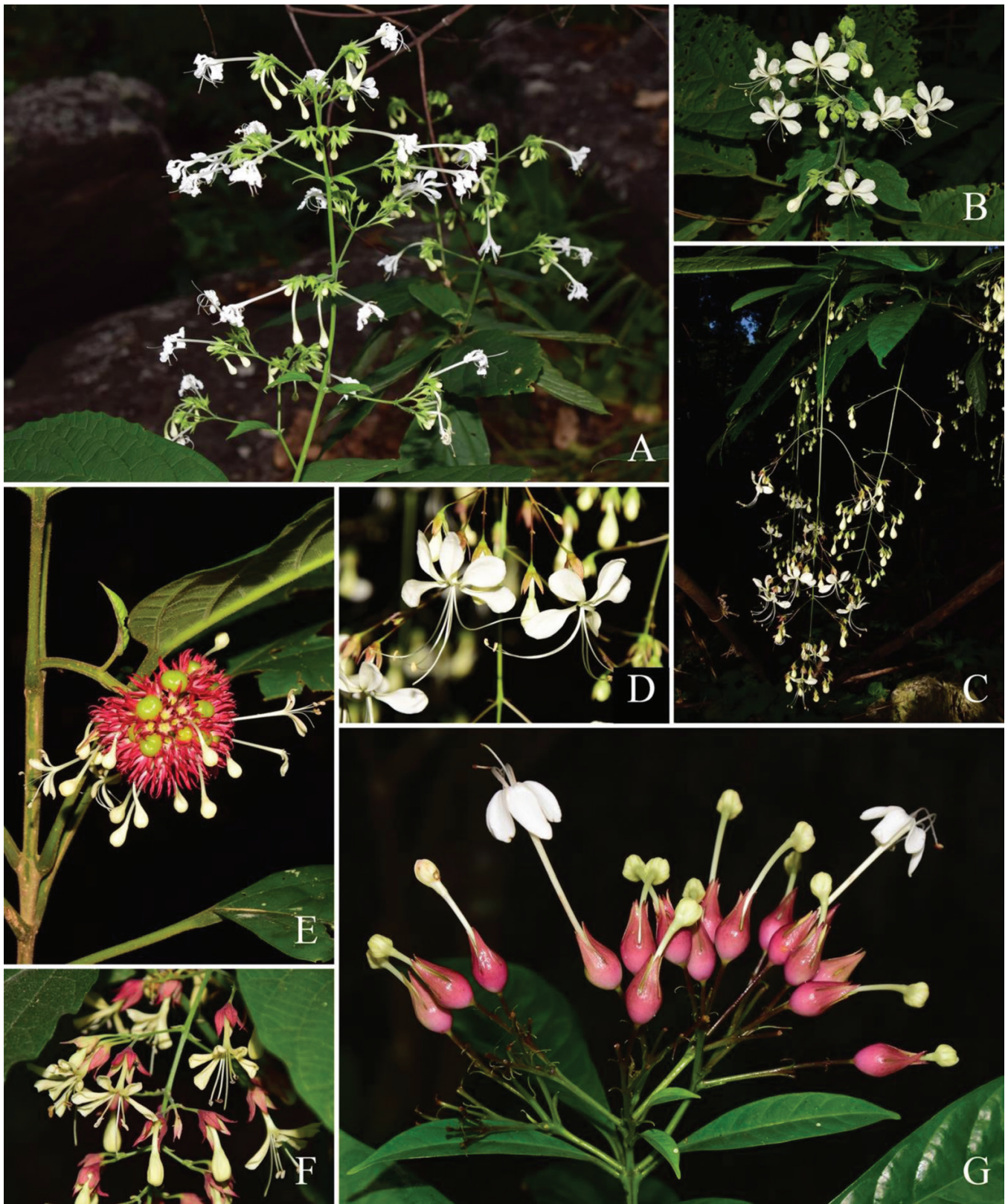


Figure 7. Selected diagnosis characters of sect. *Albiflora* (A–G). A, Upright inflorescence of *C. godefroyi*. B, Flowers of *C. lloydianum*. C, Lax and pendulous inflorescences of *C. nutans*. D, Flowers of *C. nutans*. E, Condensed and pendulous inflorescence of *C. deflexum*. F, Flowers of *C. schmidtii*. G, Upright inflorescence of *C. smitinandii* showing urceolate calyx shape. All photos by J. Sathaphorn.

(Fig. 3, Clades A–L) did not match previously recognized groups from morphology-based infrageneric classifications (brackets after species name in Fig. 3; Supporting Information, Figs S2–S4,

Table S1) and are either African and Malagasy or Asian and Australian in distribution. Subsect. *Axilliflora* (*sensu* Schauer, 1847 and Lam, 1919) accommodated species in both continents

(Table 1, Fig. 3). Previously recognized taxa were considered on the basis of the placement of their type species with respect to these clades (Schauer 1847, Lam 1919, Verdcourt 1992, Wearn *et al.* 2019). The clades within the Asian and Australian Clade are examined first, followed by the seven clades within the Malagasy and African Clade. Morphological differences between the recognized taxa are summarized in Table 3 and a key is provided in the Taxonomic Treatment.

There are five recognized clades for Asian and Australian *Clerodendrum* species (Clades A–E) that can be referred to six morphology-based sections, with Clade B being divided into two sections as discussed next (Figs 3, 4). Our findings show that most published infrageneric taxa (sections and subsections) proposed by Schauer (1847), Lam (1919), and Wearn *et al.* (2019) are non-monophyletic as noted by Steane *et al.* (1997). Yuan *et al.* (2010) illustrated two sister clades within Asian and Australian *Clerodendrum* consisting of long and narrow corolla groups (e.g. *C. floribundum*, *C. indicum* (L.) Kuntze, and *C. quadriloculare* (Blanco) Merr.) sister to the clade of remainder species. However, this study shows that *C. quadriloculare* is in a different clade to the other species and neither clade is a sister to the rest of the Asian species.

In the African and Malagasy Clade, seven clades are identified that correspond to sections recognized by Verdcourt (1992), except Clade F (Figs 3, 4, Clades G–L). In Verdcourt's treatment, sections are mainly based on calyx characteristics and although our results support Verdcourt's classification, African species have been less well-sampled than the Asian species in this analysis. Within the African and Malagasy Clade, Clade F containing species restricted to Madagascar is sister to Clades G–L comprising species from both mainland Africa and Madagascar, and Indian *C. phlomidis*. Yuan *et al.* (2010) reported *C. hildebrandtii* as a sister to the remaining African species, but that work did not sample any species recognized here belonging to Clade F.

Two sister clades of *Clerodendrum* (Clades A–E and F–L) separate representatives from Asia and Australia (except *C. phlomidis*), and Africa and Madagascar that can be recognized as two subgenera. The clade accommodating Asian and Australian *Clerodendrum* contains the type of the genus and is recognized as subgen. *Clerodendrum* here. The clade containing African and Malagasy representatives, including Indian *C. phlomidis*, is recognized as *Clerodendrum* subgen. *Afroclerodendrum* in this study and formally described in the Taxonomic Treatment.

The Asian and Australian Clade

Clade A (Figs 3–4, Section *Clerodendrum*)

Species within this clade are shrubby Asian and Australian species having a villose stem, terminal, upright, lax thyrsoid inflorescences, and white to creamy-white flowers with or without pink blotches at base of corolla lobes (Fig. 5A–C, Table 3). The clade shows a sister relationship to all the other clades within the Asian and Australian Clade with strong support. Most species in this clade (e.g. *C. infortunatum*, *C. villosum* Blume, *C. lanuginosum* Blume, *C. porphyrocalyx* Lauterb. & K. Schum., and *C. tracyanum*) were found to be in the subsect. *Paniculata* in previous studies of Schauer (1847) and Lam (1919), but Wearn *et al.* (2019) subsequently placed these species in sect. *Clerodendrum*, which held a large number of Malesian species on the basis of a short corolla

tube (< 4 cm long), in contrast to sect. *Siphonanthus* with a much longer corolla tube. However, the length of corolla tube discussed by Wearn *et al.* (2019) is variable across several sections and is not diagnostic for the clade. This clade is named as section *Clerodendrum*, because it includes the type of *Clerodendrum*.

Clade B (Figs 3, 4, Sections *Fortunata* and *Densiflora*)

Clerodendrum fortunatum distributed in southeast China, Taiwan, Hong Kong, and Vietnam is sister to the rest of Clade B with strong support. However, this species has unique morphological characters that are not found in other species in the same clade. It differs from the rest species in Clade B by having an axillary inflorescence (vs. terminal) and large calyx lobes concealing corolla tube (as opposed narrowly triangular calyx lobes and exposed corolla tube). The presence of an axillary inflorescence resembles some members of Clade D, but all species in the latter clade have a significantly long corolla tube (> 30 mm long rather than 7–28 mm) and glabrous leaves, while *C. fortunatum* exhibits hairy leaves. In addition, this species has not been placed within any previous infrageneric classification. Consequently, a new monotypic section *Fortunata*, based on the type species, *C. fortunatum*, is proposed here (Table 3, Figs 4, SD, E).

