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Phylogenetic Relationships among Dracaenoid Genera (Asparagaceae: Nolinoideae) Inferred from Chloroplast DNA Loci

Pei-Luen Lu[1] and Clifford W. Morden[1,2]

[1]Department of Botany and Pacific Cooperatives Studies Unit, University of Hawaii at Manoa, 3190 Maile Way, Honolulu, Hawaii 96822, U. S. A.
[2]Author for correspondence (cmorden@hawaii.edu)

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Abstract*—**The global evolutionary pattern among the dracaenoid plant genera *Dracaena*, *Pleomele*, and *Sansevieria* has remained ambiguous. Their classification has been disputed due to different taxonomic interpretation and the difficulty in morphological characterization of the species and genera. This study explores the phylogenetic analysis of 95 species representing all three genera using four combined chloroplast intergenic spacer DNA regions (*trnL-trnF, ndhF-rpl32, trnQ-rps16*, and *rpl32-trnL*). The combined dataset was analyzed using parsimony, maximum likelihood, and Bayesian analysis. Results show that 1) dracaenoids are monophyletic; 2) the Hawaiian *Pleomele* species are the sister group to the remainder of the dracaenoid clade; 3) species of *Dracaena* and the remaining *Pleomele* are intermixed; 4) *Sansevieria* is monophyletic, but nested within *Dracaena*; 5) the Central American species *D. americana* and *D. cubensis* are the sister group to the remainder of the non-Hawaiian dracaenoid species. The Hawaiian *Pleomele* are morphologically and phylogenetically distinct from the remaining dracaenoids and are recognized as a distinct genus, ***Chrysodracon, and new species combinations are made. *Dracaena* is paraphyletic in regards to *Sansevieria* and those species should be recognized as species of *Dracaena*. The polyphyletic status of *Pleomele* species nested within *Dracaena* confirms previous morphology based studies that combined these genera.

***Keywords*—**Biogeography, *Chrysodracon*, *Dracaena*, evolution, *Pleomele, Sansevieria*.

Taxonomic issues surrounding the three globally important genera *Dracaena* Vand., *Pleomele* Salisb., and *Sansevieria* Thunb. (Asparagaceae subfamily Nolinoideae) have been ongoing since the 18th century. The three plant genera, collectively referred to as the dracaenoids, represent an unusual clade within tropical and subtropical Asia, Africa, Central America, and in the remote Hawaiian Islands (Rudall et al. 2000; APG II 2003; APG III 2009). In addition, they have valued application in horticulture, medicine, the fiber industry, and in ceremonies of different cultures (Lee 1975; Koller and Rost 1986; Chun 1994; Neuwinger 1996; Bos 1998; Binojkumar 2002; Langenheim 2003; Staples and Herbst 2005; Haldar et al. 2010). The three genera have been variously classified in the families Liliaceae (Brown 1914, 1915), Agavaceae (Cronquist 1968, Takhtajan 1969; Hutchinson 1973), Dracaenaceae (Salisbury 1866; Watson and Dallwitz 1992; Bos 1998), Ruscaceae (APG II 2003), and now the Asparagaceae (APG III 2009). Dracaenoids share the derived characteristics of having soft berries that lack phytomelanin in the seed testa (Rudall et al. 2000).

Dracaena s. s. comprises 60–80 species worldwide, mainly in the tropics and the subtropics with the exception of South America where there are only two extant species recorded (Bos 1992, 1998; Staples and Herbst 2005; Judd et al. 2007; Mabberley 2008). One of the common names recognized for *Dracaena* is "dragon tree" (Milburn 1984) and several *Dracaena* species are the source of "dragon's blood," a red exudate derived from the tree sap (Lee 1975; Edward et al. 2001; Langenheim 2003) that has been shown to have medicinal properties (Gupta et al. 2008). Because of their adaptation to harsh conditions and interesting patterns of leaf variegation, several *Dracaena* species are also popular horticultural plants, particularly in temperate zones (Bos 1998; Staples and Herbst 2005). Africa is thought to be the center of diversity for *Dracaena* (Bos 1984; Bos 1998; Marrero et al. 1998; Mwachala and Mbugua 2007). Species are mainly native to Africa with some in Madagascar, Asia, Socotra, the Mediterranean regions, Central America, Micronesia, northern Australia, and the Pacific islands (Gwyne 1966; Wu and Raven 1994; Bos 1998; Marrero et al. 1998; Staples and Herbst 2005). Great morphological variation has been shown in *Dracaena*, with species generally categorized into two groups: arborescent and arbustial dracaenas (Marrero 2000). Arborescent dracaenas are usually restricted to semi-desert regions surrounding the Red Sea, whereas the arbustial dracaenas form the remainder of the species distribution (Bos 1998).

Pleomele s. s. consists of 40–50 species worldwide, mainly in the tropics and the subtropics with the exception of the Americas (Brown 1914; Wagner et al. 1990). There are six endemic *Pleomele* species in the Hawaiian Islands (Wagner et al. 1990), where indigenous people have used it as a cold medicine and for ceremonial functions (the sap has not been used externally, as has dragon's blood). *Pleomele* has been regarded as a monophyletic lineage based on morphological characteristics (Brown 1914; St. John 1985; Wagner et al. 1990). To date, little phylogenetic information is available.

Sansevieria comprises ca. 60 species worldwide, mainly in dry or arid areas of the Old World tropics and subtropics (Brown 1915; Marais 1973; Bos 1998; Staples and Herbst 2005; Mabberley 2008). Africa is the center of diversity for *Sansevieria* (Brown 1915; Morgenstern 1979; Mabberley 2008), with some species distributed in the Arabian Peninsula, South Asia, and Southeast Asia (Brown 1915; Morgenstern 1979; Carlquist and Schneider 2007). Plants are usually xerophytic perennials that are often rhizomatous, and they can be herbs, shrubs, or trees (Staples and Herbst 2005). Some species have medicinal and horticultural value (Neuwinger 1996; Bos 1998; Khalumba and Mbugua 2005; Staples and Herbst 2005). Common English names for these species are snake plant or bowstring-hemp along with "mother-in-law's tongue" for the widely cultivated horticultural plant *S. trifasciata* (Staples and Herbst 2005).

Pleomele has an uncertain relationship to the genus *Dracaena*. Brown (1914) distinguished *Pleomele* from *Dracaena* on the basis of differences in floral morphology. *Dracaena* has a short perianth tube with the tepals divided to the base, and thickened staminal filaments. In contrast, the perianth tube of *Pleomele* is slender and longer with tepals fused at least

one-third their length, and with filiform staminal filaments. However, other authors have found these characteristics to be variable and treated *Pleomele*, including the type species *P. fragrans*, as a synonym of *Dracaena* (Ker Gawler 1808; Stevens 2001; Staples and Herbst 2005; Mabberley 2008; Jankalski 2008). Recently, Jankalski (2008) combined the two genera and recognized them as subgenera of *Dracaena* (subg. *Dracaena* and subg. *Pleomele*) and this relationship was recognized in APG III (2009). Jankalski (2008) also recognized a third new subgenus for the Hawaiian species, subg. *Chrysodracon*, because those taxa do not fit subg. *Dracaena* or subg. *Pleomele*, and have longer flowers with broader floral tubes and yellow (rather than white, green, or purple) tepals. He further proposed that the Hawaiian species were most closely related to the two species from Central America, *D. americana* Donn. Sm. and *D. cubensis* Vict.

Like *Pleomele*, *Sansevieria* has also been variously treated in relation to *Dracaena* (Baker 1875; Brown 1914; Bos 1984). Several authors have placed *Sansevieria* in synonomy with *Dracaena* based on their similar floral characteristics (Bos 1998; Mabberley 2008). However, *Sansevieria* continues to be recognized as a genus by several botanists (Harms 1904; Marais 1973; McVaugh 1974; Newton 2002; Jankalski 2003) because of its usually shorter stature and herbaceous habit, thick leathery leaves, and creeping rhizome.

Several issues exist in the classification of the three dracaenoid genera. The systematic relationships among them are unclear, and no thorough examination of their biogeographic and evolutionary history has been made. Most recent molecular phylogenetic studies have focused only on the large-scale relationships at the family level among Agavaceae, Dracaenaceae, Ruscaceae, and Asparagaceae (Bogler and Simpson 1995, 1996; Rudall et al. 2000; Kim et al. 2010). These studies only sampled one to two species of each genus (and did not include type species) to show they are closely related, but did not further resolve their relationships. A preliminary examination of a small subset of *Dracaena* and *Pleomele* species (without *Sansevieria* represented) confirmed their close affinity and suggested a polyphyletic relationship among the genera (Lu and Morden 2010). The present study employed molecular systematic analyses of all three genera to assess their circumscription, the evolution of dracaenoids, and their biogeographic affinities.

Materials and Methods

***Taxon Sampling*—**A total of 31 *Dracaena* species, 30 *Pleomele* species, and 34 *Sansevieria* species representing the global distribution of these genera were examined in this study (Appendix 1). Six undescribed *Dracaena* species native to Thailand discovered by Paul Wilkin (Kew Herbarium, London, U. K.) were also included. Sources of DNA for sequencing included freshly collected leaves, herbarium specimens, and the DNA Bank at Royal Botanic Gardens, Kew, United Kingdom. Appendix 1 includes specimen source, voucher information, locality, and collection number. All novel sequences generated for this study are deposited in GenBank. The selection of five outgroup taxa from the Asparagaceae (Nolinoideae) was based on the results of previous studies and were shown to be closely allied to dracaenoid genera (Bogler and Simpson 1996; Rudall et al. 2000; Kim et al. 2010). Four of the outgroup species (*Comospermum yedoensis, Disporopsis pernyi, Liriope muscari, Speirantha gardenii*) are distributed from East Asia and one is from Africa (*Eriospermum flagelliforma*).

