SANSEVIERIA

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The Genus Sansevieria: An Introduction to Molecular (DNA) Analysis and Preliminary Insights to Intrageneric Relationships

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Summary

Molecular biology, particularly as it involves the analysis of DNA, is growing in importance within plant taxonomy to resolve how families and genera are related and to even resolve plant species from one another. Here, we review some of the concepts of molecular biology with an emphasis on how it may help to unravel certain long-debated issues within the genus *Sansevieria* as well as the placement of this genus among other related genera. We provide some preliminary data and offer a few insights but caution against jumping to any conclusions about Sansevierias without considerable additional data.

Introduction

A well-respected succulent plant and cactus collector and researcher from England reportedly refers to DNA as "Damned Nasty Answers" because he doesn't particularly care for what molecular biology has to contribute to the understanding of plant species and families compared with more traditional, character-based taxonomy. Point taken: molecular biology is based on the genetic instructions for all these structural characters of which we are so fond, hidden deep inside each tiny cell, unseen to the naked eye. Using such data is upsetting the species cart in the world of plant taxonomy well beyond the little universe of succulent plants and cacti. We believe that stirring DNA sequence data into the pot that includes character data enhances the discussion of organization of species, and may, or should, eventually help determine what makes these species distinct from one another. After all, now we can distinguish among individual humans with such reliability that such data have been admissible in the court systems since 1986: why not among plant species? So, in this article, pretend that the genus *Sansevieria*, and the use of molecular biology, is on trial and you are the jury: will you vote for conviction or acquittal?

Biogeography

As the readers of this journal are well aware, *Sansevieria* is a cosmopolitan genus that occurs in Africa, the Middle East, and the Asian subcontinent. The diversity in form is rather astonishing, ranging from tiny little plants, some with stout, spiky leaves and others with thin, flat ones, to formidable shrubs 2-4 m in height. What holds this group of plants together within the genus *Sansevieria* are the similar flowers and seeds, but some believe that the flowers and seeds aren't so unique to exclude larger, related plants currently within the genus *Dracaena* (Bos, 1984), and some molecular data bear this out (Lu and Morden, 2014). One of the limits of character-based assignment of plants into groups – whether a variable group of plants into a species, or a set of species with shared characteristics into families – is that personal opinion eventually comes into play. Molecular data in the form of DNA sequences is supposed to eliminate or at least reduce the influence of personal opinion.

Using his opinion based largely on dried specimens or living collections, Brown (1915) compiled the first comprehensive review of the genus *Sansevieria*, including the description of many new species. Most of the species occur in East Africa, particularly Kenya but also Tanzania and Uganda (Newton, 2001). Other species are in South Africa (Obermeyer, 1992; van Jaarsveld, 1995), Madagascar (Perrier, 1938), southeastern Africa (especially Zimbabwe and Malawi: Thiede, 1993; la Croix, 2010; Rulkens and Baptista, 2009, 2013), west-

ern Africa, Ethiopia and Somalia (Teketay, 1995, Thulin, 1995; Sebsebe and Nordal, 2010), Yemen and Oman (Vrskovy, 2009), India (Binojkumar, 2002), Sri Lanka, and Myanmar. In our current opinion, the genus contains 73 species (Table 1) and 20 subspecies or varieties; at least another 12 undescribed species, subspecies, or varieties are in cultivation.

Sansevieria occur in a variety of habitats ranging from tropical forests in West Africa to savannah and desert habitats in East Africa and the Arabian Peninsula, although some species (e.g., *S. kirkii*) are coastal in their northerly distribution and likely have at least some salt tolerance. They grow within a spectrum of full shade to full sun, and some have a tolerance to brief freezing conditions (Myklebust, this volume). They range in morphology from broad- leaf (e.g., *Sansevieria masoniana*) to cylindrical-leaf (e.g., *S. cylindrica*) and in height from

Fig. 1 - Robert Webb (Arid Lands Nursery) comparing *Sansevieria pinguicula* (in pot) with *S. dumetescens* (in foreground). There are substantial differences in all characteristics of these species except the inflorescence (not shown), which branches for both species.

dwarf (e.g., *S. eilensis*) to arborescent (e.g., *S. arborescens*). All species offset vegetatively, either by stolons or rhizomes, and young plants – whether reproduced sexually or vegetatively – frequently differ in morphology from juvenile to adult plants, leading to confusion in the description of some species. This wide range of morphological variation within the genus should result from specific phenotypes with phylogenetic inheritance or be the result of ecological adaptation (or both).