The remaining species in Clade B display terminal, condensed, rounded, somewhat corymbose inflorescences, with white to creamy-white flowers directed upwards and with narrowly triangular calyx lobes (Table 3, Fig. 5F–H). Most species have calyx lobes shorter than calyx tube (except *C. chinense* (Osbeck) Mabb.) and their fruiting calyx is expanded and cup-shaped and sheath-like. With the exception of *C. cyrtophyllum* Turcz., all species develop the extrafloral nectary glands at the base of the lower surface of the leaves that can be found only in representatives in this clade (Fig. 5G). This occurrence plays an ecological function to attract insects, especially ants that may protect the plant (Blüthgen and Reifenrath 2003). Schauer (1847) and Lam (1919) placed *C. macrostegium* Schauer and *C. deflexum* Wall. in subsect. *Densiflora* on the basis of a cordate leaf and compacted inflorescences. However, in this study, these species fall in Clades A and E, respectively. This new placement of these species is more morphologically congruent with representatives in each clade. Moreover, Schauer (1847) and Lam (1919) placed *C. chinense* in subsect. *Densiflora* and Verdcourt (1992) raised the placement of this species to sectional rank, sect. *Densiflora*, with the indication of *C. chinense* as the type of the section. Since species in Clade B (except *C. fortunatum*) form a monophyletic group and display shared morphological characters, this group containing type of sect. *Densiflora* (Verdcourt 1992) is named sect. *Densiflora*.

Clade C (Figs 3, 4, Section *Tridens*)

Clade C is diagnosed morphologically by the shrubby habit and having peltate scales on the lower leaf surface (except *C. myrmecophilum* Ridl.), a band of hairs just above nodes, terminal, upright thyrsoid inflorescences, 3–5 lobed calyxes, and 12–22 mm long corolla tubes. In fresh field collections, the inflorescence, calyx, and corolla are conspicuous by the red (rarely yellow to orange) colour (Fig. 6A–C).

Most species in Clade C can be referred the previously recognized sect. *Squamata* as noted by Steane *et al.* (1997) based

Table 4. Comparison of diagnosed characters of African and Malagasy sections of the subgenus *Afroclerodendrum*.

| Characters | Sect. <i>Capitata</i> | Sect. <i>Cylindrocalyx</i> | Sect. <i>Eurycalyx</i> | Sect. <i>Macrocalyx</i> | Sect. <i>Megaflorea</i> | Sect. <i>Oxycalyx</i> | Sect. <i>Siphonocalyx</i> |
|------------------------|---------------------------------|--|---------------------------|---------------------------|---|-----------------------------|-----------------------------|
| Habit | Shrub, 0.3–4 m tall | Shrub to small tree, 3–5 m tall | Scandent shrub | Liana | Shrub to small tree, 2.5–3.5 m tall | Shrub, 2–3 tall | Liana |
| Inflorescence position | Terminal and axillary | Terminal and axillary | Terminal | Terminal and axillary | Terminal | Terminal | Terminal and axillary |
| Inflorescence type | Upright | Upright | Upright | Upright | Upright | Upright | Upright or pendulous |
| Inflorescence shape | Rounded | Spike-like to pyramidal | Spike-like to pyramidal | Spike-like to pyramidal | Spike-like to pyramidal | Spike-like to pyramidal | Spike-like to pyramidal |
| Cymes | Lax to condensed | Condensed | Condensed | Lax to condensed | Lax to condensed | Lax to condensed | Condensed |
| Calyx shape | Campanulate | Cylindrical | Campanulate | Campanulate | Cylindrical | Campanulate | Cylindrical-campanulate |
| Calyx tube length | 3–6 mm | Up to 10 mm | 2–2.5 mm | 3–7 mm | 1.1–4.5 cm | 1.2–6 mm | 2–5 mm |
| Calyx lobes length | 10–25 mm, much longer than tube | 3–5 mm, shorter than tube, splitting from 1/4 to 1/2 of its length | 1–2 mm, shorter than tube | 4–16 mm, longer than tube | 2–10 mm, shorter than tube, dividing 1/5 to 2/5 of its length | 4.5–10 mm, longer than tube | 0.8–2 mm, shorter than tube |
| Corolla tube length | 7–15 cm | 1.8–2.5 cm | 5–7.5 mm | 12–20 mm | 2.5–15.5(-22) cm | 1.4–4 cm | 6.5–25 mm |
| Corolla lobe length | 9.5–15 mm | 6–9 mm | 2–2.5 mm | 6.5–10 mm | 1.2–3.5 cm | 2.5–5.5 mm | 3–5.5 mm |

on having peltate scales and hairs just above the nodes (Schauer 1847, Lam 1919) and *C. japonicum* (Thunb.) Sweet (= *C. kaempferi* (Jacq.) Sieb.) was indicated as the type. However, the use of the rank section in sect. *Squamata* by Steane *et al.* (1997) was incorrect because the treatment of Moldenke (1985) using sectional rank was invalid due to lacking a reference to the basionym. *Clerodendrum brassii* E.Beer & H.J.Lam and *C. magnificum* Warb. form a sister relationship nested within Clade C (Fig. 3), and display a three-lobed calyx that places them within sect. *Tridens* established by Lam (1919) and was later supported by Wearn *et al.* (2019). Sect. *Tridens* was based on the type *C. elbertii* Hallier f. [syntypes L (L0017217!, L0003866!)] from south-eastern Malesia, which was noted to be conspecific with *C. brassii* by Wearn *et al.* (2019). Sect. *Tridens* is the only valid name at sectional rank for Clade C.

Clade D, (Figs 3, 4, Section *Siphonanthus*)

This clade contains Asian and Australian species that have glabrous leaves, terminal or axillary, lax inflorescences, white to creamy-white flowers, long corolla tube (3–10 cm long), and broadly triangular calyx lobes dividing to half of the calyx length (Fig. 6E, F). This clade is congruent with the existing morphology-based sect. *Siphonanthus* (Schauer 1847, Lam 1919, Yuan *et al.* 2010, Wearn *et al.* 2019) (Table 3). *Clerodendrum floribundum* was previously placed in subsect. *Axilliflora* of sect. *Clerodendrum* by Lam (1919), but this species resembles those of representatives in Clade D in morphology. The differences between species in this clade compared to its relative Clade E are discussed next. *Clerodendrum indicum* is treated as the type of the section (Steane *et al.* 1997, Wearn *et al.* 2019).

Clade E (Figs 3, 4, Section *Albiflora*)

Clade E in our study includes 24 species distributed from southern China to Australia. This clade is one of the most under-represented clades in prior studies, with only *C. quadriloculare* included (Yuan *et al.* 2010). Species in this section are morphologically variable, for example, shrub to tree habit, upright or pendulous elongated inflorescences, small to large calyx size and short to long corolla tube (Fig. 7A–G) but all species have a white to creamy-white corolla (rarely pale-yellow) on terminal inflorescences (Table 3). Most representatives in Clade E were treated in sect. *Clerodendrum sensu* Wearn *et al.* (2019) according to their corolla tube length being < 4 cm long. However, there are some species in Clade E with a long white corolla tube that may resemble those of sect. *Siphonanthus* (Clade D) by a combination of traits. *Clerodendrum smitinandii* Moldenke from this section is distinguished from those in sect. *Siphonanthus* by having an urceolate calyx shape (vs. campanulate in sect. *Siphonanthus*). *Clerodendrum quadriloculare* in this section has a calyx tube longer than lobes (vs. tube shorter or equal to lobes in sect. *Siphonanthus*). *Clerodendrum fistulosum* Becc. has pubescent stem and leaves and condensed cymes (vs. glabrous and lax cymes in sect. *Siphonanthus*).

Although Asian species with pendulous inflorescences can be found only in this clade, the presence of this character is homoplasious (red and blue arrows in Fig. 3) as species with the upright inflorescences, *C. longisepalum* Dop and *C. sp.1* [Du *et al.* HNK3478 (K001282560!)] are inserted among species with

pendulous inflorescences (single asterisk in Fig. 3). Likewise, *C. sp.2* [Kuznetsov *et al.* 1664 (K!)], a species with pendulous inflorescences (double asterisk in Fig. 3), is nested within a subclade of species with the upright inflorescences (dashed arrow in Fig. 3). Schauer (1847) recognized species with pendulous inflorescences in unranked *Penduliflora* and this concept was supported by Lam (1919) as subsect. *Penduliflora* including, e.g. *C. laevifolium*, *C. nutans*, and *C. umbratile* King & Gamble (red arrow in Fig. 3). These species could be considered as the possible type of the subsect *Penduliflora* (Schauer) H.J.Lam. However, this previous concept did not include another group of species having pendulous inflorescences (blue arrow in Fig. 3) such as *C. deflexum*, *C. garrettianum* Craib, and *C. schmidtii* C.B.Clarke. Since the morphological character of pendulous inflorescences is homoplasious, there is no reason to recognize species with pendulous inflorescences as separate sections or subsections based on this character. About half the number of species in the broader clade retain the character of upright inflorescence. No name has been applied to species in this clade at the rank of section, so species in Clade E are placed in a new section, sect. *Albiflora* and *C. nutans* is chosen to be the type of this section.

Clerodendrum in Africa and Madagascar

Clade F (Figs 3, 4, Section *Megaflora*)

This clade consists of endemic species from Madagascar producing distinctly large floral structures, especially calyx tube length (1.1–4.5 cm long), corolla tube 2.5–7 cm long, exceptionally long corolla tubes of certain species (mentioned next), corolla lobes size (1.2–3.5 cm long by 0.8–1.8 cm wide), on terminal and upright inflorescences, which are sometimes cauliflorous (Table 4, Fig. 8A–C). This clade is sister to the rest of the African clades and most representative species in this study have been unplaced in previous infrageneric taxa. In addition, these species cannot be morphologically referred to the existing infrageneric classification of Thomas (1936) and Verdcourt (1992). The one exception to this is *C. Sylvestre* Moldenke. This species was placed in invalid sect. *Siphonocalyx* by Thomas (1936), but it is morphologically incongruent with that section due to having a long calyx tube, at least 1.1 cm long (vs. up to 5 mm long in sect. *Siphonocalyx*). One Malagasy species in this study, *C. aucubifolium* Hemsl. exhibits a much longer corolla tube (15–15.5 cm long) than other species in this clade and roughly resembles those of species in Clade L but differs in having a longer calyx tube length. A long corolla tube is also found in *C. kamhyoae* Phillipson & Allorge (not included in this study), which has a 19–22-cm long corolla tube and c. 4-cm long calyx (Phillipson and Allorge 2016). This clade is circumscribed as the new section *Megaflora* and *C. aucubifolium* is designated as its type (Fig. 8A).