***DNA Extraction and Amplification*—**Total genomic DNA was extracted from 1.0 g of fresh or 0.2 g of silica gel-dried leaves using the CTAB method (Doyle and Doyle 1987) with modification (Morden et al. 1996), or using the Qiagen DNeasy plant mini kits (Qiagen Corporation, Valencia, California) following manufacturer specifications. DNA samples were accessioned into the Hawaiian plant DNA library (Morden et al. 1996).

Four chloroplast intergenic spacer regions were examined for this study: *trnL-trnF*, *ndhF-rpl32*, *trnQ-rps16*, and *rpl32-trnL*. The *trnH-psbA* spacer had been used in preliminary analyses (Lu and Morden 2010), but was not further pursued because it was not as variable as the selected gene regions. The PCR was performed using an Eppendorf (Westbury, New York) Mastercycler gradient or MJ Research Thermal PCR machine (GMI, Inc. Ramsey, Minnesota). PCR reactions were performed in 25 μl reaction mixtures containing 1 × GoTaq Flexi PCR buffer, 15 mM $MgCl_2$, 0.1% bovine serum albumin, 0.2 mM each dNTP, 0.2 mM each amplification primer, and 1 U GoTaq polymerase (Promega, Madison, Wisconsin). The *rpl32-trnL* and *trnQ-rps16* regions were amplified using primer pairs from Shaw et al. (2007) and amplified under the following PCR conditions: 5 min at 80°C, followed by 30 cycles at 95°C for 1 min, 50°C for 1 min (a ramp 0.3°C/sec to 65°C), 65°C for 4 min, plus a final extension of 5 min at 65°C. The *ndhF-rpl32* region was amplified using the primer pairs from Scarcelli et al. (2011). Alternative parameters were used to amplify this region: one with the PCR conditions of 3 min at 94°C, followed by 35 cycles at 94°C for 30 sec, 42°C for 30 sec, 72°C for 1 min, plus a final extension of 10 min at 72°C, and the other with the PCR conditions of 5 min at 80°C, followed by 35 cycles at 94°C for 1 min, 42°C for 1 min (increasing 3°C/sec/cycle), 65°C for 4 min, plus a final extension of 10 min at 65°C. The *trnL-F* region was amplified using the primer pair described in Taberlet et al. (1991) with the PCR conditions of 80°C for 5 min followed by 29 cycles at 94°C for 1 min, 60°C for 1 min, 72°C for 4 min, plus a final extension of 5 min at 72°C (Shaw et al. 2005). All amplifications were verified on 1.5% agarose gels.

The PCR products were prepared for sequencing using ExoSAP-IT (USB Corporation, Cleveland, Ohio) or similar treatment with shrimp alkaline phosphatase and exonuclease I following the USB ExoSAP-IT PCR product cleanup protocol of incubation for 37°C for 15 min followed by 80°C for 15 min. Samples were bidirectionally sequenced using each amplification primer at the University of Hawaii's ASGPB Sequencing Facility (http://cgpbr.hawaii.edu/) using BigDye Terminator chemistry (Applied Biosystems, Foster City, California) and visualized on an ABI 3730XL capillary-based DNA sequencer (Applied Biosystems).

***Sequence Alignment and Phylogenetic Analysis*—**Contiguous strands were assembled and edited for all *trnL-trnF*, *ndhF-rpl32*, *trnQ-rps16*, and *rpl32-trnL* sequences using MEGA 5 (Tamura et al. 2011). All sequences were aligned initially in ClustalW (ver. 2.1; Larkin et al. 2007) and Muscle (Edgar 2004) and then manually adjusted in MEGA 5 following the guidelines of Kelchner (2000) to minimize indels. Sequences from all four cpDNA regions were combined into one dataset and indels were excluded from subsequent phylogenetic analyses; no data cells were scored as missing data (TreeBASE study number 13430). Modeltest version 3.7 (Posada and Crandall 1998) was used to determine the most suitable nucleotide substitution model. The best-fit models as determined in the evolutionary models were selected by Akaike information criterion (AIC; Akaike 1974) for each partition and the combined dataset. The GTR + G model (a general time reversible model with a gamma-shaped distribution of rates across sites) was chosen for the four regions combined data matrix as the best-fitting among the 24 models compared and was used to construct the ML and Bayesian trees. Sequences were concatenated and aligned in a NEXUS file and PHYLIP file prior to conversion by Mesquite 2.7.4 (Maddison and Maddison 2010) into the appropriate file format necessary for the tree search applications.

Maximum parsimony (MP), maximum likelihood (ML), and Bayesian methods were used to estimate phylogenies for the combined chloroplast data set. Maximum parsimony searches were conducted using PAUP* 4.0b10 (Swofford 2002). In all MP analyses, heuristic searches were done using a starting tree built from stepwise addition with 1,000 random addition replicates and TBR branch swapping. Bootstrap analyses based on 1,000 replicates with 10 random additions per replicate were used to assess confidence in clades (Felsenstein 1985; Pattengale et al. 2010).

Maximum likelihood (ML) analyses were carried out by RAxML through the CIPRES portal (Stamatakis et al. 2008) for 10,000 replicates, and repeated 10 times to generate 100,000 replicates. The ML analysis was also repeated using the likelihood ratchet method in PAUP* (Swofford 2002). Bootstrap values were estimated with 1,000 replicates. ML analyses as an optimality criterion for tree estimation (Felsenstein 1981) was implemented using RAxML (Stamatakis 2006; Stamatakis et al. 2008). Maximum likelihood bootstrap proportions (MLBS) >70% were considered strong support (Hillis and Bull 1993).

MrBayes v3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist et al. 2005) was used to conduct Bayesian phylogenetic analyses without a molecular

clock model. Markov Chain Monte Carlo (MCMC) was repeated twice to assure parameter convergence. The MCMC algorithm was run for 1,000,000 generations with one cold and three heated chains, starting from random trees and sampling one out of every 100 generations. Tree samples and parameter estimates from the first 0.25% of all trees (2,500) were designated as the burn-in period and discarded. Remaining trees were used to construct 50% majority-rule consensus trees. Posterior probability (PP) values greater than 0.95 were considered strong support for individual clades (Erixon et al. 2003; Huelsenbeck and Rannala 2004).

Results

A total of 404 new sequences were generated from the four gene regions and the 100 species examined for a combined aligned length of 3,263 bp. GenBank accession numbers for each sequence are available in Appendix 1. A complete list of gene regions, their aligned length, and combined data matrix statistics is given in Table 1. Of the four sampled regions, *trnQ-rps16* was the longest region sampled (1,003 bp) and *trnL-trnF* was the shortest (380 bp). Of the combined data, 10% of all characters were parsimony informative; *ndhF-rpl32* was the most parsimony informative gene region with 13.0% of the variable sites informative while *rpl32-trnL* was the least parsimony informative with 6.6% of the variable sites informative.

***Parsimony Analysis*—**Maximum parsimony (MP) analysis was conducted on the combined dataset of all regions. The strict consensus tree of 1,008 equally parsimonious trees is shown with bootstrap percentages (BP) greater than 50% associated with the branches (Fig. 1). The dracaenoids were strongly supported (90% BP) as a monophyletic lineage relative to the outgroup genera. However, *Dracaena, Pleomele*, and *Sansevieria* as traditionally delimited were polyphyletic. Representatives of all sampled species of *Sansevieria* except *S. sambiranensis* constituted a clade (80% BP). The monophyly of Hawaiian *Pleomele* was strongly supported (90% BP) and positioned as the sister group to a large clade containing the remainder of ingroup taxa. The two Central American species, *D. americana* and *D. cubensis*, were supported as the sister group to the remaining ingroup species (90% BP) followed by *D. cinnabari* from Socotra (85% BP). Species in the sister group to *D. cinnabari* are variously distributed throughout Africa or Asia.

***Maximum Likelihood Analysis*—**Maximum likelihood (ML) analysis of the combined dataset produced a topology similar to that of the MP strict-consensus tree (Fig. 2). Positions of some species differ from the MP tree although overall relationships are similar. The monophyly of all dracaenoids was strongly supported (100% BP). As previously described, *Dracaena, Pleomele* and *Sansevieria* were polyphyletic with *Sansevieria* species in a terminal position within the clade and *Dracaena* and *Pleomele* species intermixed. The monophyly of Hawaiian *Pleomele* were strongly supported (95% BP), as was their sister relationship to all other dracaenoids (90% BP). All *Sansevieria* species were monophyletic in a well-supported clade (88%).

***Bayesian Analysis*—**The majority rule consensus tree from the combined Bayesian analysis with posterior probabilities (PP) is summarized from the set of recovered post-burn-in trees (Fig. 3). The resolved clades were similar overall to what was found in the MP and ML analyses. Dracaenoids were strongly supported as a monophyletic lineage (1.0 PP), but species of the three genera were not. The African *Sansevieria* were monophyletic (1.0 PP), but were nested within a large clade that included *Dracaena* and *Pleomele* species rendering the assemblage polyphyletic. The Hawaiian *Pleomele* were supported as monophyletic (1.0 PP) and as sister to the clade containing all other dracaenoid species (1.0 PP). The relation of *D. cubensis*, *D. americana* (Central America) and *D. cinnabari* (Socotra) as the basal taxa in the remainder of the dracaenoid clade is also strongly supported and consistent with other analyses.

Table 1. Statistics for the chloroplast gene regions analyzed in the maximum parsimony (MP) analysis. PIC = parsimony informative characters; CI = consistence index; RI = retention index. CI and RI values based on most parsimonious trees. Constant and variable sites do not account for gaps inserted into sequences for the aligned length.

Statistic	*trnL-trnF*	*rpl32-trnL*	*trnQ-rps16*	*ndhF-rpl32*	combined cpDNA
Aligned length	380	975	1,003	905	3,263
Constant sites	332	887	831	723	2,931
Variable sites	36	68	183	125	432
PIC	32	65	111	117	325
CI	0.51	0.68	0.56	0.59	0.67
RI	0.66	0.78	0.69	0.53	0.70

Discussion

***Dracaenoid Phylogeny*—**Dracaenoids are a well-supported monophyletic group, consistent with previous molecular phylogenetic analyses at the family level (Bogler and Simpson 1995, 1996; Rudall et al. 2000). The combined analysis provides evidence of a primary division within the dracaenoid radiation into three main clades. Hawaiian species of *Pleomele* constitute a clade that is sister to the remainder of the dracaenoid species (*Dracaena* s. l.). Support for this relationship was strong in all three analyses. Other species of *Pleomele* and those of *Dracaena* are intermixed in the tree; *Sansevieria* species constitute a clade in the ML and Bayesian trees.

