Phylogenetic relationships between *Clerodendrum* (Lamiaceae) and other Ajugoid genera inferred from nuclear and chloroplast DNA sequence data

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Abstract

Over the last two centuries the circumscription of the large, pan-tropical genus *Clerodendrum* (Lamiaceae) has changed frequently, as different authorities have added or removed taxa on the basis of various morphological characters. With the development of molecular methods for systematic research the process of circumscribing taxa has become increasingly analytical. When morphology signals the possibility that taxa are closely related, molecular methods can be used to test the hypothesis objectively. *Aegiphila*, *Amasonia*, *Huxleya*, and *Kalaharia* are similar morphologically to *Clerodendrum*. In this paper we use nuclear ribosomal ITS and chloroplast *ndh*F sequence data to clarify the positions of these four genera relative to *Clerodendrum*. We show that the Australian monotypic genus *Huxleya* evolved from within *Clerodendrum*. Accordingly, we sink *Huxleya* into *Clerodendrum* and make a new combination, *Clerodendrum linifolium*.
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1. Introduction

Throughout its taxonomic history *Clerodendrum* (Ajugoideae; Lamiaceae) has been delimited in many ways, some delimitations being more inclusive than others. *Clerodendrum s.l.* has been divided between as many as a dozen different genera; sometimes these smaller genera were divided among different families (e.g., De Necker, 1790; Westman, 1744). Nineteenth and 20th century taxonomic and phylogenetic studies did much to rectify this, but even now, especially with the development of molecular systematic methods, the delimitation of *Clerodendrum* continues to be modified.

Cladistic analyses using chloroplast DNA (cpDNA) restriction site data (Steane et al., 1997) and ITS (internal transcribed spacer) sequence data from the nuclear ribosomal DNA (nrDNA; Steane et al., 1999) resulted in the separation of a large group of species from *Clerodendrum s.l.*, placing them in the resurrected genus *Rotheca* Raf. (Steane and Mabberley, 1998). Two tropical genera, *Oxera* Labill. and *Faradaya* F. Muell. formed the sister group to the clade containing the remaining species of *Clerodendrum*. *Clerodendrum* (*sensu* Steane and Mabberley, 1998) comprises ca. 350 species distributed through the tropical/subtropical regions of Africa, Asia, and Pacific Oceania, with fewer representatives in the New World. Sequence data from the chloroplast *ndh*F gene (Steane et al., 1997) provided preliminary evidence that *Clerodendrum* is polyphyletic, and that the North American genus *Tetraclea* A. Gray should be included therein. In this paper we examine the taxonomic positions of four more labiate genera in relation to *Clerodendrum*: *Aegiphila* Jacq., *Amasonia* L.f., *Huxleya* Ewart and Rees, and *Kalaharia* Baillon. We also examine the positions of these taxa in the broader context of subfamily Ajugoideae.

During studies on the systematics of *Oxera*, *Faradaya*, and *Hosea*, the problem of the relative placement

of *Huxleya* became prominent (De Kok, 1997). *Huxleya linifolia* is endemic to the Northern Territory of Australia and is similar in growth form to another northern Australian endemic, *Clerodendrum tatei* (F. Muell.) Munir. However, when it was first described, *Huxleya* was placed with *Oxera* and *Faradaya* in the Verbenaceae subtribe Oxereae (Ewart and Rees, 1912). Recent morphological and chemical analyses (De Kok et al., 2000) suggested that *Huxleya* is, in fact, closer to *Clerodendrum* than to *Oxera*, *Faradaya* or *Hosea*.

Another genus from the Australian/Indomalesian region that may have close affinities with *Clerodendrum* is *Glossocarya* Wallich ex Griffith (9 species in Indomalesia and Australia). This genus shares a particular "*Clerodendrum*" pollen type (Raj, 1983) with *Clerodendrum*, *Aegiphila*, *Amasonia*, several species of *Caryopteris*, *Faradaya*, *Hosea*, *Huxleya*, *Kalaharia*, *Oncinocalyx*, *Oxera*, and *Tetraclea*. Unfortunately no material of *Glossocarya* was available for this study.