Clade G (Figs 3, 4, Section *Cylindrocalyx*)

Species in Clade G display a long calyx tube (c. 1 cm long) with very short calyx lobes splitting one-quarter to one-third of its length, 1.8–2.5-cm long corolla tubes on the terminal and axillary condensed inflorescences and accrescent calyces larger than fruits (Table 4, Fig. 8D, E). There are two species



Figure 8. Selected diagnostic characters of sect. *Megaflora* (A–C), sect. *Cylindrocalyx* (D and E) and sect. *Eurycalyx* (F and G). A, Flowering branch of *C. aucubifolium*. B, Flower of *C. moramangense*. C, Flowers of *C. rubellum*. D, Flowering branch of *C. hildebrandtii*. E, Flowering branch of *C. phlomidis*. F, Flowers of *C. volubile*. G, Flowers of *C. melanocrater*. All photos by J. Saththaphorn. Specimens: A [Rakotonasola 1062 (K)], B [Razafimandimbison 185 (K)], C [Razafimandimbison 724 (K)], D [Polhill & Paulo 743 (K)], E [Drummond 26186 (K)], F [Newbould & Harley 4263 (K)], and G [Drummond & Harley 4578 (K)].

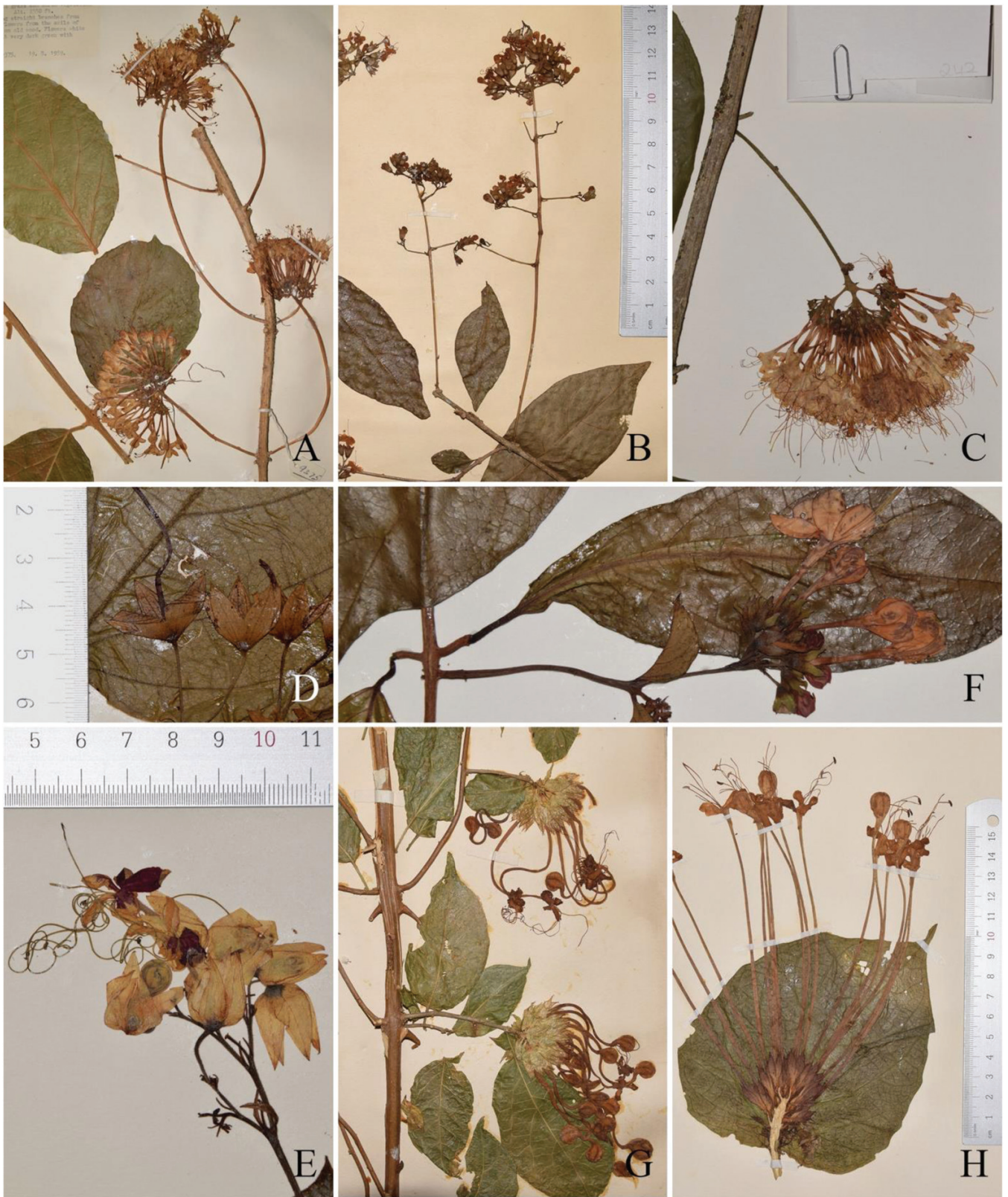


Figure 9. Selected diagnostic characters of sect. *Siphonocalyx* (A–C), sect. *Macrocalyx* (D and E), sect. *Oxycalyx* (F) and sect. *Capitata* (G–H). A, Flowering branch of *C. schweinfurthii*. B, Flowering branch of *C. silvanum*. C, Inflorescence of *C. schweinfurthii*. D, Calyx of *C. welwitschii*. E, Inflorescence of *C. fuscum*. F, Axillary inflorescence of *C. splendens*. G, Flowering branch of *C. capitata*. H, Inflorescence of *C. poggei*. All photos by J. Sattaphorn. Specimens: A & C [Harley 9375 (K)], B [Drummond 4433 (K)], D [Lisowski 16871 (K)], E [Eilu 243 (K)], F [Diabate et al. 1230 (K)], G [Howells 5 (K)], and H [Eggleing 3703 (K)].

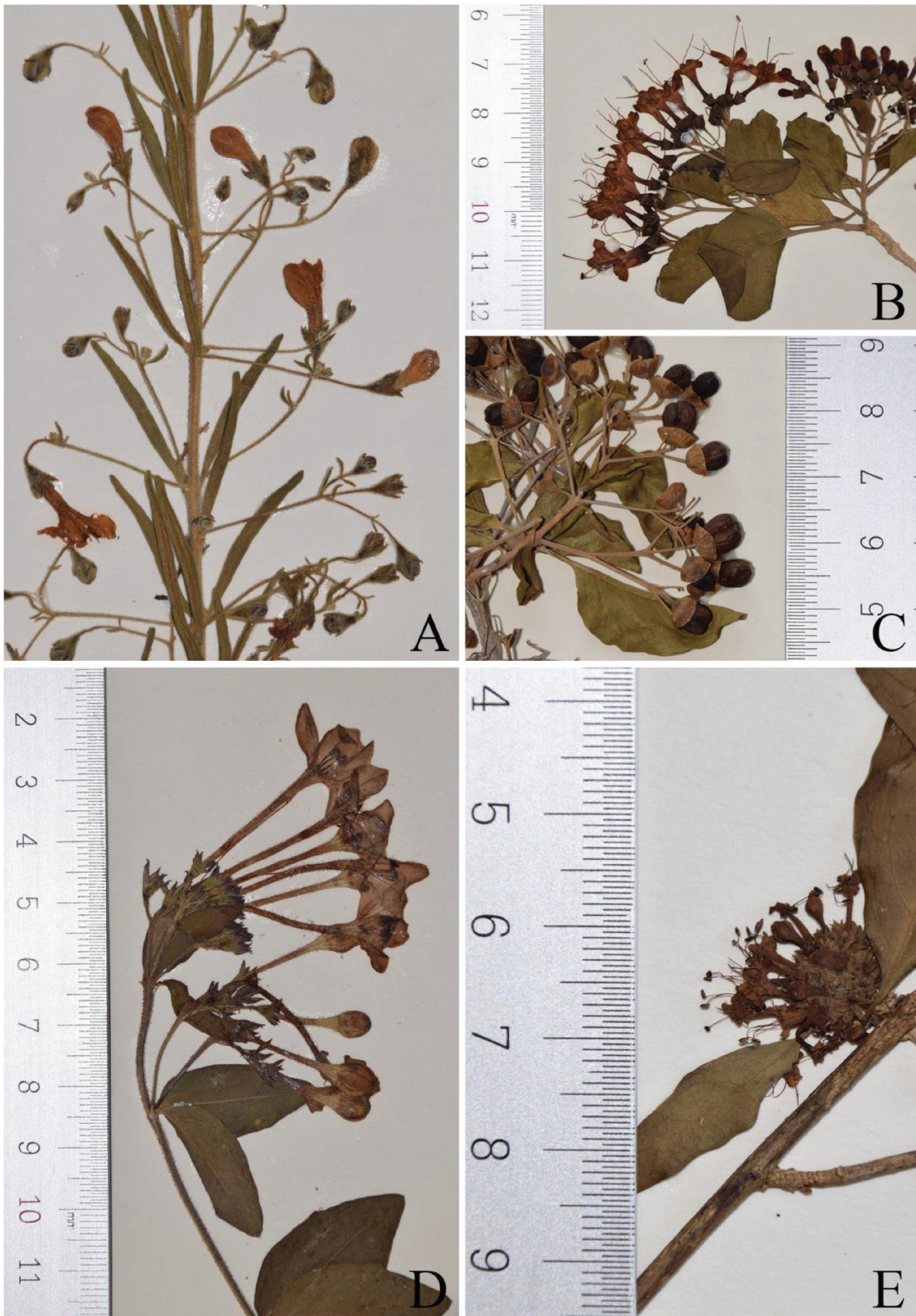


Figure 10. Clerodendrum species nested within the New World clade. A, Flowering branch of *C. parvulum* [Clarkson 4812 (K)]; B, flowering branch of *C. laciniatum* [Coode 4307 (K)]; C, fruiting branch of *C. laciniatum* [Coode 4307 (K)]; D, flowering branch of *C. tatei* [Evans 3578 (K)]; and E, flowering branch of *C. globosum* [Phillipson & Raharilala 4110 (K)].