***Monophyly of the Hawaiian Dracaenoids*—**The relationship of Hawaiian *Pleomele* have long been debated (Brown 1914; Bos 1984, 1998; St. John 1985; Wagner et al. 1990). Results here demonstrate that the six extant Hawaiian species are strongly supported as a monophyletic group and support Jankalski's (2008) classification separating them as a distinct taxon from the remainder of *Dracaena* and *Pleomele*.

Although classified within *Pleomele*, the Hawaiian species do not conform well to the morphological description of the genus by Brown (1914). Hawaiian *Pleomele* species are unique in having yellow tubular flowers that are long and wide, and in pendent panicles, possibly an adaptive shift toward bird pollination (Jankalski 2008). The non-Hawaiian *Pleomele* species have white or greenish slender tubular flowers that are much smaller than those of Hawaiian species. Also, Hawaiian species of *Pleomele* have a diurnal flowering and fragrant cycle, in contrast to the nocturnally fragrant flowering of *Pleomele*, *Dracaena*, and *Sansevieria* (Bos 1984, 1992, 1998; Mwachala 2005; Jankalski 2008; P.-L. Lu pers. obs.). These traits in the Hawaiian species led Jankalski (2008) to place them in a separate subgenus, *Dracaena* subg. *Chrysodracon.*

Results here indeed support Jankalski's (2008) separation of the Hawaiian clade as a distinct taxon although they do not support his assumption that they descended from *D. americana* or *D. cubensis* from central America. The species evidently constitute a clade and form the sister group to the remainder of the dracaenoids. Based on these morphological differences and the evident phylogenetic distinction of the

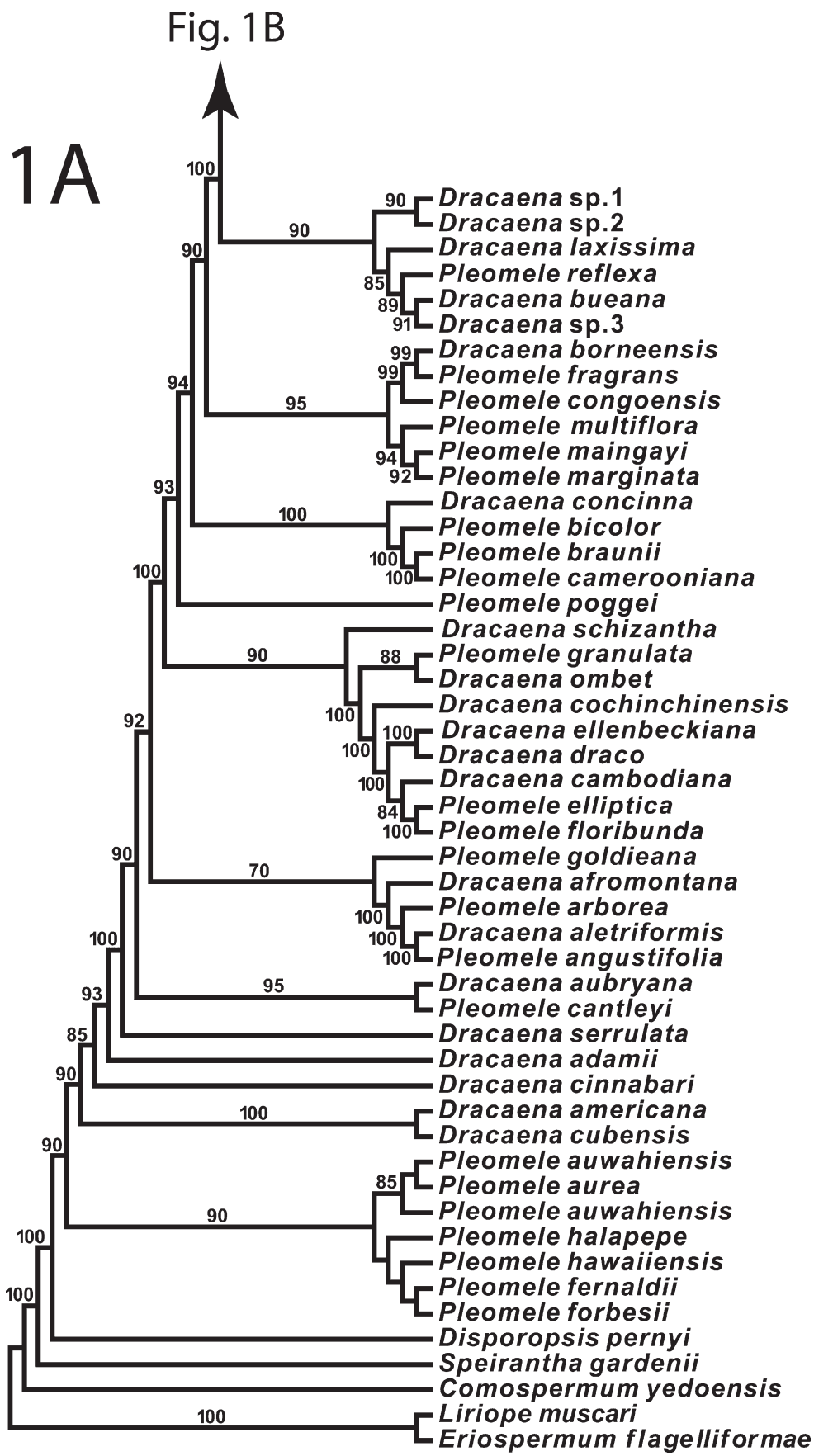

FIG. 1A, B. Strict consensus of the 1008 most parsimonious trees resulting from maximum parsimony analysis of the combined dataset (*trnL-trnF*, *ndhF-repl32*, *trnQ-rps16*, and *rpl32-trnL*) illustrating relationships of species among the three dracaenoid genera, rooted with five closely related non-dracaenoid members of the Asparagaceae (Kim et al. 2010). Numbers above the branches represent bootstrap values above 50%.

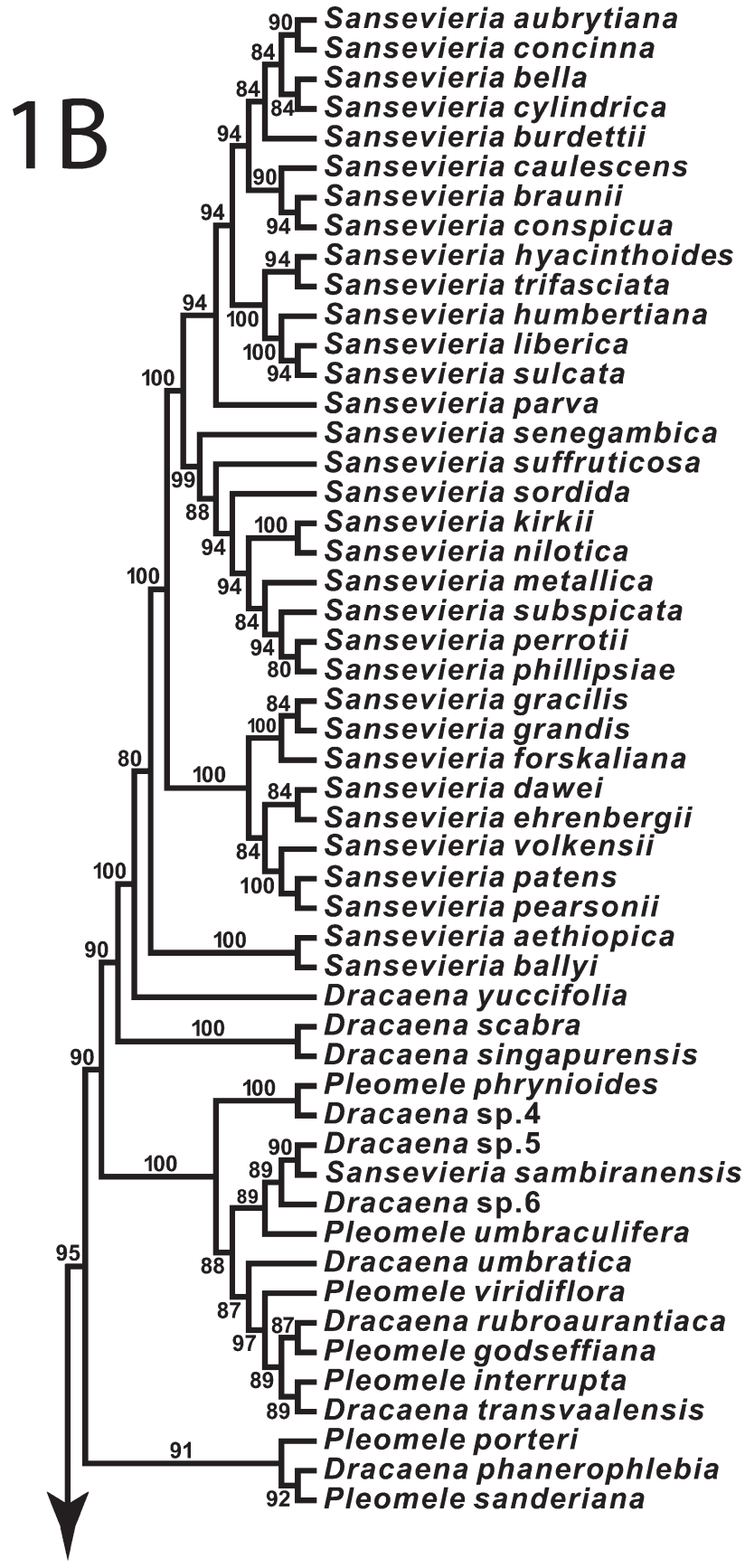

FIG. 1A, B. Continued.