The plant upon which Schinz (1890) founded his *Clerodendrum uncinatum* was collected in the north-west Kalahari, hence the generic name *Kalaharia* (Baillon, 1892; Pearson, 1912). *Kalaharia uncinata* (Schinz) Mold. was incorporated into *Clerodendrum* as a monotypic subgenus by Thomas (1936), on the basis of the form of the four-locular ovary and the drupaceous fruit that divides into four one-seeded pyrenes. Since then the ranking of the taxon has been inconsistent, with Moldenke (1985) maintaining it as a genus, Cantino et al. (1992) including it in *Clerodendrum*, Verdcourt (1992) giving it subgeneric status within *Clerodendrum s.l.*, and Herman and Retief (2002) placing it in the genus *Rotheca*.

Two tropical American genera are included in this study. *Aegiphila* comprises 150 species and *Amasonia* has just eight. In his morphological study of the Lamiaceae, Cantino (1992a) found *Aegiphila* and *Amasonia* to belong to a monophyletic group with genera of tribes Clerodendreae and Caryopterideae. Their exact positions within that clade (as well as the positions of *Huxleya*, *Kalaharia* and many of the infrageneric taxa of *Clerodendrum s.l.*) were unresolved.

In this paper we use nuclear ribosomal ITS sequence data to clarify the positions of *Kalaharia* and *Huxleya* relative to *Clerodendrum*. In addition, we have expanded our previous *ndh*F data set (Steane et al., 1997) to include *Aegiphila*, *Amasonia*, *Huxleya*, and *Kalaharia*, and four other taxa from subfamily Ajugoideae.

2. Materials and methods

Table 1 lists the new samples that were not used in the previous studies (Steane et al., 1997, 1999). Forty-two ITS sequences were included in the analyses, including 23 accessions of *Clerodendrum*, 10 of *Rotheca*, and nine representing other genera of Lamiaceae subfamily Ajugoideae. Most of these sequences were used by Steane et al. (1997, 1999), except for *Amasonia*, *Huxleya*, *Kalaharia*, and *Tetraclea*. The *ndh*F data set consists of 26 Ajugoideae taxa, including *Aegiphila*, *Amasonia*, *Huxleya*, *Kalaharia*, and six other genera not included by Steane et al. (1997), plus 10 non-Ajugoideae outgroups. Total DNA was extracted from fresh or silica gel dried leaf tissue (Chase and Hills, 1991) using the protocol of Doyle and Doyle (1990). The 5.8S nrDNA and flanking ITS regions were amplified and sequenced using the protocols described by Steane et al. (1999). The chloroplast gene *ndh*F was amplified and sequenced as described by Olmstead and Sweere (1994) and Olmstead and Reeves (1995). New sequences were aligned by eye to the aligned ITS sequences from Steane et al. (1999) and the *ndh*F data set from Steane et al. (1997). Alignment gaps were scored as separate binary characters following the 'simple gap coding' method of Simmons and Ochoterena (2000). Parsimony analyses were carried out using PAUP* ver. 4.0b10 (Swofford, 2002) using heuristic searches with 1000 replicates, each with ten random order entry starting trees, TBR branch swapping, and saving multiple trees at each step (MULTREES on). Taxa that were common to the two data sets were incorporated into a combined ITS/*ndh*F data set. In some cases the two data sets contained different species of a genus (e.g., *Caryopteris incana* and *Caryopteris clandonensis*; *Oxera pulchella* and *Oxera macrocalyx*), and these data were combined for the third data set. There were no ITS data for *Aegiphila*, but because of its importance to this study, it was included in the "combined" data set with the ITS data coded as missing. Four outgroup taxa for which there were no ITS data (*Lamium purpureum*, *Pogostemon cablin*, *Holmskioldia sanguinea*, and *Scutellaria bolanderi*) were also included in the combined data set. All data sets were bootstrapped 1000 times following DeBry and Olmstead (2000), using 10 random order entry starting trees per replicate, TBR branch swapping and MULTREES off. The incongruence length difference (ILD) test of Farris et al. (1994) was calculated to determine whether the ITS and *ndh*F data sets were significantly different from random subsets of the same size drawn from a combined data set.