in this clade, *C. hildebrandtii* and *C. phlomidis*, and this clade is sister to Clades H–L (Fig. 3). The east African *C. hildebrandtii* was placed in sect. *Cylindrocalyx* by Thomas (1936) and was validated and typified as a monotypic section by Verdcourt (1992). A previous study based on a parsimony analysis of ITS sequences found *C. phlomidis* and *C. hildebrandtii* to form a clade (MohanMarugaRaja and Devarajan 2017). We confirm that *C. phlomidis*, a native to the western Indian subcontinent, forms a strongly supported sister relationship with *C. hildebrandtii* and morphological characters of these two species are similar. The phylogenetic position of *C. phlomidis* embedded in the African and Malagasy Clade suggests that the origin of *C. phlomidis* may be in Africa or Madagascar.

There are other cases of genera in Lamiaceae that display an Asian–African disjunction within a clade. This relationship of an Asian species embedded in an African Clade was also reported by Paton *et al.* (2018) in the case of *Plectranthus gardneri* Twaites and by Ryding (1998) in the case of *Leucas milanjaniana* Gürke. By contrast, some species originated from Asia and moved to Africa. For example, the north-eastern African species *Otostegia integrifolia* Benth. (= *Rydingia integrifolia* (Benth.) Scheen & V.A. Albert) was found to embed within an Asian clade (Scheen and Albert 2009). A similar example is as the African *Isodon ramosissimus* (Hook.f.) Codd and *I. schimperi* (Vatke) J.K. Morton (Yu *et al.* 2014). The common ancestors of these species showing a disjunct distribution with relatives may have evolved and migrated across the African/Asian boundary in humid and arid periods during the early Miocene, 20–14 Myr during the uplift of eastern Africa (DeMenocal 2004, Wolfenden *et al.* 2004, Trauth *et al.* 2005).

Clade H (Figs 3, 4, Section *Eurycalyx*)

This clade comprises species having morphologically distinctive characters from other African species due to their very short calyx length (2–5 mm long) with lobes dividing to two-thirds to half of its length and very short corolla tube, < 1 cm long on terminal and upright inflorescences (Table 4, Fig. 8F, G). Two species, *C. volubile* P.Beauv. and *C. melanocrater* Gürke, belong to this clade. Based on their similar morphology, Thomas (1936) and Verdcourt (1992) placed these species in sect. *Eurycalyx* and Verdcourt (1992) indicated *C. volubile* as the type species.

Clade I (Figs 3, 4, Section *Siphonocalyx*)

Species in Clade I share the characters of liana habit and condensed, terminal, or axillary and upright or pendulous inflorescences with a cylindrical-campanulate calyx with lobes shorter than the tube, 0.8–2 vs. 2–5 mm long, and corolla tubes 6.5–25 mm long (Table 4, Fig. 9A, B). Representatives in this clade were treated under different sections in previous studies. Thomas (1936) recognized sect. *Siphonocalyx* by having a cylindrical-tubular calyx with short-triangular lobes and sect. *Microcalyx* by having campanulate-infundibular calyx with the calyx widened toward apex, and acute calyx lobes (Table 4, Fig. 9A, B). Verdcourt (1992) designated *C. silvanum* Henriq. as the type of sect. *Siphonocalyx* and *C. formicarum* Gürke (not included in our study) as the type of sect. *Microcalyx*. From investigation of specimens, these two sectional type species have a wide range of calyx shape. Variation is continuous between the two states

cylindrical-tubular or campanulate-infundibular. This variation of calyx shape can be also found in *C. hircinum* in Clade I (Fig. 3). In the same treatment, *C. johnstonii* Oliv. was placed in sect. *Microcalyx*, while *C. schweinfurthii* Gürke was placed in sect. *Siphonocalyx*, although they are sister species in our study. *Clerodendrum hircinum*, *C. johnstonii* and *C. schweinfurthii*, including the types of sections, show similarities regarding calyx shape and can be referred to both the existing sect. *Siphonocalyx* and sect. *Microcalyx*. The molecular phylogenetic placement and morphological investigation (Fig. 3, Clade I) support the synonymy of sect. *Microcalyx* under the earlier established sect. *Siphonocalyx*.

Clade J (Figs 3, 4, Section *Oxycalyx*)

This clade accommodates two African species: *C. pleiosciadium* and *C. welwitschii* and is sister to Clade K plus Clade L. Species in this clade are erect shrubs having campanulate calyces with lobes longer than the tube and a 1.4–4-cm long corolla tube. One of these, *C. pleiosciadium* is the type of the sect. *Oxycalyx* (Verdcourt 1992). The section was previously diagnosed by having calyx length of 0.5–1 cm, with lanceolate lobes and 1.2–3-cm long corolla tubes (Moldenke 1985, Verdcourt 1992). Our results show that *C. welwitschii*, a species previously placed in sect. *Macrocalyx* (Thomas 1936), is sister to *C. pleiosciadium* with a strong support, but this species has a calyx > 1 cm long, resembling those of Clade I. The habit of this species is a shrub similar to *C. pleiosciadium*, whereas species in Clade I are all lianas. It also has longer corolla tube than those in Clade I, being 1.4–4 cm long (vs. 1.2–2 cm long). Therefore, we recognize Clade J as sect. *Oxycalyx* (Table 4, Fig. 9D).

Clade K (Figs 3, 4, Section *Macrocalyx*)

Clade K comprises lianas with terminal or axillary, upright, lax to condensed inflorescences, calyx lobes being longer than tube and with a short corolla tube, up to 2 cm long. According to the existing infrageneric classification, Verdcourt (1992) recognized *C. thomsoniae* Balf.f. as the type of sect. *Macrocalyx* based on its 1–3-cm long calyx on lax inflorescences. Thomas (1936) divided this section into three subsections: subsect. *Capitata*, subsect. *Spicata* and subsect. *Laxiflora*. Verdcourt (1992) later raised subsect. *Capitata* and subsect. *Spicata* to sect. *Capitata* that are shrubs with long corolla tubes, 7–15 cm (see Clade L next). From the morphological investigations, most species of this Clade K have red corollas (except *C. Umbellatum* Poir.) and have several shared characters with *C. thomsoniae*, such as habit, calyx size, and corolla length. This clade is named sect. *Macrocalyx*.

Clade L (Figs 3, 4, Section *Capitata*)

Clade L consists of species sharing their terminal or axillary upright and rounded inflorescences with 7–15-cm long corolla tubes, calyx lobes being longer than the tube, and white to creamy-white corolla colour. Thomas (1936) proposed subsect. *Capitata* of sect. *Macrocalyx* was later raised to the sectional rank by Verdcourt (1992) with an indication of *C. capitatum* (Willd.) Schumacher as the type of section. Steane *et al.* (1997) suggested that *C. capitatum* with *C. buchneri* Gürke and *C. cephalanthum* Oliv. are in the same group but noted the poor support. However, this study fully supports the relationship (and

these species have similar characters regarding habit, calyx, and corolla) (Table 4, Fig. 9G, H). This clade is hence referred to existing sect. *Capitata* based on the type of section, *C. capitata*.

Impact of methodology on topology

Both trimmed datasets of exons and supercontigs were selected to construct phylogenetic trees; these results represent better phylogenetic resolution, because missing data prior to trimming can affect tree topology due to phylogenetic noise (Shah *et al.* 2021b). Minor differences of topologies and dissimilar species placements were observed based on the different datasets and approaches. However, these conflicts between topologies are mostly found within the Asian clade and might result from fast-evolving sites treated by the concatenated approach (Xi *et al.* 2014). In this study, the supercontigs dataset is favoured because it has intronic regions that contain more variable informative and rapidly evolving sites (Dodsworth *et al.* 2019). This dataset also includes more variable sites and a greater alignment length (Table 2). Results using the supercontigs datasets have supported the morphology-based taxa concepts and produced well-resolved trees even with missing data in previous studies, e.g. Nute *et al.* (2018), Larridon *et al.* (2020, 2021).