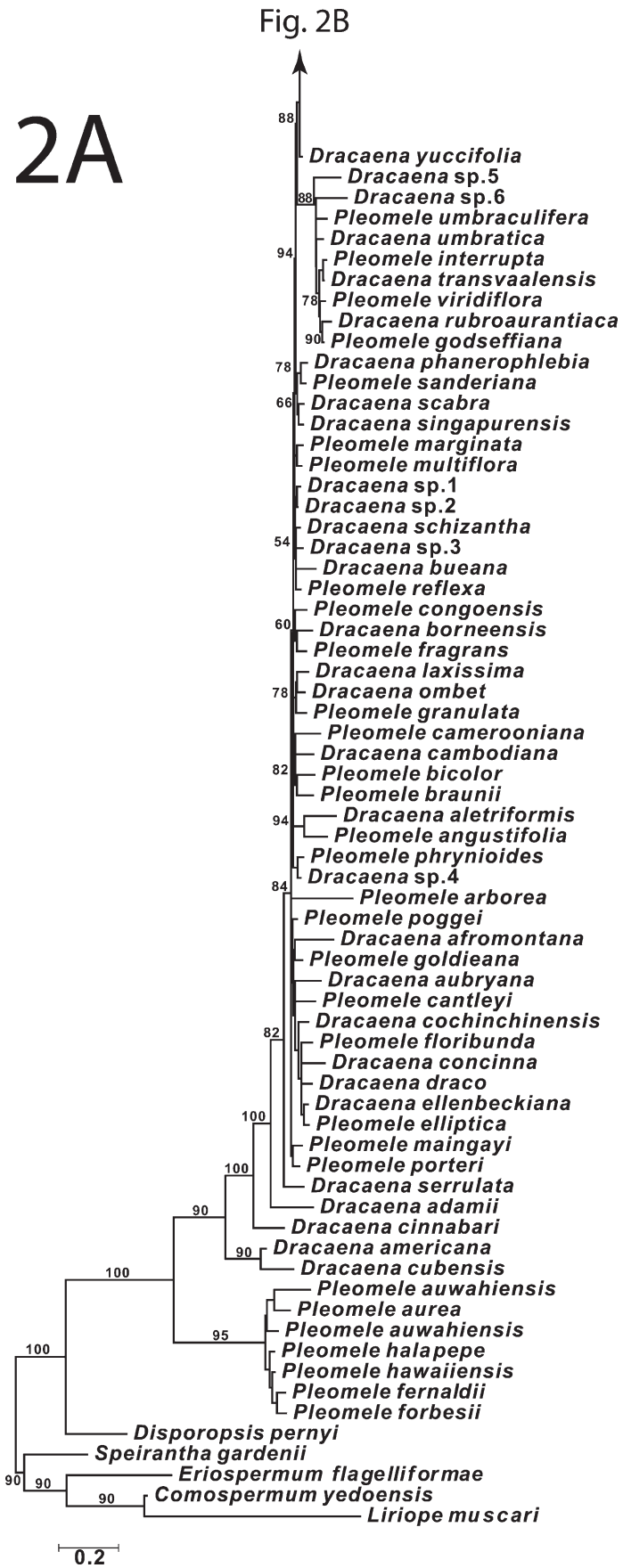

FIG. 2A, B. Results of Maximum-likelihood analysis of the combined data set (*trnL-trnF*, *ndhF-repl32*, *trnQ-rps16*, and *rpl32-trnL*) illustrating relationships of species among the three dracaenoid genera, rooted with five closely related non-dracaenoid members of the Asparagaceae (Kim et al. 2010). Numbers above the branches represent bootstrap values above 50%.

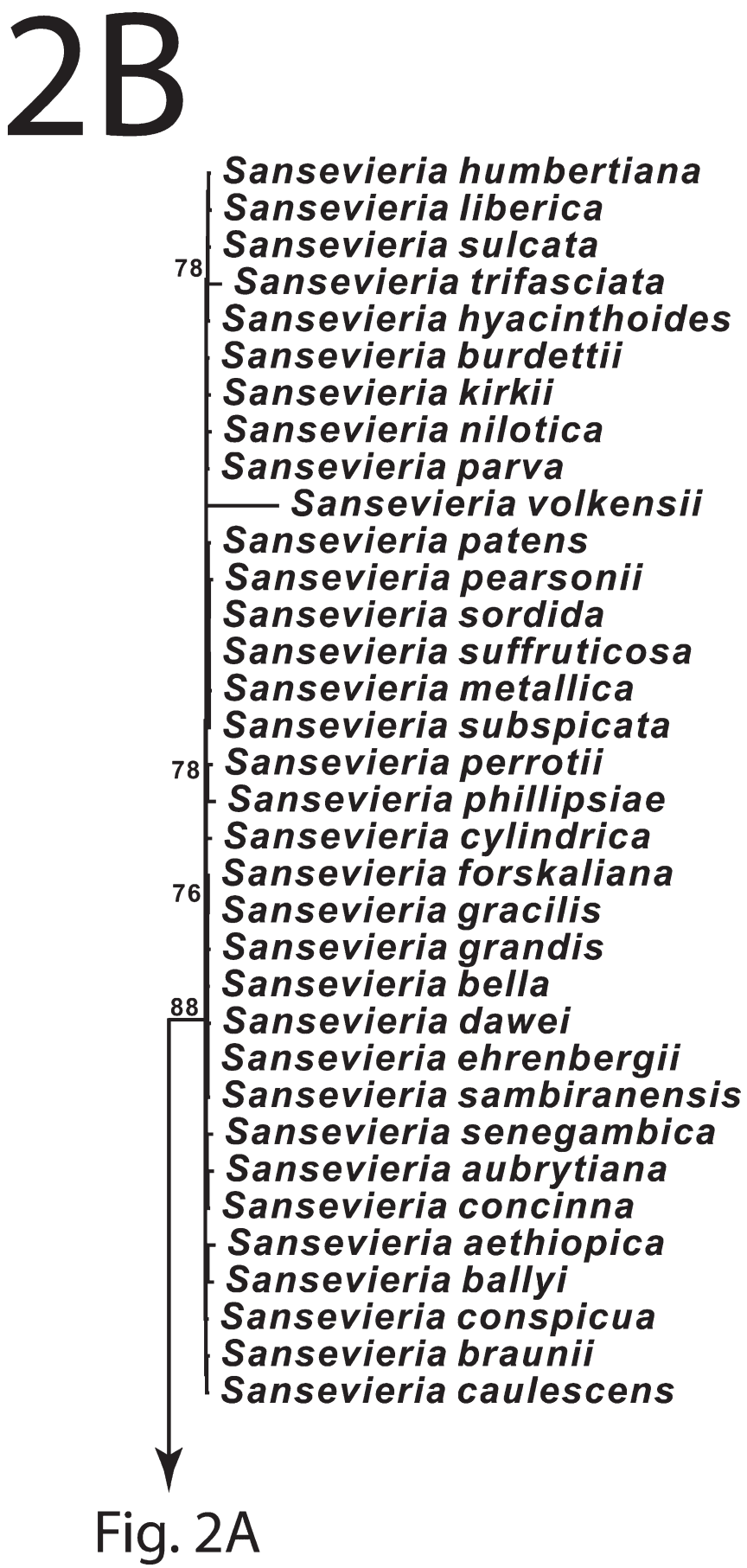

FIG. 2A, B. Continued.