Questions abound, including how the intrageneric structure of *Sansevieria* should be arranged (or not), the relationship of *Sansevieria* to *Dracaena*, and the family to which both genera belong (e.g., Agavaceae, Dracaenaceae, or the current favorite, Asparagaceae). Several authors have proposed either three groups (Pfennig, 1977, used without attribution by Mbugua, 2007) or sections (Jankalski, 2009) within *Sansevieria*. For our initial purposes, we retain the informal group designation, and the groups are *Sansevieria* (64 taxa), *Capitatus* (10 species), and *Paniculatus* (9 species) on the basis of inflorescence structure (Table 1). Group *Capitatus* produces capitate inflorescences, usually directly out of the ground; group *Paniculatus* has branching inflorescences, usually from leaf axils near the apical tip; and plants in group *Sansevieria* produce unbranched inflorescences from the leaf axils, which in some species can also be from subterranean points.

One obvious problem with this grouping scheme is that other rather obvious morphological characteristics are ignored. For example, one could easily devise a grouping scheme on the basis of flat, flexible leaves; stiff, broad, and channeled leaves; upright, more or less cylindrical leaves held in a more-or-less distichous arrangement; and spiky leaves with short channels. A grouping based strictly on flowering arrangements ignores other characteristics that may have a stronger genetic signal (or not), and this could cause rather severe conflicts between molecular and character data.

While some traditional taxonomists may sneer at the importance of molecular data, it is often hard to argue the point that additional data can be useful to addressing questions where strict morphological data leaves one a bit baffled. For example, how does *Sansevieria pinguicula*, a small, rosette-forming species, fit in with *Sansevieria dumetescens*, a rather large, thicket-forming shrub (Fig. 1)? The answer, of course, is that both have branching inflorescences, but other than that no one would necessarily believe that these two species are closely related. Given the complexity and questions within the genus *Sansevieria* described above, we propose that an additional molecular data set could potentially offer some resolution.