CONCLUSION

Clerodendrum is monophyletic with the exception of four Australian and Indian ocean species (*C. globosum*, *C. laciniatum*, *C. tatei*, and *C. parvulum*), which are more closely related to *Volkameria inermis* and share morphological similarities with that species. Further work is required to determine whether other Australian species belong to the *Volkameria* Clade. The remainder of *Clerodendrum* is divided in two sister clades: an Asian and Australian Clade and an African and Malagasy Clade. These two major clades are formally recognized here as different subgenera, subgen. *Clerodendrum* and the new subgen. *Afroclerodendrum*, according to different geographical regions Asia and Australia, and Africa and Madagascar, respectively, although the western Indian *C. phlomidis* falls within subgen. *Afroclerodendrum*. Previous sectional classifications within the Asian and Australian Clade are not supported, but the clade can be divided into six sections on the basis of morphologically diagnosable clades. Of these, sect. *Albiflora* and sect. *Fortunata* are proposed in this study. Within the African and Malagasy Clade, a Malagasy clade is sister to the remainder of the African Clade and sect. *Megaflora* is proposed for this clade. The remainder of the African Clade can be divided into six monophyletic sections that mostly match with the treatment of Verdcourt's classification. Molecular evidence has shed light on the phylogenetic relationships. This understanding allows further study of morphological variation and provides important insights into the infrageneric classification. The phylogenetic placement of *C. phlomidis* encourages further biogeographic study to explore the continental disjunction. Regional or monographic revisions and biogeographic study are required to delimit *Clerodendrum*

species and to better understand the natural history of the genus in the future.

Taxonomic treatment

In this study, we included some species that are not sampled in the molecular study (Supporting Information, Table S5), but are likely to belong in one of the following sections based on morphological similarity. The unsampled species mentioned in this work highlight particular morphological characters to demonstrate variation or assumed relationships. Taxa recognized here are based on the results of the analysis and herbarium based morphological study. The key below allows placement of most species into one of the recognized sections within subgen. *Clerodendrum* (Clades A–E) or subgen. *Afroclerodendrum* (Clades F–L). Information of geography is needed to identify the subgenus and a combination of morphological characters is necessary to place species at sectional rank. The aim is to provide an infrageneric treatment that accounts for previously published infrageneric taxa and the combination of morphological characters observed in species of *Clerodendrum* that can be tested by further phylogenetic research.

Some Australian and Indian ocean *Clerodendrum* that are found to be closely related with *Volkameria inermis* (Fig. 3) and their morphological characters can be referred to the member of the genus *Volkameria* discussed by Yuan *et al.* (2010) (Fig. 10). Hence, these species are transferred to the genus *Volkameria* and the combination is made formally at the end of the Taxonomic Treatment next.

***Clerodendrum* L.**, Sp. Pl. 2: 637. 1753 & Gen. Pl. ed. 5: 285. 1754. Type: *Clerodendrum infortunatum* L. (lectotype, designated by Moldenke & Moldenke, 1983).

= *Siphonanthus* L., Sp. Pl. 1: 109. 1753 & Gen. Pl. ed. 5: 47. 1754. Type: *Siphonanthus indicus* L.

= *Cryptanthus* Osbeck, Dagb. Ostind. Resa: 215. 1757, *nom. Rej.* Type: *Cyrptanthus chinensis* Osbeck.

= *Valdia* Boehm., Defin. Gen. Pl.: 39. 1760, *nom. Superfl.*

= *Marurang* Adans., Fam. Pl. 2: 226. 1763. Type: not indicated.

= *Bellevalia* Scop., Intr. Hist. Nat.: 198. 1777, *nom. Illegit.*

= *Montalbania* Necker, Elem. Bot.: 273. 1790, *nom. Illegit.*

= *Volkmannia* Jacq., Pl. Hort. Schoenbr. 3: 48. 1798. Type: *Volkmannia japonica* Jacq.

= *Agricolaea* Schrank, Denkschr. Königl. Akad. Wiss. München 1808: 98. 1808. Type: *Agricolaea fragrans* Schrank.

= *Egena* Raf., Fl. Tellur. 2: 85. 1837. Type: *Egena emirnenensis* (Bojrt ex Hook.) Raf.

= *Adelosa* Blume, Ann. Mus. Bot. Lugduno-Batavi 1: 176. 1849. Type: *Adelosa microphylla* Blume.

= *Cleianthus* Lour. Ex B.A. Gomes, Mem. Acad. Real Sci. Lisboa, 2 Cl. Sci. Moraes, n.s., 4(1): 28. 1868. Type: *Cleianthus coccineus* Lour. Ex Gomes.

= *Siphoboea* Baill., Bull. Soc. Linn. Paris 1: 722. 1888. Type: *Siphoboea commersonii* Baill.

= *Archboldia* E. Beer & H.J. Lam, Blumea 2: 31. 1936. Type: *Archboldia ericoides* E. Beer & H.J. Lam.

Key to sections of *Clerodendrum*

- 1 Asian or Australian plants (excluding Indian *C. phlomidis*, sect. *Cylindrocalyx*) 2
 1' African plants (including Indian *C. phlomidis*) 7
 2 Corolla red, rarely yellow to orange; stem nodes with a band of hairs **6. sect. *Tridens***
 2' Corolla white to creamy-white, pink, rarely pale-yellow to yellow; stem nodes without a band of hairs 3
 3 Inflorescences rounded, somewhat corymbose; cymes condensed; flowers upright; lower surface of leaves bearing sessile glands at base (except *C. canescens* and *C. cyrtophyllum*) **3. sect. *Densiflora***
 3' Inflorescences spike-like to pyramidal, rarely globose; cymes lax to condensed; flowers downward-pointing or spreading; lower surface of leaves without sessile glands at base 4
 4 Shrubs; corolla tube always > 3 cm long **5. sect. *Siphonanthus***
 4' Shrubs to trees; corolla tube usually up to 3 cm (if longer than 3 cm, then a tree) 5
 5 Inflorescences axillary **4. sect. *Fortunata***
 5' Inflorescences terminal 6
 6 Calyx lobe usually broadly ovate; corolla with or without pink blotches; stems villose; inflorescences upright
 **2. sect. *Clerodendrum***
 6' Calyx lobes usually triangular; corolla without pink blotches; stems glabrous to pubescent or pilose; inflorescence upright or pendulous **1. sect. *Albiflora***
 7 Plants lianas 8
 7' Plants shrub, scandent shrub, or tree 9
 8 Calyx lobes ≤ 2 mm long, shorter than tube; corolla lobes < 6.5 mm long; inflorescences upright or pendulous, cymes condensed. **13. sect. *Siphonocalyx***
 8' Calyx lobes > 2 mm long, longer than tube; corolla lobes at least 6.5 mm long; inflorescences upright, cymes lax to condensed **10. sect. *Macrocalyx***
 9 Calyx tube at least 11 mm long **11. sect. *Megaflora***
 9' Calyx tube < 11 mm long 10
 10 Corolla tube ≤ 7.5 mm long **9. sect. *Eurycalyx***
 10' Corolla tube > 7.5 mm long 11
 11 Calyx tube cylindrical (sides parallel), longer than lobes **8. sect. *Cylindrocalyx***
 11' Calyx tube campanulate, shorter than lobes 12
 12 Corolla tube ≤ 4 cm long, lobes 2.5–5.5 mm long **12. sect. *Oxycalyx***
 12' Corolla tube > 4 cm long, lobes 9.5–15 mm long **7. sect. *Capitata***

Subgenus *Clerodendrum*

This subgenus includes Asian and Australian *Clerodendrum*, and can be recognized by having a shrub, small tree to tree habit, campanulate to urceolate calyx with a 0.5–8 mm long tube. Six sections belong to *Clerodendrum* subgenus *Clerodendrum*

1. *Clerodendrum* section *Albiflora* Satthaphorn, sect. nov.
Type: *Clerodendrum nutans* Wall. ex Jack.

= *Clerodendrum* unranked *Penduliflora* Schauer in DC., Prodr. 11: 663. 1847.

= *Clerodendrum* subsection *Penduliflora* (Schauer) H.J.Lam, Verben. Malay. Archip.: 264. 1919.

Shrub or tree, 0.4–10 m tall. **Stem** slender to robust, ±quad-rangular in cross-section, glabrous to pubescent or pilose; nodes without a band of hairs. **Leaves** variable in shape, 3–39 cm long, 1–18 cm wide, glabrous to pubescent or pilose, lower surface of leaves without large sessile glands at base. **Inflorescence** thyrsoid, spike-like to pyramidal, rarely globose, terminal, upright or pendulous, glabrous to pubescent or pilose; cyme lax to condensed; flowers downward-pointing or spreading. **Calyx** white to greenish-white, green, reddish-green, yellowish-green, pink to red, rarely dark purple, campanulate or urceolate, glabrous to pubescent or pilose, with or without glandular hairs (capitate glandular or peltate glandular trichomes), without dark sessile glands; tube 0.5–6

mm long; lobes usually triangular, spreading, 2–18 mm long, shorter or longer than tube; fruiting calyx accrescent, reflexed or not. **Corolla** white to creamy-white, rarely pale-yellow to yellow, lacking pink blotches at centre, glabrous to pubescent or pilose, with or without glandular hairs; tube 0.8–3 cm long (3.4–4 cm long in *C. smitinandii*, 7–8 cm long in *C. quadriloculare*); lobes obovate or oblong to oblong-obovate in outline, 4–22 mm long, rarely undulate. **Fruits** subglobose, green to red, ripening black.

Species included: 29 species ([Supporting Information, Table S5](#)).

Distribution: Indian subcontinent to south China, Indo-China, and Malesia.

Note: *Clerodendrum* section *Albiflora* superficially resembles members of related sect. *Siphonanthus* in having white to creamy-white corolla colours. Sect. *Albiflora* is distinguishable by having shorter corolla tube being < 3 cm long, while those of sect. *Siphonanthus* are > 3 cm long. With some exceptions, a combination of traits is required to identify the section. *Clerodendrum quadriloculare* and *C. smitinandii*, belonging to sect. *Albiflora*, have corolla tubes > 3 cm long, but they differ from members of sect. *Siphonanthus* by exhibiting a tree habit (vs. shrub in sect. *Siphonanthus*).