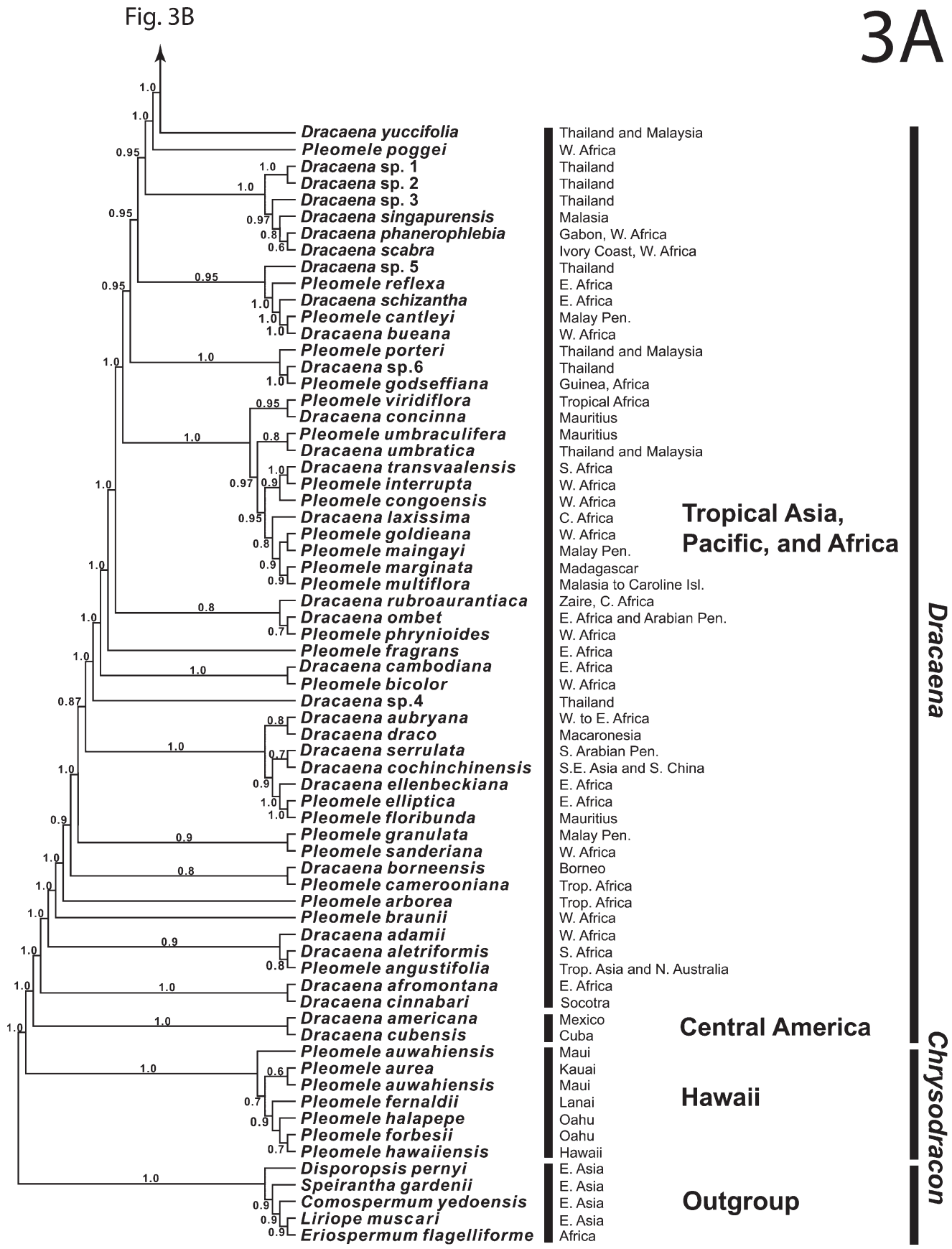

FIG. 3A, B. Results of Bayesian analysis of the combined dataset (*trnL-trnF*, *ndhF-repl32*, *trnQ-rps16*, and *rpl32-trnL*) illustrating relationships of species among the three dracaenoid genera, rooted with five closely related non-dracaenoid members of the Asparagaceae (Kim et al. 2010). The 50% majority rule consensus tree is shown. Posterior probabilities consistent with the consensus tree are shown above each branch, but values below 0.50 are not indicated. Geographic region of each species is given. Generic names for the species as determined in this study are shown along the bracket at right.

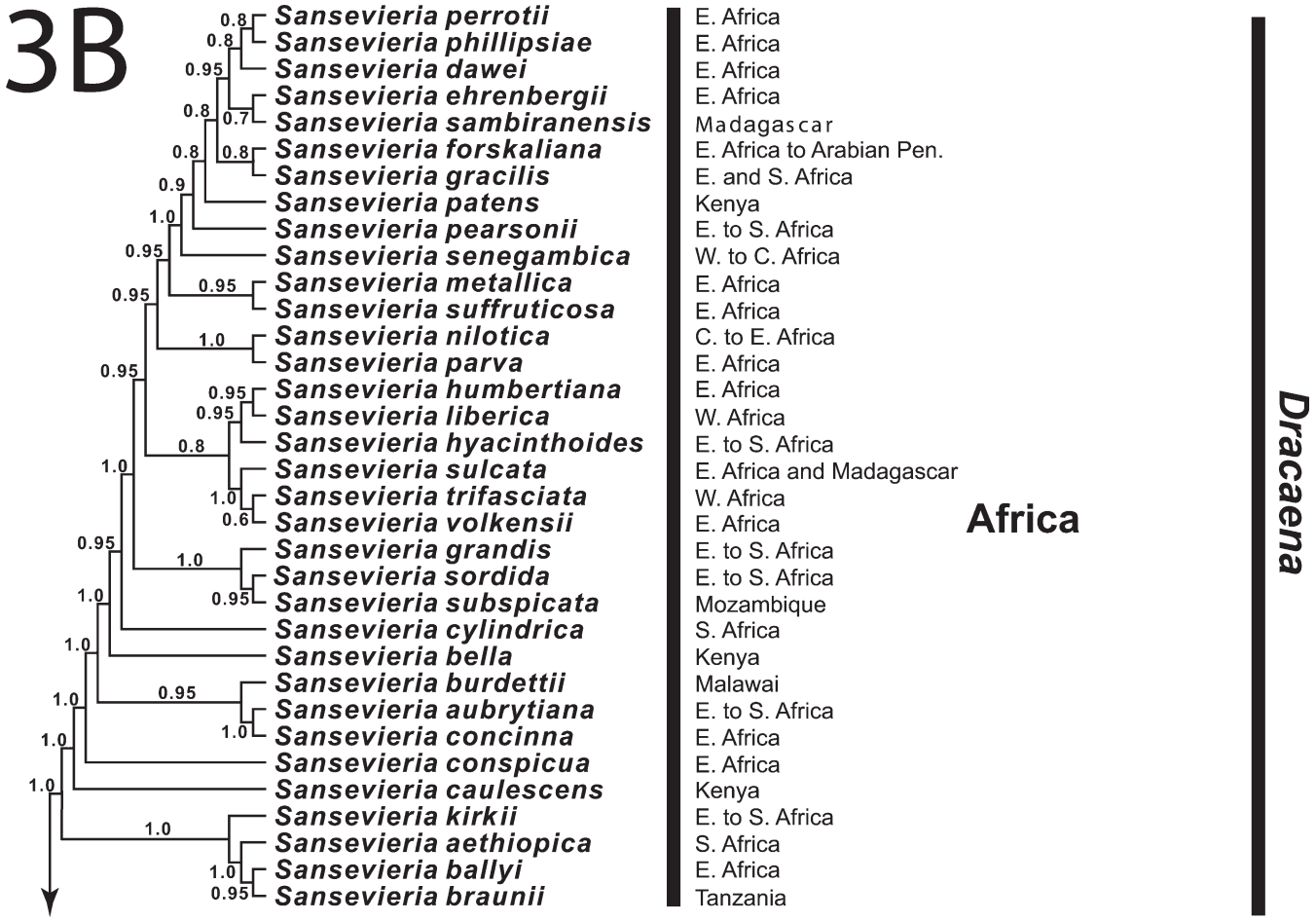

Fig. 3A

FIG. 3A, B. Continued.

Hawaiian species from the remainder of the dracaenoids, this unique clade should be elevated to the rank of genus.

Relationships Among Dracaena and Pleomele—Excluding the Hawaiian clade, the relationships among species of *Pleomele* and *Dracaena* do not conform to Brown's (1914) or Jankalski's (2003) generic classifications. Brown (1914) separated *Pleomele* from *Dracaena* based on differences in the division of perianth parts and filament thickness. Jankalski (2008) retained *Dracaena* and *Pleomele* as subgenera of *Dracaena* based on these morphological distinctions. The results here thus suggest that variation in these traits is convergent rather than homologous and, as such, the two genera should be treated as a single genus with no subgeneric designation.

The relation between arborescent and arbustial dracaenoids was examined and results here demonstrate that differences in woody habit are homoplasious (Fig. 4A). Sequence analysis does not support Brown's (1914) classification for *Dracaena* to separate arborescent *Dracaena* from arbustial *Dracaena*. If the arbustial condition is considered to be ancestral within the phylogeny, being present also among outgroup taxa and the Hawaiian species, then arborescence could have arisen independently several times.

Phylogenetic Relationship of African Sansevieria—The 34 *Sansevieria* taxa mostly form a well-supported clade that is nested within *Dracaena*. (*Sansevieria sambiranensis* is nested in a clade with *Dracaena* and *Pleomele* species near the *Sansevieria* clade in the MP analysis, but is nested within the *Sansevieria* clade in both ML and Bayesian analyses). Although monophyletic, its position within the phylogeny makes *Dracaena* s. l. a paraphyletic assemblage and, as such, *Sansevieria* must be considered a clade within the broader interpretation of *Dracaena*. The genus name *Dracaena* Vandelli ex Linnaeus (1767) has priority over *Sansevieria* Thunberg (1794) and *Pleomele* Salisbury (1796), and *Dracaena* must be used as the genus name for the species in this clade if all are treated as congeneric, as proposed here. These results support the classifications of Bos (1984, 1998) that subsume *Sansevieria* into *Dracaena*, rather than the classification of Jankalski (2003) that maintains its separation as a distinct genus. All *Sansevieria* species in this analysis are native to Africa; there are four species native to Asia described by Brown (1915) that were unavailable for analysis and should be analyzed to understand the relationships of those taxa. Biogeographical patterns among sampled species of the clade suggest that it dispersed from east Africa to southern and west Africa.

Brown (1915) hypothesized that species with cylindrical leaves originated from ancestral forms having flattened leaves based on plant ontogeny (juvenile plant leaves are flattened to concave and transition to adult plant leaves that are thicker and eventually become cylindrical). However, this unique cylindrical leaf-type is not a synapomorphic character state as is evident in Fig. 4B. The trait is present in

FIG. 4. Reconstruction of (A) arborescent vs. arbustial habit and (B) cylindrical vs. flat leaf structure overlayed on the 50% majority rule consensus tree produced by Bayesian inference (see Fig. 3). Origin of arborescent and cylindrical leaf traits are shown with bold lines and the species with these traits are boxed.

nine species that are polyphyletic within the tree suggesting that it may have evolved on multiple occasions. Compared to the other dracaenoid species, *Sansevieria* species are better adapted to extreme drought and high solar irradiation conditions (Sreenivasan et al. 2011). Their thick, leathery leaves combined with their rhizomatous nature make them efficient at water use. The round leaf forms are even more water efficient in this regard (Sreenivasan et al. 2011).

Sansevieria taxa radiated rapidly with little genetic differentiation among the species. This is best exemplified in the ML analysis where branch lengths are very short. Bayesian analysis showed clear resolution among the species of *Sansevieria* and with strongly supported clades. However, phylogenetic relationships of species among the three analyses are not concordant. Additional gene regions should be examined to resolve these species relationships.

Biogeography of Dracaenoids—Results previously reported by Kim et al. (2010) and confirmed here indicate that the dracaenoids are most closely related to Asparagaceae subfamily Nolinoideae genera native to the temperate and subtropical regions of Asia. Previous hypotheses were that dracaenoids arose in Africa where their center of diversity is located (Bos 1984, 1998; Mwachala 2005). However, the closest relatives of the dracaenoids are from tropical and subtropical Asia. Dracaenoids form a sister clade to the genera *Ruscus*, *Damae*, and *Semele* (Kim et al. 2010), genera of Macronesian-Mediterranean distribution that were previous recognized as constituting the family Ruscaceae s. s. (Stevens 2001, APG II 2003) prior to their present recognition in the more broadly encompassing Asparagaceae (APG III 2009). A split in the common ancestor of these lineages gave rise to Ruscaceae s. s. to the west across temperate regions of central Asia and Europe, and dracaenoids remaining in the east and dispersing west via tropical and arid regions to Africa.