Maximum likelihood (ML; PAUP* ver. 4.0b10, Swofford, 2002) and Bayesian (MrBayes 2.01, Huelsenbeck and Ronquist, 2001) analyses were conducted for all three data sets using substitution models estimated using Modeltest v. 3.06 (Posada and Crandall, 1998). Because the results from all these analyses were congruent with the results of the maximum parsimony analyses, the results of the Bayesian and ML analyses are not presented here.

Table 1
New samples not previously sequenced for *ndh*F and/or ITS by Steane et al. (1997) and Steane et al. (1999)

Taxon	Subfamily	Voucher	Genbank Accession No.	
			*ndh*F	ITS
Aegiphila costaricensis	Teucrioideae	*Wendt et al., 3622* TEX	AY310121	n.a.
Ajuga reptans	Teucrioideae	*S. Wagstaff 89-07* BHO	L36391	n.a.
Amasonia sp.	Teucrioideae	*Giulietti et al., PCD 6176* K	AY310122	AY307079
Amethystea caerulea	Teucrioideae	*P. Cantino 1329* BHO	AY310123	n.a.
Callicarpa mollis	Viticoideae	Living specimen, Missouri B.G. accession no. 897684	AY310134	n.a.
Caryopteris divaricata	Teucrioideae	No voucher	U78679	n.a.
Caryopteris odorata (= *C. bicolor*)	Teucrioideae	*Spooner & Jha 6916* WIS	U78680	n.a.
Clerodendrum buchanani	Teucrioideae	*M. Hedren s.n.* UPS	AY310124	Steane et al., 1999 (U77742)
Clerodendrum schweinfurthii	Teucrioideae	*Steane 82*, FHO	AY310125	Steane et al., 1999 (U77768)
Clerodendrum splendens	Teucrioideae	NBGZ*	AY310126	Steane et al., 1999 (U77770)
Congea tomentosa	Symphorematoideae	*Anon. 36821* FTG	U78689	n.a.
Faradaya splendida	Teucrioideae	*H. Rimpler 2144* FB	AY310127	Steane et al., 1999 (U77773)
Huxleya linifolia	Teucrioideae	*I. D. Cowie 8213, iii. 1999,* CANB, DNA and K	AY310128	AY307078
Kalaharia uncinata	Teucrioideae	*Goyder et al., 3838*, K	AY310130	n.a.
Kalaharia uncinata	Teucrioideae	*Goyder et al., 3799*, K	AY310129	AY307080
Karomia speciosa	Teucrioideae	*Steane 71*, FHO	AY310131	Steane et al., 1999 (U77774)
Oxera pulchella	Teucrioideae	*H. Rimpler 1328* FB	AY310132	n.a.
Prostanthera rotundifolia	Chloanthoideae	Wagstaff et al., 1995; no voucher	U78702	n.a.
Spartothamnella teucriiflora	Teucrioideae	*Keighery & Gibson 1740* PERTH	AY310133	n.a.
Tectona grandis	Unassigned	No voucher	U78705	n.a.
Tetraclea coulteri	Teucrioideae	*K.-J. Kim 10026* TEX	U78706	AY307081
Teucridium parviflorum	Teucrioideae	*Olmstead & Wagstaff 92-228* WTU	U78684	n.a.
Vitex agnus-castus	Viticoideae	*K.-J. Kim 2804* TEX	U78707	n.a.

*NBGZ, National Botanic Garden, Zimbabwe.