This new section is based on Asian species having upright or pendulous inflorescences with white to creamy-white (rarely pale-yellow) corollas. Sect. *Albiflora* includes some species with pendulous inflorescence that were treated in subsect. *Penduliflora*, some species with an upright inflorescence were also placed within subsect. *Axilliflora* by Schauer (1847) and Lam (1919) such as *C. calamitosum* L., *C. disparifolium*, and *C. lankawiense* King & Gamble. As names only have priority at the rank at which they were published, neither *Penduliflora* nor *Axilliflora* need to be used as epithets as the basis for the name at sectional rank. *Penduliflora* would be inappropriate as not all species have pendulous inflorescences. Schauer's unranked *Axilliflora* could be typified with species now placed in *Volkameria*, since that genus has axillary inflorescences, and most species treated in subsect. *Axilliflora* have been transferred to *Ovieda* and *Volkameria*. The typification of unranked *Axilliflora* will be considered with further work on the species that fall into the *Volkameria* Clade.

The name of this section refers to the shared characteristic of species having white to creamy-white corolla colour.

1.2. *Clerodendrum* section *Clerodendrum* Schauer in DC., Prodr. 11: 658. 1847; Wearn *et al.* in Bramley *et al.*, Fl. Malesiana 23: 92. 2019. Type: *Clerodendrum infortunatum* L.

= *Clerodendrum* unranked *Paniculata* Schauer in DC., Prodr. 11: 666. 1847.

= *Clerodendrum* subsection *Paniculata* (Schauer) H.J.Lam, Verben. Malay. Archip.: 270. 1919, *nom. illegit.*

shrub, 1–3 m tall. **Stem** robust, quadrangular in cross-section, with villose hairs; nodes without a band of hairs. **Leaves** subcoriaceous, variable in shape, mostly broadly ovate or cordate, 5–26 cm long, 2.5–20 cm wide, pubescent on both sides, lower surface of leaves without large sessile glands at base. **Inflorescence** thyrsoid, spike-like to pyramidal, terminal, upright, pubescent; cymes lax to condensed; flowers spreading. **Calyx** green to reddish-green, campanulate, pubescent with capitate glandular and peltate glandular trichomes, without dark sessile glands; tube 2–4 mm long; lobes usually broadly ovate, 2.5–13 mm long, longer or equal to calyx tube; fruiting calyx accrescent, reflexed, white or red. **Corolla** white to creamy-white, with pink blotches at centre, pubescent; tube 7–25 mm long; lobes oblong, 4–15 mm long, margin usually undulate. **Fruits** subglobose, green to black.

Species included: Eight species (Supporting Information, Table S5).

Distribution: Indian subcontinent to south and south-eastern China, Japan, Indo-China, Malesia, and northern Australia.

Note: This section accommodates *C. infortunatum*, the type species of the genus that had been placed in subsect. *Paniculata* (Lam 1919) and unranked *Paniculata* (Schauer 1847). As the type of the genus *Clerodendrum*, it must belong to sect. *Clerodendrum*. Verdcourt (1992) corrected the nomenclature, and the change was supported by Wearn *et al.* (2019).

The morphological characters of species within sect. *Clerodendrum* resemble those of sect. *Albiflora*. A combination of characters is needed to identify sectional rank, such as the type of hairs on stem, shape of calyx lobes, and the presence of

pendulous inflorescences. Some species in this section, such as *C. infortunatum* and *C. villosum*, display pink blotches at the central area of the corolla that can be used to consider the sectional placement of these species. This study requires further revision to clarify the taxonomic characters and placement within sect. *Clerodendrum*.

1.3. *Clerodendrum* section *Densiflora* (Schauer) Verdcourt, Fl. Trop. E. Africa, Verben.: 85. 1992. Type: *Clerodendrum chinense* (Osbeck) Mabb.

= *Clerodendrum* subsection *Densiflora* (Schauer) H.J.Lam, Verben. Malay. Archip.: 259. 1919.

= *Clerodendrum* unranked *Densiflora* Schauer in DC., Prodr. 11: 664. 1847.

Shrub to small tree, 1–6 m tall. **Stem** robust, ±quadrangular in cross-section, glabrous to pubescent; nodes without a band of hairs. **Leaves** subcoriaceous, variable in shape, 5.5–30 cm long, 3.2–27 cm wide, pubescent on both sides, or villose, lower surface bearing large sessile glands at base (except *C. cyrtophyllum* and *C. canescens*). **Inflorescence** thyrsoid, congested, rounded to corymbose, terminal, upright, pubescent; cymes condensed; flowers upright. **Calyx** green or reddish-green, to red, campanulate, pubescent, with or without sessile glands; tube 1.5–8 mm long; lobes triangular, 0.8–12 mm long, shorter or equal to calyx tube length (except in *C. chinense*); fruiting calyx cup-shaped, green to red, spreading and flattening out in fruit. **Corolla** white to creamy-white, pinkish-white or pink; tube 3.5–28 mm long; lobes ovate, oblong to oblong-obovate, 1.5–15 mm long. **Fruits** globose, green to red, ripening black.

Species included: Eight species (Supporting Information, Table S5).

Distribution: Himalaya to south China, Indo-China, and Malesia.

Note: Lam (1919) recognized the unranked *Densiflora* of Schauer (1847) at subsection level in *Verbenaceae of the Malayan Archipelago*. Verdcourt (1992) validly raised it to section for the *Flora of Tropical East Africa* based on the cultivated Asian species in Africa and designated *C. chinense* as the lectotype of this section.

1.4. *Clerodendrum* section *Fortunata* Sathaphorn, **sect. nov.** Type: *Clerodendrum fortunatum* L.

Shrub, 1–1.5 m tall. **Stem** slender, ±quadrangular in cross-section, densely pubescent; nodes without a band of hairs. **Leaves** chartaceous, elliptic to oblong-elliptic, 5.5–18 long, 1.2–4 cm wide; upper surface, glabrous, pubescent on veins; lower surface densely pubescent especially on veins, without large sessile glands at base. **Inflorescence** a compound cyme, spike-like to pyramidal, axillary, upright, 3.5–5.5 cm long, densely pubescent; cymes lax; flowers spreading. **Calyx** red to purple, campanulate, conspicuous, pubescent at base and margin, without dark sessile glands; tube 0.8–1 mm long; lobes ovate-triangular, 9–12 by 5.5–7 mm; fruiting calyx not reflexed, red to purple, lobes 9–15 by 4–5 mm. **Corolla** white to creamy-white, glabrous to slightly pubescent; tube 9–12 mm long; lobes oblong, 6–8.5 by 3.5–4.5 mm. **Fruit** subglobose, 5–8 mm in diameter, 2–4-lobed, ripening black.

Species included: Only one species, *C. fortunatum*.

Distribution: South-east China, Taiwan, Hong Kong, and Vietnam.

Note: *Clerodendrum* sect. *Fortunatum* is unique from other Asian and Australian sections as the only species, *C. fortunatum*, has an axillary inflorescence and short corolla tube (9–12 mm long). Species with axillary inflorescences can be found in sect. *Siphonanthus*, but the corolla tube of these species are more than 3-cm long. This species is also distinguishable by its morphology from its sister group sect. *Densiflora* (Table 3, Figs 3–SD, E). Further study is needed to investigate the closest relatives of *C. fortunatum*.

1.5. *Clerodendrum* section *Siphonanthus* Schauer in DC., Prodr. 11: 670. 1847; H.J.Lam, Verben. Malay. Archip.: 248. 1919; Wearn *et al.* in Bramley *et al.*, Fl. Malesiana 23: 93. 2019. *Type:* *Clerodendrum indicum* (L.) Kuntze.

= *Clerodendrum* subgenus *Siphonanthus* (L.) Moldenke, Phytologia 57: 339. 1985, *nom. inval.*

Shrub, 1–3 m tall. **Stem** robust, quadrangular in cross-section, glabrous; nodes without a band of hairs. **Leaves** subcoriaceous, linear, elliptic to oblong-elliptic, 4–27 cm long, 0.7–11 cm wide; upper surface glabrous; lower surface glabrous to glabrescent, without large sessile glands at base. **Inflorescence** compound cyme or thyrsoïd, spike-like, terminal, or axillary, upright, glabrous; cymes lax to condensed; flowers downward or spreading. **Calyx** green to reddish-green, campanulate, glabrous, without dark sessile glands; tube 2–7 mm long; lanceolate to broadly triangular, 3.5–8 mm long, longer or equal to tube; fruiting calyx accrescent, red, reflexed. **Corolla** white to creamy-white, glabrous, with capitate glandular trichomes; tube (3–)5–10 cm long; lobes oblong or elliptic to oblong-obovate, 10–15 mm long. **Fruits** subglobose, deeply lobed, green to red, ripening black.

Species included: Six species (Supporting Information, Table S5).

Distribution: Indian subcontinent to south China, Indo-China, Malesia, and northern Australia.

Note: Schauer (1847) described this section based on species presenting a long corolla and afterwards it was adopted by Lam (1919) for Malesian species. Moldenke (1985) raised this section to the subgenus level but the subgeneric name was considered as invalid due to the lack of a full and direct citation of the basionym (Turland *et al.* 2018; Article 41.5). Wearn *et al.* (2019) retained Schauer (1847) and Lam (1919)'s sect. *Siphonanthus*.

1.6. *Clerodendrum* section *Tridens* H.J.Lam. Verben. Malay. Archip.: 316. 1919. *Type:* *Clerodendrum elbertii* Hallier f.

= *Clerodendrum* unranked *Squamata* Schauer in DC., Prodr. 11: 668. 1847.