Species	Group	Year Described	Leaf Morphology
Sansevieria aethiopica Thunberg	*Sansevieria*	1794	narrow, flattened
Sansevieria arborescens Cornu ex Gérôme & Labroy	*Paniculatus*	1903	elliptical, guttered
Sansevieria ascendens L.E. Newton	*Paniculatus*	2010	elliptical, guttered
Sansevieria aubrytiana Carriere	*Sansevieria*	1861	broad-leaf
Sansevieria bacularis Pfennig ex Butler & Jankalski	*Sansevieria*	2010	cylindrical, grooved
Sansevieria bagamoyensis N. E. Brown	*Paniculatus*	1913	narrow, flattened
Sansevieria ballyi L.E. Newton	*Sansevieria*	2004	cylindrical
Sansevieria bella L.E. Newton	*Sansevieria*	2000	cylindrical
Sansevieria braunii Engler & K. Krause	*Sansevieria*	1911	broad-leaf
Sansevieria burdettii Chahinian	*Sansevieria*	2000	cylindrical
Sansevieria burmanica N. E. Brown	*Sansevieria*	1915	narrow, flattened
Sansevieria canaliculata Carrière	*Capitatus*	1861	cylindrical, grooved
Sansevieria concinna N. E. Brown	*Capitatus*	1915	spoon-shaped
Sansevieria conspicua N. E. Brown	*Sansevieria*	1913	broad-leaf
Sansevieria cylindrica Bojer ex Hooker	*Sansevieria*	1859	cylindrical
Sansevieria dawei Stapf	*Sansevieria*	1906	broad-leaf
Sansevieria dooneri N. E. Brown	*Sansevieria*	1915	narrow, flattened
Sansevieria downsii Chahinian	*Sansevieria*	2000	elliptical, guttered
Sansevieria dumetescens L.E. Newton	*Paniculatus*	2009	broad, flattened
Sansevieria ebracteata (Cavanilles) C. R. Suresh	*Sansevieria*	1988	cylindrical, guttereed
Sansevieria ehrenbergii Schweinfurth ex Baker	*Paniculatus*	1875	elliptical, guttered
Sansevieria eilensis Chahinian	*Sansevieria*	1995	elliptical, guttered
Sansevieria elliptica (Chiovenda) Cufodontis	*Sansevieria*	1971	broad-leaf
Sansevieria erythraeae Mattei	*Sansevieria*	1918	elliptical
Sansevieria fasciata Cornu ex Gérôme & Labroy	*Sansevieria*	1903	broad-leaf
Sansevieria fischeri (Baker) Marais	*Capitatus*	1986	cylindrical
Sansevieria formosa Chahinian	*Sansevieria*	2012	elliptical, guttered
Sansevieria forskaliana (Schultes *fil*.) Hepper & Wood	*Sansevieria*	1983	broad-leaf
Sansevieria francisii Chahinian	*Sansevieria*	1995	bract-like
Sansevieria frequens Chahinian	*Sansevieria*	2000	broad-leaf
Sansevieria gracilis N. E. Brown	*Sansevieria*	1911	cylindrical
Sansevieria gracillima Chahinian	*Sansevieria*	2005	cylindrical
Sansevieria grandicuspis Haworth	*Sansevieria*	1812	broad-leaf
Sansevieria hallii Chahinian	*Capitatus*	1996	elliptical, thickened
Sansevieria hargeisana Chahinian	*Sansevieria*	1994	cylindrical
Sansevieria humiflora D.J. Richards	*Capitatus*	2004	elliptical, thickened
Sansevieria hyacinthoides (Linné) Druce	*Sansevieria*	1914	broad-leaf
Sansevieria kirkii Baker	*Capitatus*	1887	broad-leaf
Sansevieria liberica Gérôme & Labroy	*Sansevieria*	1903	broad-leaf
Sansevieria lineata T.G. Forrest	*Sansevieria*	2013	broad-leaf
Sansevieria longiflora Sims	*Sansevieria*	1826	broad-leaf
Sansevieria longistyla la Croix	*Sansevieria*	2004	broad-leaf
Sansevieria lunatifolia Newton	*Sansevieria*	2014	elliptical, guttered
Sansevieria masoniana Chahinian	*Capitatus*	2000	broad-leaf
Sansevieria metallica Gérôme & Labroy	*Sansevieria*	1903	broad-leaf
Sansevieria newtoniana T.G. Forrest	*Sansevieria*	2014	broad-leaf
Sansevieria nilotica Baker	*Sansevieria*	1875	broad-leaf
Sansevieria nitida Chahinian	*Sansevieria*	2001	broad-leaf
Sansevieria parva N. E. Brown	*Sansevieria*	1915	narrow, flattened
Sansevieria patens N. E. Brown	*Sansevieria*	1915	elliptical, guttered
Sansevieria pearsonii N. E. Brown	*Sansevieria*	1911	elliptical, guttered
Sansevieria pedicellata la Croix	*Sansevieria*	2004	broad-leaf
Sansevieria perrotii Warburg	*Paniculatus*	1901	elliptical, guttered
Sansevieria pfisteri D.J. Richards	*Sansevieria*	2009	elliptical, guttered
Sansevieria phillipsiae N. E. Brown	*Sansevieria*	1913	cylindrical
Sansevieria pinguicula P. R. O. Bally	*Paniculatus*	1964	conical, guttered
Sansevieria powellii N. E. Brown	*Paniculatus*	1915	elliptical, guttered
Sansevieria powysii L.E. Newton	*Paniculatus*	2010	elliptical, guttered
Sansevieria raffillii N. E. Brown	*Sansevieria*	1915	broad-leaf
Sansevieria rhodesiana N. E. Brown	*Sansevieria*	1915	elliptical, guttered
Sansevieria robusta N. E. Brown	*Sansevieria*	1915	elliptical, guttered
Sansevieria rorida (Lanza) N. E. Brown	*Sansevieria*	1915	elliptical, guttered
Sansevieria roxburghiana Schultes	*Sansevieria*	1829	cylindrical, guttereed
Sansevieria scimitariformis D.J. Richards	*Capitatus*	2002	elliptical, thickened
Sansevieria senegambica Baker	*Sansevieria*	1875	broad-leaf
Sansevieria sinus-simiorum Chahinian	*Capitatus*	2002	elliptical, guttered
Sansevieria stuckyi Godefroy-Lebeuf	*Capitatus*	1903	cylindrical
Sansevieria subspicata Baker	*Sansevieria*	1889	broad-leaf
Sansevieria subtilis N. E. Brown	*Sansevieria*	1915	broad-leaf
Sansevieria suffruticosa N. E. Brown	*Sansevieria*	1915	cylindrical
Sansevieria trifasciata Prain	*Sansevieria*	1903	broad-leaf
Sansevieria volkensii Gürke	*Sansevieria*	1895	cylindrical
Sansevieria zeylanica (Linné) Willdenow	*Sansevieria*	1799	narrow, flattened

Table 1. List of *Sansevieria* species that we accept to be used in this study. We are generally not using subspecies, varieties, known hybrids or cultivars, or species with indefinite provenance except for certain tests (with some notable exceptions).

A Brief Introduction
To Molecular Biology

All living organisms are made up of cells (excepts for viruses, if one considers viruses as 'alive'). In sexually reproducing organisms, the first cell is formed from the fusion of male and female gametes, each bringing with them half the genetic material required to make a fully functioning organism. That first cell, now with a full set of genetic information, divides multiple times, as do the resulting daughter cells. The result is a multicellular organism with each cell containing the same genetic information as all other cells and as the original cell. Thus, removing a leaf tip from a *Sansevieria* plant provides tissue with the same genetic code for that individual as would other plant parts, such as roots or flowers.