3. Results

3.1. Phylogenetic analysis of ITS sequence data

The ITS data set comprised 41 taxa, 941 aligned bases and 15 binary gap characters. Of the 908 unambiguously aligned bases (see below), 261 were potentially informative for parsimony analysis (469 were constant, 193 were autapomorphic). Fifteen phylogenetically informative alignment gaps were coded as binary characters. The method of alignment followed that of Steane et al. (1999), where one particular sequence tract in ITS 1 (ca. 120 bp) was aligned easily within *Clerodendrum* and *Rotheca* individually, but not between these genera. To overcome alignment problems while preserving phylogenetic information within each genus, gaps were inserted alternately in this region in each group of taxa. Specifically, aligned positions 62–184 consisted of sequence data in *Clerodendrum* and gaps in *Rotheca*; positions 185–309 comprised gaps in *Clerodendrum* and

sequence data in *Rotheca*; sequence data were alignable between these genera from base 1 to base 61 and from base 310 onwards. Sequence data within this region (bases 62–309) were omitted from the outgroup taxa because alignment with either one of the two genera was ambiguous. In addition to this large region of ambiguity, five short segments of the aligned ITS sequence (totalling 33 bases) could not be aligned unambiguously and were excluded from the analysis.

Parsimony analysis of the ITS data resulted in four most parsimonious trees of 1049 steps (consistency index, CI = 0.633; retention index, RI = 0.738). Fig. 1 shows the four major clades identified by Steane et al. (1997): I, Asian *Clerodendrum* (96% bootstrap support); II, African *Clerodendrum* (96%); III, pan-tropical *Clerodendrum* (91%); IV, *Rotheca* (100%). *Huxleya* is sister to *Clerodendrum inerme* in clade III (99% bootstrap support for *Huxleya* + *C. inerme*). *Kalaharia* is resolved as sister to a clade composed of *Clerodendrum* + *Huxleya*, *Tetraclea*, and *Amasonia*.
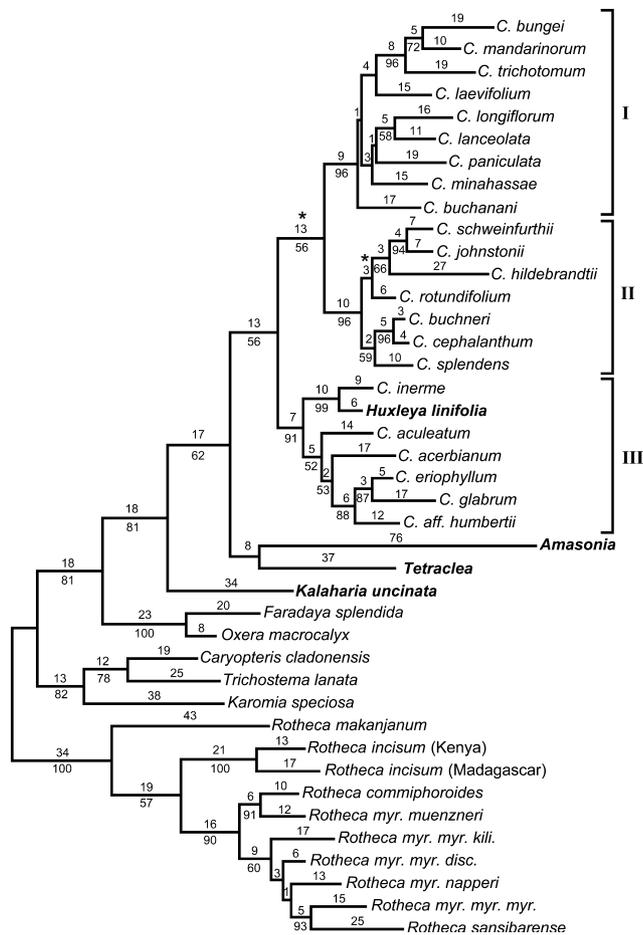
Fig. 1. One of four most parsimonious trees of 1049 steps (CI = 0.633; RI = 0.738) obtained from cladistic analysis of nuclear ribosomal ITS sequence data. Clades I, II, and III of *Clerodendrum* (Steane et al., 1997, 1999) are shown. Genera that have been suggested to be close to, or congeneric with, *Clerodendrum* are shown in bold. Branch lengths are shown above branches. Bootstrap percentages greater than 50% are shown below branches. Asterisks mark branches that collapse in the strict consensus. *Rotheca* abbreviations: *myr, myricoides*; *disc, discolor*; and *kili, kilimandscharense*.
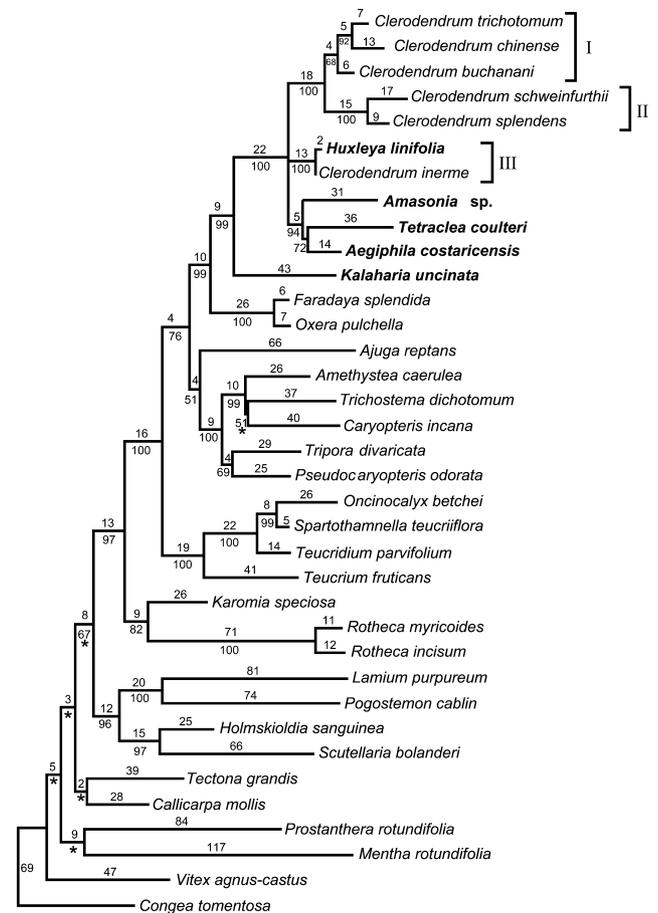