= *Clerodendrum* subsection *Squamata* (Schauer) H.J.Lam, Verben. Malay. Archip.: 294. 1919. *Type:* *Clerodendrum japonicum* (Thunb.) Sweet.

= *Clerodendrum* section *Oxycalyx* subsection *Fallax* Verdcourt, Fl. Trop. E. Africa, Verben.: 85. 1992, **syn. nov.** *Type:* *Clerodendrum speciosissimum* Jacob-Makoy (= *C. fallax* Lindl.).

Shrub, 1–2.5 m tall. **Stem** slender to robust, quadrangular in cross-section, glabrous to pubescent; nodes with a band of hairs. **Leaves** subcoriaceous, broadly ovate or cordate in outline, unlobed to deeply 3–7-lobed, 4–40 cm long, 4–36 cm wide, pubescent on both sides, lower surface with scattered peltate glandular scales, without large sessile glands at base. **Inflorescence** thyrsoïd, spike-like to pyramidal, terminal, upright, pubescent, with or without with capitate glandular trichomes; cymes condensed; flowers spreading. **Calyx** green or red, rarely yellow to orange, campanulate, pubescent, with or without peltate glandular trichomes, without dark sessile glands; tube 1–5 mm long; lobes 5, elliptic, lanceolate to oblong-lanceolate or triangular, 3–15 mm long, longer than tube; fruiting calyx reflexed, red. **Corolla** red, rarely yellow to orange, pubescent, with or without capitate glandular trichomes; tube 12–22 mm long; lobes oblong to oblong-obovate, 5–14 mm long, margin entire to undulate, reflexed. **Fruits** subglobose, green to red, turning black when mature.

Species included: Nine species (Supporting Information, Table S5).

Distribution: Indian subcontinent to southeast China, Indo-China, and Malesia.

Note: This section consists of most species previously placed in subsect. *Squamata* with the type, *C. japonicum* (= *C. kaempferi*) (Schauer 1847, Steane *et al.* 1997). However, our results reveal that representatives of sect. *Tridens* (*C. brassii* and *C. magnificum*) assigned by Lam (1919) and Wearn *et al.* (2019) are nested with species previously placed in subsect. *Squamata*.

Verdcourt (1992) established subsect. *Fallax* under African sect. *Oxycalyx* that was based on the Asian cultivated species *C. speciosissimum* Jacob-Makoy (= *C. fallax* Lindl.) as type. Nevertheless, this species is found to be within sect. *Tridens* in our study and the sect. *Oxycalyx* subsect. *Fallax* is synonymized under sect. *Tridens* here.

2. *Clerodendrum* subgenus *Afroclerodendrum* Sathaphorn, subgen. nov.

Species in this subgenus can be found in mainland Africa and Madagascar and characterized by being shrubs, scandent shrubs, lianas (absence in Asian and African *Clerodendrum*), or small trees. The calyx ranges found from campanulate to cylindrical with 1.2–45 mm long tube, and corolla tube length is up to 22 cm long. This subgenus includes one western Indian species, *C. phlomidis*, belonging to sect. *Cylindrocalyx*. The calyx characters of *C. phlomidis* distinguish it from all Asian or Australian species in having a cylindrical shape and being up to 10 mm long. Seven sections belong to *Clerodendrum* subgenus *Afroclerodendrum*.

2.1. *Clerodendrum* section *Capitata* Verdcourt, Fl. Trop. E. Africa, Verben.: 85. 1992. *Type:* *Clerodendrum capitatum* (Willd.) Schumach.

Shrub, 0.3–4 m tall. **Stem** robust, more or less quadrangular in cross-section, pubescent; nodes without a band of hairs. **Leaves** chartaceous, variable in shape, 3–23 cm long, 2.5–13.5 cm wide, surface, pubescent on both sides, without large sessile

glands at base. **Inflorescence** thyrsoid, rounded, terminal and axillary, upright, pubescent; cymes lax to condensed; flowers upright, showy. **Calyx** green or purplish-red, campanulate; tube 3–6 mm long; lobes lanceolate, 10–25 mm long, much longer than tube; fruiting calyx accrescent, not reflexed, mostly enclosing fruits, red. **Corolla** white to creamy-white; tube 7–15 cm long; lobes oblong-ovate, 9.5–15 mm long. **Fruits** subglobose, usually deeply lobed, green to red, turning black when mature.

Species included: Seven species ([Supporting Information, Table S5](#)).

Distribution: Tropical Africa.

2.2. *Clerodendrum* section *Cylindrocalyx* Verdcourt, Fl. Trop. E. Africa, Verben.: 85. 1992. *Type:* *Clerodendrum hildebrandtii* Vatke.

Shrub to small tree, 3–5 m tall. **Stem** robust, terete to quadrangular in cross-section, much branched, glabrous; nodes without a band of hairs. **Leaves** subcoriaceous and somewhat fleshy, orbicular to ovate, length and width subequal, 0.8–8.5 cm long, 0.8–9.5 cm wide, pubescent on both sides, without large sessile glands at base. **Inflorescence** thyrsoid, spike-like to pyramidal, terminal, or axillary, upright, glabrous; cymes condensed; flowers upright. **Calyx** green, cylindrical (parallel sided); tube up to 10 mm long; lobes triangular, 3–5 mm long, shorter than tube, splitting from a quarter to half of its length; fruiting calyx accrescent, reflexed, smaller than fruits, red. **Corolla** white to creamy-white; tube 1.8–2.5 cm long; lobes oblong-ovate, 6–9 mm long. **Fruits** subglobose, deeply four-lobed, green to red, turning black when mature.

Species included: Only two species were included: *C. hildebrandtii* and *C. phlomidis* ([Supporting Information, Table S5](#)).

Distribution: East Ethiopia to north-east Mozambique (*C. hildebrandtii*) and Indian subcontinent (*C. phlomidis*).

2.3. *Clerodendrum* section *Eurycalyx* Verdcourt, Fl. Trop. E. Africa, Verben.: 85. 1992. *Type:* *Clerodendrum volubile* P. Beauv.

Scandent shrub. **Stem** slender, more or less quadrangular in cross-section, much branched, glabrous; nodes without a band of hairs. **Leaves** chartaceous, variable in shape, mostly elliptic in outline, 6–16 cm long, 2–6 cm wide, glabrous on both sides, without large sessile glands at base. **Inflorescence** thyrsoid, spike-like to pyramidal, terminal, upright, pubescent; cymes condensed; flowers spreading. **Calyx** green to whitish-green or yellow, campanulate, pubescent; tube 2–2.5 mm long; lobes triangular, 1–2 mm long, shorter than tube; fruiting calyx accrescent, not reflexed, spreading to sheet, smaller than fruit. **Corolla** white to creamy-white or yellowish-green, pubescent; tube 5–7.5 mm long; lobes oblong, 2–2.5 mm long. **Fruits** globose to subglobose, deeply 2–4-lobed, green to red, turning black when mature.

Species included: Two species: *C. volubile* and *C. melanocrater* ([Supporting Information, Table S5](#)).

Distribution: Tropical Africa.

2.4. *Clerodendrum* section *Macrocalyx* Verdcourt, Fl. Trop. E. Africa, Verben.: 85. 1992. *Type:* *Clerodendrum thomsoniae* Balf.f.

= *Clerodendrum* section *Oxycalyx* subsection *Apiculata* Verdcourt, Fl. Trop. E. Africa, Verben.: 85. 1992, **syn. Nov.** *Type:* *Clerodendrum splendens* G. Don.

Liana. **Stem** slender, ± quadrangular in cross-section, glabrous to pubescent; nodes without a band of hairs. **Leaves** chartaceous, variable in shape, elliptic in outline, 2.5–14.5 cm long, 1.5–7 cm wide, pubescent on both sides, without large sessile glands at base. **Inflorescence** thyrsoid, spike-like to pyramidal, terminal and axillary, upright, pubescent; cymes lax to condensed; flowers spreading. **Calyx** white, green to whitish-green or greenish-red, campanulate; tube 3–7 mm long; lobes triangular, 4–16 mm long, longer than tube; fruiting calyx accrescent, reflexed, turning red when mature. **Corolla** white to greenish-white or red, sometimes with pink at centre; tube 12–20 mm long; lobes oblong-ovate, 6.5–10 mm long. **Fruits** globose to subglobose, 2–4-lobed, green to red, turning black when mature.

Species included: Four species ([Supporting Information, Table S5](#)).

Distribution: West central, west tropical Africa.

Note: Verdcourt (1992) designated *C. splendens* as the type of subsect. *Apiculata* within sect. *Oxycalyx*. This species falls within sect. *Macrocalyx* in our phylogenetic study. We formally synonymize sect. *Oxycalyx* subsect. *Apiculata* under sect. *Macrocalyx* here.

2.5. *Clerodendrum* section *Megaflora* Sathaphorn, **sect. nov.** *Type:* *Clerodendrum aucubifolium* Hemsl.

Shrub to small tree, 2.5–3.5 m tall. **Stem** robust, terete, glabrous, light to dark brown, lenticellate; nodes without a band of hairs. **Leaves** opposite, coriaceous, thick cuticle, elliptic to oblong-ovate, 4–23 cm long, 2–10 cm wide, apex acute to acuminate, based cuneate or rounded, margin entire, glabrous or pubescent on both sides, without large sessile glands at base. **Inflorescence** thyrsoid, spike-like to pyramidal, terminal, upright, sometimes cauliflorous, glabrous; cymes lax to condensed; flowers upright, showy. **Calyx**, green, cylindrical, glabrous to pubescent; tube much longer than lobes, 1.1–4.5 cm long; lobes 2–10 mm long, shorter than tube, minutely triangular, shorter than tube, dividing from less than one- to two-fifths of its length; fruiting calyx accrescent, not reflexed, enclosing fruit. **Corolla** white to pink, sometimes with pink to purple blotches at base of corolla lobes, glabrous; tube 2.5–15.5(–22) cm long; lobes oblong, usually longer than tube, 1.2–3.5 cm long. **Fruits** subglobose, unlobed to four-lobed, green, turning black in mature, enclosed by accrescent calyx.