Although results suggest that the likely origin of the dracaenoids was in East Asia, it is apparent that the early lineages from this region have since gone extinct. The earliest diverging lineages of dracaenoids are represented by the Hawaiian and Central American taxa; the Hawaiian dracaenoids are the sister group of the remaining dracaenoid taxa, and the two Central American species are the earliest diverging taxa of the remaining dracaenoids. This would suggest that the sister Asian lineage went extinct after dispersal to the remote Hawaii Archipelago and elsewhere. Dispersal patterns such as this with Hawaiian species seemingly ancestral to large world-wide clades is not unprecedented. A similarly surprising result was found in the Begoniaceae where the monotypic genus *Hillebrandia sandwicensis,* endemic to Hawaii, is sister to all other species of *Begonia* (ca. 1400 species) located throughout Africa, America, and Asia (Clement et al. 2004). Their hypothesis was that *H. sandwicensis* represents a relict species dating back to an early colonization of now subsided high Hawaiian Islands 20 million years ago (MYA) and followed a progression rule model (Hennig 1966; Funk and Wagner 1995) down the chain as new islands formed. Similar hypotheses of colonization to now submerged islands to the northwest followed by stepping stone colonization to newly formed islands has been made for a minority of other extant lineages in Hawaii (Price and Clague 2002; Givnish et al. 2008) and is consistent with what has been found in the study here. The discovery of *Dracaena*-like pollen from the Neogene period (ca. 23 MYA; Van Campo and Sivak 1976) is consistent with such a model.

While we have not performed a rigorous biogeographic analysis here, it is interesting to speculate on the dispersal events that may have led to the present day distribution of the dracaenoids, based on the available data. Extant taxa occur widely in tropical and subtropical regions of the continents of Asia, Africa, and Central America (Brown 1914; Bos 1998; Mwachala 2005). Dracaenoids also occur on many oceanic islands that are in close proximity to a continental land mass (Bos 1998), the isolation of the Hawaiian radiation being the lone exception to this. With the origins of dracaenoids being in the south or Southeast Asia region (above), the bird-mediated dispersal (Bos 1998) that gave rise to extant lineages is complex. First, an early separation to the Pacific islands leading to the Hawaiian radiation must have taken place. This suggests that colonization is likely to have occurred to a previous high island that has now subsided, followed by a stepping stone dispersal from the older to younger islands as they formed. The oldest high island in the Hawaiian archipelago is Kauai dated to ca. 5 MYA (Carson and Clague 1995).

The second dispersal event was a similarly long distance event from either the original source region in Asia or the Hawaiian Islands to Central America. Central American dracaenoids did not radiate extensively, as in other regions or, if they did, the other species have gone extinct. The third dispersal event occurred from the original source region in Asia to the Arabian Peninsula and subsequently Africa. The lineages to branch following the American species are *D. cinnabari*, endemic to Socotra Islands (Yemen), and then a clade with African species including *D. adamii*, *D. aletriformis*, and *D. angustifolia,* the latter with populations distributed in areas of Asia and islands of the Pacific Ocean (Bos 1984; Mwachala 2005). This in turn led to a large radiation of species into mainland Africa and subsequently to Madagascar (and Mauritius), Australia and Papua New Guinea, with periodic dispersal back to South and Southeast Asia. The alternative hypothesis of dispersal from Central America to Asia and Africa cannot be discounted although the immense distances involved make it unlikely. At some point following this third major dispersal event, the original source population went extinct.

The center of diversity among species of *Dracaena* was identified to be in West Africa (Bos 1984) or East Africa (Mwachala 2005). Although numerous species from both African regions and Asia were used in this analysis, there were no obvious subclades of species from a specific region. In contrast, the several subclades present have representative taxa from both Africa and Asia. Hence, there does not appear to be any strong correlations between phylogenetic relationships among species and their current biogeographical distribution. This pattern suggests that dispersal between Africa and Asia was common and supports the suggestion of Bos (1998) that birds, and likely migratory birds, are the most probable dispersal agents for dracaenoids. Such patterns suggest that bird mediated dispersal between these two continents may have been important in mediating speciation.

Taxonomic Treatment

Here, we establish the genus *Chrysodracon* to accommodate the Hawaiian dracaenoid species. Jankalski (2008) recognized these species as a distinct subgenus within *Dracaena* (subg. *Chrysodracon*) and the name recognizes these species as

golden-flowered dragon tree's because of the yellow tubular funnelform flowers in the pendent leafy panicles. Other features that distinguish this genus include the foliaceous nature of the panicles, the large flower size (often exceeding 4 cm long), and flattened staminal filaments (Jankalski 2008). Although results here suggest that new combinations of other species of *Pleomele* and *Sansevieria* as species of *Dracaena* are in order, taxonomic studies by others on these genera are on-going and recognition of species and subsequent revisions will be left for their determination.

Chrysodracon (Jankalski) P.-L. Lu & Morden, stat. and comb. nov.—TYPE: *Chrysodracon aurea* (H. Mann) P.-L. Lu & Morden, based on *Dracaena aurea* H. Mann. Proc. Amer. Acad. Art. Sci. 7: 207, 1867.

Trees with stems few to many-branched, younger ones with conspicuous leaf scars. Phylotaxy spirally arranged, leaves subcoriaceous, clustered at ends of branches, leaves linear to sword-shaped. Panicles terminal, branches subtended by leafy bract ½ to equaling panicle branch length, narrow and slender to broad and stout, peduncles 6–25 cm long, usually abruptly recurved. Flowers perfect, numerous in clusters, perianth yellow or greenish-yellow to yellowish-orange, connate into a well-developed tube ½ – ¾ the length of the perianth, 23–70 mm long, constricted into narrow tube basally 2–6 mm long, prominently lobed above with lobes slightly spreading to reflexed, 8–18 mm long. Stamens 6, inserted at base of perianth; filaments flattened and subulate; anthers 3.5–6 mm long. Ovary superior, 3-celled, ovules 1 per cell, styles filiform, equaling or extending slightly beyond perianth, stigmas slightly 3-lobed. Fruit a berry, red at maturity, 8–17 mm long. Seeds 1, occasionally 2 or 3, 4–9 mm long.

Species of *Chrysodracon* have been variously treated by recent authors (as species of *Pleomele* or *Dracaena*). St. John (1985, 1987) recognized 10 species as island endemics with three on Hawaii, two on Oahu and Kauai, and one each on Maui, Molokai, and Lanai. Wagner et al. (1990, 2012) subsequently recognized only six species (combining those on Hawaii and those on Maui and Molokai) bringing several of St. John's taxa into synonomy. Jankalski (2008) recognized seven species including one (*P. stenophylla*) not addressed by Wagner et al. (1990, 2012). Interestingly, Jankalski (2008) recognized two species by names placed in synonomy of other species by Wagner et al. (1990) when he reclassified them as species of *Dracaena*. Here, we make the nomenclatural changes for the six species presently recognized in Wagner et al. (1990). Subsequent publications will address more fully the evolution and biogeography of *Chrysodracon* species and their populations.

Chrysodracon aurea (H. Mann) P.-L. Lu & Morden, comb. nov. *Dracaena aurea* H. Mann, Proc. Amer. Acad. Arts Sci. 7: 207 (1867). *Pleomele aurea* (H. Mann) N. E. Brown, Kew Bulletin 1914: 277. *Draco aurea* (H. Mann) O. Kuntze, Rev. Gen. Pl. 2: 710 (1891).—TYPE: U. S. A. Hawaiian Islands, Kauai Island: Koloa. *H. Mann* & *W. T. Brigham 362* (lectotype: GH; isolectotypes: BISH-497015!, BH-50817!, F, G, MASS-11916, MO-2867249!, NY-320094).

Chrysodracon auwahiensis (St. John) P.-L. Lu & Morden, comb. nov. *Pleomele auwahiensis* St. John, Pacific Science 39(2): 175. 1985.—TYPE: U. S. A. Hawaiian Islands, Maui Island: Auwahi, 3,800 ft alt., trees to 10 m × 40 cm., flowers greenish yellow, fruit carmine, oblate globose, 30 June 1972, *H. St. John 26869* (holotype: BISH-494592!, 494940!; isotype: PTBG-027438!).

Chrysodracon fernaldii (St. John) P.-L. Lu & Morden, comb. nov. *Pleomele fernaldii* St. John, Contrib. Gray Herb. 165: 39 pl3 (1947). *Dracaena fernaldii* (St. John) Jankalski, Sansevieria 18: 20 (2008). *Dracaena hawaiiensis* Fosberg, Occas. Papers Bishop Mus. 23(2): 32 (1962). *Pleomele lanaiensis* Degener, Fl. Hawaiiensis: Fam. 68 (1932), *nom. nud*.—TYPE: U. S. A. Hawaiian Islands, Lanai Island: south ridge of Holopoe Gulch, Mahana, lower edge of forest, 2,000 ft alt. tree 8 m. × 2 dm., flowers yellowish green, 6 April 1947, *H. St. John & R. S. Cowan 22666* (holotype: BISH-497364!; isotype: GH, BISH-497367!).

Chrysodracon forbesii (Degener) P.-L. Lu & Morden, comb. nov. *Pleomele forbesii* Degener, Fl. Hawaiiensis: Fam. 68 (1932). *Dracaena forbesii* (Degener) Jankalski, Sansevieria 18: 21 (2008).—TYPE: U. S. A. Hawaiian, Oahu Islands: Waianae Mtns., Valley east of Kawaihapai, dry bare ridge in decadent forest, 28 September 1930, *O. Degener & K. K. Park 4195* (holotype: BISH-497368!).