Fig. 2. One of 18 most parsimonious trees of 1574 steps (CI = 0.649; RI = 0.691) obtained from cladistic analysis of chloroplast *ndh*F sequence data. Clades I, II, and III of *Clerodendrum* (Steane et al., 1997, 1999) are indicated with Roman numerals. See legend to Fig. 1 for more details.

3.2. Phylogenetic analysis of ndhF data

The *ndh*F data set comprised 36 taxa and 2107 aligned bases (1341 constant, 360 autapomorphic, and 406 parsimony informative) plus four parsimony-informative gaps coded as binary characters. Parsimony analysis yielded 18 most parsimonious trees of length 1574 (CI = 0.649, RI = 0.691). The topology of the *ndh*F tree (Fig. 2) is consistent with that from the ITS data except for the position of *Karomia*. *Huxleya* and *Clerodendrum inerme* form a clade (representing "Clade III" in Fig. 2; 100% bootstrap support). A "New World" clade comprising *Amasonia*, *Tetraclea*, and *Aegiphila* (94%) is monophyletic and together with *Clerodendrum* + *Huxleya* forms a more inclusive clade (100%). The *ndh*F data concur with ITS in finding *Kalaharia* to be sister to *Clerodendrum* plus *Huxleya*,

Tetraclea, *Aegiphila*, and *Amasonia* (inclusive bootstrap = 99%). Also in agreement with the ITS data, *Faradaya* and *Oxera* form a monophyletic group that is sister to *Kalaharia*, *Clerodendrum*, *Aegiphila*, *Amasonia*, *Huxleya*, and *Tetraclea* (inclusive bootstrap support = 99%). *Karomia speciosa* appears to be sister to *Rotheca* (inclusive bootstrap support = 82%), although connected by a very short branch (Fig. 2). The above-mentioned taxa represent subfamily Ajugoideae (or clade Teucrioideae *sensu* Cantino et al., 1997), a taxon that in this analysis has 97% bootstrap support.