Species included: Nine species ([Supporting Information, Table S5](#)).

Distribution: Madagascar.

Note: *Clerodendrum* sect. *Megaflora* is confined to Malagasy species. The morphological characters of the species members may resemble those of sect. *Capitata* by having a showy floral structure, especially corolla tube (2.5–15.5 cm long in sect. *Megaflora* vs. 7–15 cm long in sect. *Capitata*). The calyx tube length is different as those of sect. *Megaflora* are at least 11 mm long, as opposed to 3–6 cm long in sect. *Capitata*. However, some Malagasy

species fall into the sect. *Siphonocalyx*, but sect. *Megaflora* are shrubs or small trees (vs. lianas in sect. *Siphonocalyx*).

Megaflora refers to species in this clade having large flowers, especially the corolla lobes.

2.6. *Clerodendrum* section *Oxycalyx* Verdcourt, Fl. Trop. E. Africa, Verben.: 85. 1992. *Type: Clerodendrum pleiosciadium* Gürke.

= *Clerodendrum* section *Oxycalyx* subsection *Oxycalyx* Verdcourt, Fl. Trop. E. Africa, Verben.: 85. 1992.

Shrub, 2–3 m tall. **Stem** terete to multi-angular in cross-section, slightly pubescent; nodes without a band of hairs. **Leaves** chartaceous, variable in shape, 6–17.5 cm long, 5–13 cm wide, pubescent on both sides, without large sessile glands at base. **Inflorescence** thyrsoïd, terminal, spike-like to pyramidal, upright, pubescent; cymes lax to condensed; flowers upright. **Calyx** green, campanulate; tube 1.2–6 mm long; lobes triangular, 4.5–10 mm long, longer than tube; fruiting calyx accrescent, not reflex, spreading to cup shape, covering up to half-length of fruits. **Corolla** white to creamy-white; tube 1.4–4 cm long; lobes obovate-oblong, 2.5–5.5 mm long. **Fruits** globose to subglobose, deeply 2–4-lobed, green to red, turning black when mature.

Species included: Two species, *C. pleiosciadium* and *C. welwitschii* Gürke (Supporting Information, Table S5).

Distribution: South tropical to South Africa.

Note: Verdcourt (1992) recognized two subsections apart from the type of subsection: subsect. *Apiculata* Verdcourt and subsect. *Fallax* Verdcourt under sect. *Oxycalyx*. However, the first subsect. *Apiculata* is based on *C. splendens*, which is phylogenetically placed in sect. *Macrocalyx* in our study. The second subsect. *Fallax* based on the type *C. speciosissimum* falls in sect. *Tridens* in this treatment.

2.7. *Clerodendrum* section *Siphonocalyx* Verdcourt, Fl. Trop. E. Africa, Verben.: 85. 1992. *Type: Clerodendrum silvanum* Henriq.

= *Clerodendrum* section *Microcalyx* Verdcourt, Fl. Trop. E. Africa, Verben.: 86. 1992, **syn. nov.** *Type: Clerodendrum formicarum* Gürke.

Liana. **Stem** robust, terete to \pm quadrangular in cross-section, glabrous; nodes without a band of hairs. **Leaves** chartaceous, variable in shape, mostly elliptic or obovate in outline, 6.8–16 cm long, 3.8–10 cm wide, upper surface glabrous or pubescent, lower surface pubescent, without large sessile glands at base. **Inflorescence** thyrsoïd, spike-like to pyramidal, terminal and axillary, upright or pendulous, pubescent; cymes condensed; flowers spreading. **Calyx** green, cylindrical-campanulate, tube 2–5 mm long; lobes triangular, 0.8–2 mm long, shorter than tube; fruiting calyx accrescent, not reflex, spreading to cup-shaped, covering more or less to half-length of fruits. **Corolla** white; tube length variable, 6.5–25 mm long; lobes oblong, 3–5.5 mm long. **Fruits** subglobose, deeply 2–4-lobed, green to red, turning black when mature.

Species included: Ten species (Supporting Information, Table S5).

Distribution: Tropical and northeast Africa and Madagascar.

Note: From our investigation of herbarium specimens, we found that *C. formicarum*, the type species of sect. *Microcalyx*, shows the morphological similarities to members of sect. *Siphonocalyx*. For this reason, sect. *Microcalyx* is synonymized here under sect. *Siphonocalyx*. Further work is necessary to resolve the phylogenetic relationships of *C. formicarum* and its allies in the previously recognized sect. *Microcalyx*.

NEW COMBINATIONS IN VOLKAMERIA

1. *Volkameria laciniata* (Balf.f.) Saththaphorn, **comb. nov.**

≡ *Clerodendrum laciniatum* Balf.f., J. Linn. Soc., Bot. 16: 19. 1877.
Type: Mauritius, Balfour *s.n.* [holotype K (K000192977!).]

2. *Volkameria globosa* (Moldenke) Saththaphorn, **comb. nov.**

≡ *Clerodendrum globosum* Moldenke, Amer. J. Bot. 38. 324. 1951. *Type:* Madagascar, Environs de Tulear: Delta du Fiherenana, Humbert 2468 [holotype *n.v.*; isotypes G (G00366322!), K (K000192975!), MO (MO-345984!).]

3. *Volkameria parvula* (L.S.Sm.) Saththaphorn, **comb. nov.**

≡ *Clerodendrum parvulum* L.S.Sm., Contr. Queensland Herb. No. 6: 19. 1969; Moldenke, Fifth Summary Verbenac.: 345. 1971, Sixth Summary Verbenac.: 335. 1980. *Type:* Australia, Queensland, 35 miles E of Musgrave Telegraph Office, Pedley 2647 [holotype BRI (BRI-AQ0024372!).]

4. *Volkameria tatei* (Munir) Saththaphorn, **comb. nov.**

≡ *Clerodendrum tatei* (F.Muell.) Munir, J. Adelaide Bot. Gard. 11(2): 143. 1989.—*Strobilanthes tatei* F.Muell. in Trans. & Proc. Roy. Soc. South Australia 5: 81. 1882. *Type:* Australia, Northern Territory, at the Twelve Mile, McKinlay River, Arnhem Land, Tate *s.n.* [Lectotype MEL (MEL 0602001!), selected by Munir (1989); isolectotype AD (AD98802061!).]

= *Clerodendrum holtzei* F.Muell. in J. Proc. Roy. Soc. New S. Wales 24: 75. 1891; Moldenke, Resume Verbenac.: 148, 208, 264: 1959, Fifth Summary Verbenac.: 247. 345. 446. 462. 1971, Sixth Summary Verbenac.: 237. 334. 1980; Dunlop, Checklist Vasc. Pl. N. Territory: 79. 1987; Barker, J. Adelaide Bot. Gard. 9: 281. 1986. *Type:* Australia, Northern Territory, near Port Darwin, Holtze 109 [syntype G (G00366147!), KFTA (KFTA0000506!), LE (LE00016585!); Holtze 802 [syntypes MEL (MEL0098250!); Holtze 995 [syntypes MEL (MEL0098245!, MEL0098246!); Holtze *s.n.* [syntypes CM (CM211025!), G (G00366145!), K (K000910243!), MEL (MEL0098247!, MEL0098248!, MEL0098249!), NSW, *n. v.*, Z, *n. v.*].

SUPPLEMENTARY DATA

Supplementary data is available at *Botanical Journal of the Linnean Society* online.

Figure S1. Heatmap of recovery of the Angiosperms353 probes for all accessions included in this study.

Figure S2. Phylogenetic reconstruction of *Clerodendrum* based on analysis of the exons dataset. Species trees inferred in ASTRAL from RAxML gene trees. Numbers by branch represent local posterior probabilities (LPPs) and branches without number indicate full supports. Pie charts correspond to quartet support.

Figure S3. Phylogenetic reconstruction of *Clerodendrum* based on analysis of the exons dataset. Species trees of Concatenate IQTREE analysis inferred from RAxML gene trees. Numbers by nodes represent bootstrap value.

Figure S4. Phylogenetic reconstruction of *Clerodendrum* based on analysis of the supercontigs dataset. Species trees of Concatenate IQTREE analysis inferred from RAxML gene trees. Numbers by nodes represent bootstrap value.

Table S1. Voucher information, accession numbers, previous infrageneric classification of *Clerodendrum* species included in this study.

Table S2. Percentage recovery of the targeted genes by the Angiosperms353 baits for all accessions included in this study.

Table S3. A, AMAS statistics generated for the untrimmed exons dataset; B, AMAS statistics generated for the untrimmed supercontigs dataset.

Table S4. A, AMAS statistics generated for the trimmed exons dataset; B, AMAS statistics generated for the trimmed supercontigs dataset.

Table S5. Revised infrageneric classifications of *Clerodendrum* species included in this study and unsampled species.

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AUTHOR CONTRIBUTIONS

J.S. and A.J.P. designed the study and wrote the manuscript. J.S. and C.L. collected and identified specimens. J.S., A.R.Z., and R.S.C. performed the laboratory works and supported the analyses. J.S., A.J.P., and C.L. interpreted data and discussed results.

CONFLICT OF INTERESTS

The authors declare that they have no conflict of interests.

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