Chrysodracon halapepe (St. John) P.-L. Lu & Morden, comb. nov. *Pleomele halapepe* St. John, Pacific Science 39(2): 180 (1985). *Dracaena halaapepe* (St. John) Jankalski, Sansevieria 18:21 (2008).—TYPE: U. S. A. Hawaiian Islands, Oahu Island: Koolau Mts., On wooded slope, Kipapa Gulch, second north branch, Waipio, 800 Ft elev. 13 April 1930, *E.Y. Hosaka 216* (holotype: BISH-494908!; isotypes: BISH-494906!, 494907!). St. John aberrantly published the epithet as *halaapepe* based on the incorrect vernacular "hala-a-pepe"; spelling had been corrected to *halapepe* under ICBN 60.1 (Wagner et al. 1990).

Chrysodracon hawaiiensis (O. Degener & I. Degener) P.-L. Lu & Morden, comb. nov. *Pleomele hawaiiensis* O. Degener & I. Degener 1980, Fl. Hawaiiensis, Fam 68. (Not *Dracaena hawaiiensis* Fosberg)—TYPE: U. S. A. Hawaiian Islands, Hawai'i Island: at 1900 ft near Belt Road; Mauka of Pohue Bay, Kau, in ½ acre 'a'a kipuka with *Metrosideros* and *Maba*, 4 September 1977, *O. & I. Degener 34432* (holotype: NY23993, 23994!; isotypes: G-00191143, MICH-1192971, US-3277449).

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Appendix 1. Taxa, specimens examined and GenBank accession numbers for the four gene regions sequenced for molecular phylogenetic analysis. Locations of herbarium vouchers are in brackets followed by geographic origins. Living collections (LC) have accession number and botanical garden given. Abbreviations of herbaria follow Holmgren et al. (1990). Order of gene regions for GenBank numbers: *trnQ-rps16*, *trnL-trnF*, *rpl32-trnL*, and *ndhF-rpl32*.

OUTGROUP—Comospermum yedoensis (Maxim. ex Franch. & Sav.) Rauschert. U. K. Cult. source, RBG Kew, *Chase 833* (K), JX080425, JQ904928, JX015117, JX178062. ***Disporopsis pernyi*** (Hua) Diels. CHINA. Nanjing, *Chase 493* (K), JX080426, JQ904929, JX015118, JX178063. ***Eriospermum flagelliforme*** (Baker) J. C. Manning. TANZANIA. 75 km NW Tundama, *Chase 2051* (K), JX080423, JQ904926, JX015115, JX178060. ***Liriope muscari*** (Decne.) L. H. Bailey. U. S. A. Cult. source, UNC *Chase 131* (NCU), JX080424, JQ904927, JX015116, JX178061. ***Speirantha gardenii*** (Hook.) Baill. U. K. Cult. source, RBG Kew, *Chase 495* (K), JX080521, JQ905024, JX015213, JX178158.

INGROUP—Dracaena adamii Hepper. IVORY COAST. *Bos 10369* (WAG), JX080436, JQ904939, JX015128, JX178073. ***Dracaena afromontana*** Mildbr. TANZANIA. *Jannerup & Mhoro 401* (K), JX080437, JQ904940, JX015129, JX178074. ***Dracaena aletriformis*** (Haw.) Bos. SOUTH AFRICA. Kirstenbosch, *P.-L. Lu and Zenze 0100* (HAW), JX080438, JQ904941, JX015130, JX178075. ***Dracaena americana*** Donn.Sm. MEXICO. Veracruz: *Wendt 3209* (NY), JX080434, JQ904937, JX015126, JX178071. ***Dracaena aubryana*** Brongnb. ex E. Morren. U. S. A. Hawaii: Cult. source, PTBG, Kauai, *Lorence 9946* (PTBG), JX080440, JQ904943, JX015132, JX178077. ***Dracaena borneensis*** (Merr.) Jankalski. MALAYSIA. Borneo, Sabah: Sandakan, *Wood 17102* (BZ), JX080443, JQ904946, JX015135, JX178080. ***Dracaena bueana*** Engl. GHANA. *Leeuwenberg 11101* (WAG), JX080445, JQ904948, JX015137, JX178082. ***Dracaena cambodiana*** Pierre ex Gagnep. CAMBODIA. *JPZ 1* (XTBG), JX080446, JQ904949, JX015138, JX178083. ***Dracaena cinnabari*** Balf.f. YEMEN. Socotra, *Nagata 004* (HAW), JX080448, JQ904951, JX015140, JX178085. ***Dracaena cochinchinensis*** (Lour.) S. C. Chen. CHINA. Yunnan, *JY 28* (XTBG), JX080449, JQ904952, JX015141, JX178086. ***Dracaena concinna*** Kunth. U. S. A. Hawaii: Cult. source, *P.-L. Lu 0098* (HAW). JX080451, JQ904954, JX015143, JX178088. ***Dracaena cubensis*** Vict. CUBA. Prov. Guantanamo: Municipio Baracoa, *Thomas et al. 14917* (HAJB, NY), JX080435, JQ904938, JX015127, JX178072. ***Dracaena draco*** (L.) L. SPAIN. Canary Islands, *Orr and P.-L. Lu 110* (HAW), JX080453, JQ904956, JX015145, JX178090. ***Dracaena ellenbeckiana*** Engl. ETHIOPIA. *de Wilde 7327* (WAG), JX080454, JQ904957, JX015146, JX178091. ***Dracaena laxissima*** Engl. GABON. *de Wilde 11557* (WAG), JX080459, JQ904962, JX015151, JX178096. ***Dracaena ombet*** Heuglin ex Kotschy & Peyr. ETHIOPIA. *Bos 9997* (WAG), JX080462, JQ904965, JX015154, JX178099. ***Dracaena phanerophlebia*** Baker. GABON. *de Wilde s. n.* (c. s. 1983/65), JX080463, JQ904966, JX015155, JX178100. ***Dracaena rubroaurantiaca*** De Wild. NETHERLANDS. ex Burgers Zoo Acc. No.1998-0503001, *Wilkin 1197* (K), JX080468, JQ904971, JX015160, JX178105. ***Dracaena scabra*** Bos. IVORY COAST. *Bos 10350* (WAG), JX080470, JQ904973, JX015162, JX178107. ***Dracaena schizantha*** Baker. ETHIOPIA. Dire Dawa, *Chase 21514* (K), JX080471, JQ904974, JX015163, JX178108. ***Dracaena serrulata*** Baker. YEMEN. Cult. source, KHBG (06.0016), *P.-L. Lu 0099* (HAW), JX080472, JQ904975, JX015164, JX178109. ***Dracaena singapurensis*** Ridl. SINGAPORE. *AI 257* (SING), JX080473, JQ904976, JX015165, JX178110. ***Dracaena transvaalensis*** Baker. SOUTH AFRICA. Kirstenbosch, *P.-L. Lu and Zenze 0101* (HAW), JX080482, JQ904985, JX015174, JX178119. ***Dracaena umbratica*** Ridl. SINGAPORE. *Chong 359* (SING), JX080484, JQ904987, JX015176, JX178121. ***Dracaena yuccifolia*** Ridl. SINGAPORE. *Tang and Sidek 1231* (SING), JX080486, JQ904989, JX015178, JX178123. ***Dracaena* sp. 1**. border between MYANMAR and THAILAND. *Wilkin 1505* (K), JX080474, JQ904977, JX015166, JX178111. ***Dracaena* sp. 2**. THAILAND. Ching Rai: *Wilkin et al. 1508* (K), JX080475, JQ904978, JX015167, JX178112. ***Dracaena* sp. 3**. THAILAND. Loei: *Wilkin et al. 1515* (K), JX080476, JQ904979, JX015168, JX178113. ***Dracaena* sp. 4**. THAILAND. Loei: *Wilkin et al.1517* (K), JX080477, JQ904980, JX015169, JX178114. ***Dracaena* sp. 5**. THAILAND. Loei: *Wilkin et al. 1518* (K), JX080478, JQ904981, JX015170, JX178115. ***Dracaena* sp. 6**. THAILAND. Loei: *Wilkin et al. 1519* (K), JX080479, JQ904982, JX015171, JX178116. ***Pleomele angustifolia*** (Medik.) N.E. Br.