3.3. Combined analysis

Because the results of the ITS and *ndh*F analyses were largely consistent, the 16 taxa common to the two data sets, plus the *ndh*F data from *Aegiphila* and four outgroup taxa (*Lamium*, *Pogostemon*, *Holmskioldia*, and *Scutellaria*), were combined to form a third data matrix comprising 21 taxa and 3067 characters, with the goal of resolving the relationships of *Tetraclea*, *Amasonia*, and

Aegiphila with *Clerodendrum* and *Huxleya*. Thirty-three ITS positions were excluded due to alignment ambiguity and a total of 463 bases were potentially phylogenetically informative. *Caryopteris* was represented by the ITS sequence of *C. clandonensis* and the *ndh*F sequence of *C. incana*. *Oxera* was represented by the ITS sequence of *O. macrocalyx* and the *ndh*F sequence of *O. pulchella*. The ILD test was significant ($p = 0.01$); however, with *Karomia* excluded the results were not significant ($p = 0.13$). The ILD test is useful as a tool for exploring heterogeneity in data sets, but probably should not be used as an arbiter of whether data sets should be combined (Barker and Lutzoni, 2002; Yoder et al., 2001).

Analysis of the combined data set yielded two trees (Fig. 3; length = 1467, CI = 0.762, RI = 0.733). *Huxleya* is sister to *C. inerme* (100%) and the three clades of *Clerodendrum* have high bootstrap support (Fig. 3). *Tetraclea*, *Aegiphila*, and *Amasonia* form a well-supported clade (96%) with *Clerodendrum* and *Huxleya* (inclusive bootstrap 100%). *Kalaharia* is the sister taxon to the five aforementioned genera, and this all-inclusive clade has 99% bootstrap support. The results from the combined data set agreed with the *ndh*F data set in finding *Karomia* to be the sister taxon to *Rotheca*, although the bootstrap support for this in the combined
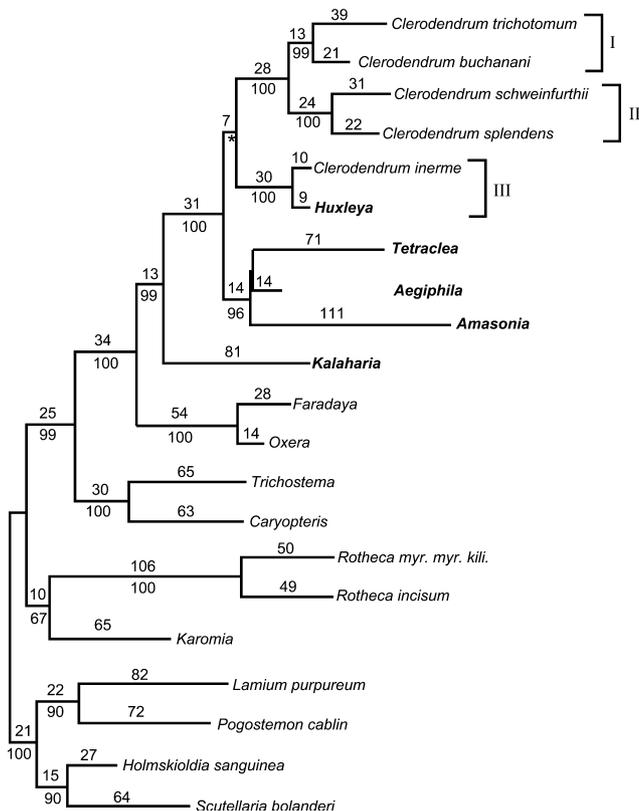

Fig. 3. One of two most parsimonious tree of 1467 steps (CI = 0.762; RI = 0.733) obtained by cladistic analysis of a combined data set comprising taxa that were common to the ITS and *ndh*F data sets. Clades I, II, and III of *Clerodendrum* (Steane et al., 1999) are indicated with Roman numerals. See legend to Fig. 1 for more details.

analysis was low (67%) relative to the *ndh*F data set (82%).

4. Discussion

Previous research (see Steane et al., 1997, 1999) showed that *Clerodendrum s.l.* is polyphyletic. In order to create a monophyletic *Clerodendrum*, Steane and Mabberley (1998) removed two groups of species (subgenus *Clerodendrum* section *Konocalyx*, and subgenus *Cyclonema*) from *Clerodendrum s.l.* and placed them in *Rotheca* Raf. However, *ndh*F data (Steane et al., 1997) indicated that *Clerodendrum* (*sensu* Steane and Mabberley, 1998) was still paraphyletic, because it appeared that the North American genus *Tetraclea* was derived from within *Clerodendrum*. Our results confirm that *Clerodendrum* is paraphyletic although, ironically, *Tetraclea* does not appear to be the offending genus (see below). Instead, we have shown that the monotypic northern Australian genus, *Huxleya*, falls as sister group to *Clerodendrum inerme*, among the pan-tropical coastal group of *Clerodendrum* species (Clade III). This result supports De Kok et al. (2000) who reported many morphological and chemical similarities between *Huxleya* and *Clerodendrum*. The placement of *Huxleya* in the "pan-tropical" clade III of *Clerodendrum* is consistent with its biogeography. Clade III taxa include species from coastal areas of Africa, Madagascar, Asia, the West Indies, and Pacific Oceania (Steane et al., 1997). This is the first report of an Australian taxon belonging to Clade III; other Australian taxa (e.g., *C. tomentosum*, *C. lanceolatum*) belong to the "Asian" Clade II. De Kok et al. (2000) commented that the habit of *Huxleya* is atypical for *Clerodendrum*, but likened it to that of *Clerodendrum tatei*, that grows on Australia's north coast. It is possible that *C. tatei* may also belong to Clade III, but molecular testing would be required to confirm this.

Our molecular data suggest that *Huxleya* should be sunk into *Clerodendrum*, and we do so here.

Clerodendrum linifolium (Ewart and B. Rees) de Kok comb. nov. *Huxleya linifolia* Ewart and B. Rees, Proc. Roy. Soc. Vic. 25: 109 (1912). Type: Northern Australia, Port Darwin, 1892, *N. Holtze 1322* (lectotype: MEL!, isolectotype: MEL!)

Tetraclea, *Aegiphila*, and *Amasonia* are American taxa. *Tetraclea* comprises two North American species, while *Amasonia* has eight and *Aegiphila* has 150 species in tropical America. Neither the *ndh*F data nor the ITS data were able to resolve with confidence the positions of *Tetraclea*, *Amasonia*, and *Aegiphila* relative to the three clades of *Clerodendrum*. Combining the two data sets does not improve resolution. The results are consistent with the monophyly of *Clerodendrum* plus *Huxleya*, but it is prudent at this point to retain *Tetraclea*, *Amasonia*, and *Aegiphila* as distinct taxa.

The latter genera form a New World clade that combine with *Clerodendrum* (plus *Huxleya*) to form a more inclusive clade. This is consistent with the geographic partitioning seen among the other clades of *Clerodendrum* (Steane et al., 1997). Clades I and II are Asian and African, respectively, and Clade III is pan-tropical, but largely restricted to coastal habitats. The New World clade comprising *Aegiphila*, *Amasonia*, and *Tetraclea* is the missing piece to the biogeographic puzzle, providing a New World component to this pan-tropical group. It would also be consistent with the fossil record, where *Clerodendrum* fossils have been found in middle Miocene deposits of North America (Wolfe, 1969).