TAIWAN. Pingtong: *P.-L. Lu 0106* (HAW), JX080441, JQ904944, JX015133, JX178078. ***Pleomele arborea*** (Willd.) N. E. Br. CAMEROON. *Westphal 10140* (WAG), JX080439, JQ904942, JX015131, JX178076. ***Pleomele auwahiensis*** H. St. John. U. S. A. Hawaii: Kanaio, Maui, *Hobdy 207* (BISH), JX080429, JQ904932, JX015121, JX178066; U. S. A. Hawaii: Makawao, Maui, *Oppenheimer H50221* (BISH), JX080427, JQ904930, JX015119, JX178064. JX080429, JQ904932, JX015121, JX178066. ***Pleomele aurea*** (H. Mann.) N. E. Br. U. S. A. Hawaii: Kauai, *Takeuchi Nualolo 17* (BISH), JX080428, JQ904931, JX015120, JX178065. ***Pleomele bicolor*** (Hook.) N. E. Br. CAMEROON. *Bos s. n.* (WAG), JX080442, JQ904945, JX015134, JX178079. ***Pleomele braunii*** (Engl.) N. E. Br. CAMEROON. *Bos 4259* (WAG), JX080444, JQ904947, JX015136, JX178081. ***Pleomele camerooniana*** (Baker) N. E. Br. IVORY COAST. *Bos 10340* (WAG), JX080447, JQ904950, JX015139, JX178084. ***Pleomele cantleyi*** (Baker) N. E. Br. SINGAPORE. *Lisa 2007.309* (SING), JX080450, JQ904953, JX015142, JX178087. ***Pleomele congoensis*** (Hua) N. E. Br. GABON. *Breteler 7636* (WAG), JX080452, JQ904955, JX015144, JX178089. ***Pleomele elliptica*** (Thunb. & Dalm.) N. E. Br. INDONESIA. Bogor, *Ariati 2010.2* (BZ), JX080455, JQ904958, JX015147, JX178092. ***Pleomele fernaldii*** H. St. John. U. S. A. Hawaii: Lanai, *Marreo 417* (BISH), JX080431, JQ904934, JX015123, JX178068. ***Pleomele floribunda*** (Baker) N. E. Br. MAURITIUS. CBG, *D. Lorence 10361* (PTBG), JX080456, JQ904959, JX015148, JX178093. ***Pleomele forbesii*** O. Deg. U. S. A. Hawaii: Oahu, *Perlman 6114* (BISH), JX080430, JQ904933, JX015122, JX178067. ***Pleomele fragrans*** (L.) Salisb. U. S. A. Hawaii: WBG, *P.-L. Lu 0103* (HAW), JX080457, JQ904960, JX015149, JX178094. ***Pleomele godseiffiana*** (Sander ex Mast.) N. E. Br. INDONESIA. Bogor, *Ariati 2010.3* (BZ), JX080481, JQ904984, JX015173, JX178118. ***Pleomele goldieana*** (W. Bull ex Mast. & Moore) N. E. Br. INDONESIA. Bogor, *Ariati 2010.4* (BZ), JX080458, JQ904961, JX015150, JX178095. ***Pleomele granulata*** (Hook.f.) N. E. Br. SINGAPORE. *Ridley 3316* (SING), JX080523, JQ905026, JX015215, JX178160. ***Pleomele halapepe*** H. St. John. U. S. A. Hawaii: Oahu, *Takeuchi 2170* (BISH), JX080432, JQ904935, JX015124, JX178069. ***Pleomele hawaiiensis*** O. Deg. & I. Deg. U. S. A. Hawaii: Puuwaawaa, Hawaii, *Takeuchi 5130* (BISH), JX080433, JQ904936, JX015125, JX178070. ***Pleomele interrupta*** (Baker) N. E. Br. IVORY COAST. *Bos 10351* (WAG), JX080522, JQ905025, JX015214, JX178159. ***Pleomele maingayi*** (Hook.f.) N. E. Br. SINGAPORE. *Sammon 300* (SING), JX080524, JQ905027, JX015216, JX178161. ***Pleomele marginata*** Lam. U. S. A. Hawaii: Cult. source, PTBG, Kauai, *Lorence 9948* (PTBG), JX080460, JQ904963, JX015152, JX178097. ***Pleomele multiflora*** (Warb. ex Sarasin) Merr. PALAU. *Kitalong 4* (PTBG, NY), JX080461, JQ904964, JX015153, JX178098. ***Pleomele phrynioides*** (Hook.) N. E. Br. CAMEROON. *Breteler 2438* (WAG), JX080464, JQ904967, JX015156, JX178101. ***Pleomele poggei*** (Engl.) N. E. Br. CAMEROON. *Leeuwenberg 8878* (WAG), JX080465, JQ904968, JX015157, JX178102. ***Pleomele porteri*** (Baker) N. E. Br. SINGAPORE. *Chong 353* (SING), JX080466, JQ904969, JX015158, JX178103. ***Pleomele reflexa*** (Lam.) N. E. Br. MAURITIUS. Nouvelle Decouverte, *P.-L. Lu 0108* (HAW), JX080467, JQ904970, JX015159, JX178104. ***Pleomele sanderiana*** (Sander) N. E. Br. U. S. A. Hawaii: Honolulu, *P.-L. Lu 0096* (HAW), JX080469, JQ904972, JX015161, JX178106. ***Pleomele umbraculifera*** (Jacq.) N. E. Br. MAURITIUS. *P.-L. Lu 1017* (HAW), JX080483, JQ904986, JX015175, JX178120. ***Pleomele viridiflora*** (Engl. & K. Krause) N. E. Br. CAMEROON. *Wieringa et al. 5824* (WAG), JX080485, JQ904988, JX015177, JX178122. ***Sansevieria aethiopica*** Thunb. U. K. Cult. source, RBG Kew, *Heath & Heath 714* (K), JX080487, JQ904990, JX015179, JX178124. ***Sansevieria aubrytiana*** Carrière. U. K. Cult. source, RBG Kew, *Kayombo 1019* (K), JX080488, JQ904991, JX015180, JX178125. ***Sansevieria ballyi*** Ballyi. U. K. Cult. source, RBG Kew, *Newton 5594* (K), JX080489, JQ904992, JX015181, JX178126. ***Sansevieria bella*** L. E. Newton. TANZANIA. Iringa Distr., Ruaha NP, *Newton 3945* (K), JX080490, JQ904993, JX015182, JX178127. ***Sansevieria braunii*** Engl. & Krause. U. K. Cult. source, RBG Kew, *Frontier-Tanzania 569* (K), JX080491, JQ904994, JX015183, JX178128. ***Sansevieria burdettii*** Chahin. MALAWI. Livingstone Falls, lower Shire Rvr., *Brummitt 10005* (K), JX080492, JQ904995, JX015184, JX178129. ***Sansevieria caulescens*** N. E. Br. KENYA. Buchuma, Mombasa-Nairobi Rd, *Powell s. n.* (K), JX080493, JQ904996, JX015185, JX178130. ***Sansevieria concinna*** N. E. Br. YEMEN. Socotra, *Wild & Leach 5234* (K), JX080494, JQ904997, JX015186, JX178131. ***Sansevieria conspicua*** N. E. Br. U. K. Cult. source, RBG Kew, *Festo et al. 2697* (K), JX080495, JQ904998, JX015187, JX178132. ***Sansevieria cylindrica*** Bojer ex Hook. U. K. Cult. source, RBG Kew, *Leistner et al. 13* (K), JX080480, JQ904983, JX015172, JX178117. ***Sansevieria dawei*** Stapf. U. K. Cult. source, RBG Kew, *Luke 9337* (K), JX080496, JQ904999, JX015188, JX178133. ***Sansevieria ehrenbergii*** Schweinf. ex Baker. U. K. Cult. source, RBG Kew, *Friis et al. 9364* (K), JX080498, JQ905001, JX015190, JX178135. ***Sansevieria forskaliana*** (Schult. & Schult.f.) Hepper & J. R. I. Wood. SOMALIA. *Friis et al. 4634* (K), JX080499, JQ905002, JX015191, JX178136. ***Sansevieria gracilis*** N. E. Br. U. K. Cult. source, RBG Kew, *Luke et al. TPR697* (K), JX080500, JQ905003, JX015192, JX178137. ***Sansevieria grandis*** Hook.f. U. K. Cult. source, RBG Kew, *Bally B8271* (K), JX080501, JQ905004, JX015193, JX178138. ***Sansevieria humbertiana*** Guillaumin. KENYA, Taita Distr.: Buchuma Plains, *s. coll. s. n.* (K), JX080502, JQ905005, JX015194, JX178139. ***Sansevieria hyacinthoides*** (L.) Druce. KENYA, *Jansen & Nuvunga PJ7665* (K), JX080503, JQ905006, JX015195, JX178140. ***Sansevieria kirkii*** Baker. MALAWI. Central Region, 19 km N of Nkhota Kota, *Mhoro 392* (K), JX080504, JQ905007, JX015196, JX178141. ***Sansevieria liberica*** Gèrôme & Labroy. GHANA. *Milne-Redhead 5120* (K), JX080505, JQ905008, JX015197, JX178142. ***Sansevieria metallica*** Gèrôme & Labroy. RÉUNION (France, DOM-ROM). étang Salé les Hauts: *Cadet 4390* (K), JX080506, JQ905009, JX015198, JX178143. ***Sansevieria nilotica*** Baker. TANZANIA. Rubondo Is., SE edge of Lake Victoria, *Barcock & FitzGibbon s. n.* (K), JX080507, JQ905010, JX015199, JX178144. ***Sansevieria parva*** N. E. Br. U. K. Cult. source, RBG Kew, *Mwangangi & Abdalla 246* (K), JX080508, JQ905011, JX015200, JX178145. ***Sansevieria patens*** N. E. Br. U. K. Cult. source, RBG Kew, *Bally 8177* (K), JX080509, JQ905012, JX015201, JX178146. ***Sansevieria pearsonii*** N. E. Br. U. K. Cult. source, RBG Kew, *Heath & Heath 447* (K), JX080510, JQ905013, JX015202, JX178147. ***Sansevieria perrotii*** Warb. U. K. Cult. source, RBG Kew, *Gillett & Hemming 24126* (K), JX080511, JQ905014, JX015203, JX178148. ***Sansevieria phillipsiae*** N. E. Br. SOMALIA, *Beckett & White 1450A* (K), JX080512, JQ905015, JX015204, JX178149. ***Sansevieria sambiranensis*** H. Perrier. MADAGASCAR. *Rakotonasolo 810* (TAN), JX080513, JQ905016, JX015205, JX178150. ***Sansevieria senegambica*** Baker. CAMEROON. *Wieringa et al. 5823* (WAG), JX080514, JQ905017, JX015206, JX178151. ***Sansevieria sordida*** N. E. Br. ETHIOPIA. Neghelli-Filtu, *Grenfell 4* (K), JX080515, JQ905018, JX015207, JX178152. ***Sansevieria subspicata*** Baker. U. K. Cult. source, RBG Kew, *Jansen et al. 7499* (K), JX080516, JQ905019, JX015208, JX178153. ***Sansevieria suffruticosa*** N. E. Br. KENYA. Naro Moru to Ngobit Rd, *Glover & Samuel 3323* (K), JX080517, JQ905020, JX015209, JX178154. ***Sansevieria sulcata*** Bojer ex Baker. U. S. A. Cult. source, WBG, *P.-L. Lu 0104* (HAW), JX080518, JQ905021, JX015210, JX178155. ***Sansevieria trifasciata*** Prain. U. S. A. Cult. source, WBG, *Lau 2852* (BISH), JX080519, JQ905022, JX015211, JX178156. ***Sansevieria volkensii*** Gürke. KENYA. 55 km W of Voi, Serengeti Plain, *Bally B13151* (K), JX080520, JQ905023, JX015212, JX178157.