The position of *Kalaharia* relative to *Clerodendrum* has long been a source of debate. Verdcourt (1992) felt that *Clerodendrum* subgenus *Cyclonema* (now *Rotheca pro parte*) and *Kalaharia* were probably closer to each other than either was to *Clerodendrum*, although he chose to maintain them both as subgenera of *Clerodendrum s.l.* until a complete morphological revision of the genus had been completed. Herman and Retief (2002) placed *Kalaharia* in *Rotheca*. The molecular data contradict this view in showing that *Kalaharia* is sister to *Clerodendrum* plus other associated genera (i.e., *Tetraclea*, *Amasonia*, *Aegiphila*, and *Huxleya*). The position of *Kalaharia* in this analysis, closely associated with *Clerodendrum* and related genera rather than with *Rotheca*, is an example of shared morphological similarity confounding taxonomic assessments. Herman and Retief (2002), Stenzel et al. (1988), and Rimpler et al. (1992) grouped *Kalaharia* with *Rotheca* (or equivalent) on the basis of morphological characters. While Herman and Retief (2002) presumably used characters suggested by Steane and Mabberley (1998; i.e., corolla symmetry, anther attachment, and stigma symmetry), Stenzel et al. (1988) and Rimpler et al. (1992) used phenetic analysis to obtain their groupings. They identified several shared floral characters in addition to corolla symmetry and stigma symmetry: the calyx at anthesis is small and green; the fruiting calyx is green, smaller than the fruit and fits the fruit base; the corolla is distinctly zygomorphic. However, while all the other members of *Rotheca* have an adaxial cleft and an abaxial median lobe in their corollas, *Kalaharia* has an abaxial "widening" (not a cleft per se; Cantino, 1992b; Verdcourt, 1992) and an adaxial median lobe. Such a corolla fits the description of *Clerodendrum*, not *Rotheca*. In the data matrix on which Cantino's (1992b) analysis was based, two corolla characters and one stomatal character distinguished *Kalaharia* from *Rotheca* (Cantino, pers. comm.). He did not find any reliable distinction between *Kalaharia* and *Clerodendrum* and, as a result, did not favor the segregation of *Kalaharia* from *Clerodendrum* (Cantino, pers. comm.; Cantino, 1992b), although he provisionally treated *Kalaharia* as a distinct unit in the analysis (Cantino, 1992b). Thus, while some morpho-

logical analyses place *Kalaharia* with *Rotheca*, and others place it with *Clerodendrum*, the molecular data indicate that *Kalaharia* is best maintained as a separate genus close to *Clerodendrum*.

Karomia has long been thought to be close to *Rotheca*, *Caryopteris*, *Trichostema*, *Teucridium*, and *Teucrium* (see Cantino, 1992a) and its phylogenetic position within this group of taxa remains unresolved. The *ndh*F and "combined" results indicate that *Karomia* is the sister to *Rotheca*, although branch lengths (Fig. 3) suggest that they are highly divergent. Interestingly, the geographic partitioning of the two genera is remarkably similar. Both genera have a single species in Asia with the remaining species (eight in the case of *Karomia*; about 40 for *Rotheca*) in Africa and Madagascar.

The *ndh*F results present the most complete sampling to date of any molecular systematic study of Ajugoideae, and support its distinction *sensu* Cantino et al. (1997) including *Ajuga*. The inclusion of a broad array of genera from Ajugoideae in this study highlights the phylogenetic distance between *Clerodendrum* and *Rotheca*.

The genus *Clerodendrum* is large, morphologically diverse, and geographically widespread. As a result, it has been a difficult genus for taxonomists to delimit and circumscribe accurately. The use of DNA technology has provided significant advances in the circumscription of the genus. The transfer of *Huxleya* to *Clerodendrum* is the second example in this genus of taxonomic changes arising from molecular analyses. There is no doubt that *Clerodendrum* type of research will continue to provide important insights into the circumscription and subdivision of this and related genera.

Acknowledgments

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