The genetic material for all life on Earth comes in the form of DNA (DeoxyriboNucleic Acid). DNA is a long double-stranded string-like molecule, affectionately called the double helix by those who discovered its structure, made of only four different subunits, called nucleotides, linked together. These nucleotides are the named guanine, adenine, cytosine, and thymine and are abbreviated G, A, C, and T. In the double-stranded arrangement, a G on one side of the DNA molecule always pairs with a C on the other side. Similarly, A always pairs with T. For this reason, amounts of DNA sequence data are measured in 'base pairs.' These base pairs, or 'letters,' create a very small 'genetic alphabet' and are chemically bound together in different orders of different lengths to spell 'words' that we call genes. As well, genes are strung together into even longer sequences to form chromosomes; members of the genus *Sansevieria* have 20-21 chromosomes in their cells. Obtaining the 'spelling' of genes is referred to DNA sequence data. If different individuals (or species) share the same genes, or the 'spelling' of genes, then they are more likely related than those individuals with different DNA sequences.

The sum total of all DNA sequence data within an organism, say a *Sansevieria* plant, is known as its genome. That could involve millions or hundreds of millions of base pairs. While the technology exists, but is still evolving, to obtain the entire genome of a plant, the analysis of all that data is daunting and typically involves the use of supercomputers. Most studies that use molecular data to evaluate the evolutionary structure or taxonomy of plants narrow down to specific regions of DNA for analysis. This is more feasible in regard to both time and money, but then the science becomes informed guessing as to which genes to analyze. The goal is to find loci, or zones within genes, that offer the appropriate level of variation for the taxonomic level being addressed. After all, if human beings share 50% of the genes of bananas, then these shared genes would likely give information for Kingdom-level relationships, but such gene sequences would be too similar within Kingdoms to offer information to intrageneric relationships. We have to therefore look for other genes that are only variable within our group of interest to determine how to separate individuals from on another.

In plants, DNA is found in several locations within each cell. While the primary location for DNA in cells (excluding bacteria) is found the nucleus, researchers often target extranuclear sources of genes, including the mitochondria, the unit (or organelle) responsible for cellular respiration, and the chloroplast, the organelle that is responsible for photosynthesis. Because most humans don't photosynthesize, analyzing chloroplast's DNA (cpDNA) is one way to distinguish humans from bananas, or plants from animals, using molecular data. Because photosynthesis is obviously so important, plant leaves have an abundance of chloroplasts and thus an abundance of DNA from this source is available for analysis. Genes located in this batch of DNA are commonly used in resolving plant relationships, and routine molecular lab protocols exist for many projects using cpDNA for evaluating plant evolutionary questions (Taberlet et al., 1991).

Genes and their specific sequences are inferred to be the result of evolution, and while most genes serve some specific purpose within the plant, such as coding for enzymes and proteins, other DNA regions do not code for tangible products. Such 'non-coding regions' were once considered "junk" DNA that served no purpose, but now molecular biologists have identified many of these regions operate as sort of as cellular traffic signals. For instance, a non-coding region in front of a gene can serve as a 'green light' that tells a cell to read the following gene, until a 'red light' is found in a non-coding region downstream from the gene.

This discussion becomes important for the following reason. Mutations, or copying errors in the DNA as cells divide, are random and can thus occur in coding or non-coding regions. However, a mutation in a coding region could lead to decreased or complete loss of that gene's function, thus evolution buffers against errors occurring here. On the other hand, mutations occurring in a non-coding region could mean the difference between a 'green light' staying on for 30 seconds versus 40 seconds. As long as the traffic signals still work, there isn't the high level of evolutionary pressure against mutations in non-coding regions. Generally speaking, there is more phylogenetic information within lower-level taxonomic groups found within non-coding regions than within genes, but finding genes within chromosomes is gener-

Sample Number	Species	Group	Data	Source
1	*Sansevieria powellii*	Paniculatus	Mwenbeni Station, Kenya; WY 1072	Webb-Yocum
2	*Sansevieria parva*	Sansevieria	Ngong Hills, Kenya; WY 1077	Webb-Yocum
3	*Sansevieria ballyi*	Sansevieria	Kasigau, Kenya (WY 1074)	Webb-Yocum
4	*Sansevieria ehrenbergii*	Paniculatus	Omani form 02-522-01	Dimmitt (Butler)
5	*Sansevieria ehrenbergii*	Paniculatus	Sala Gate, Kenya (WY 1069)	Webb-Yocum
6	*Sansevieria laevifolia*	Sansevieria	Lake Naivasha, Kenya (WY 1022)	Webb-Yocum
7	*Sansevieria suffruticosa*	Sansevieria	Gilgil, Kenya (WY 1020)	Webb-Yocum
8	*Sansevieria subspicata*	Sansevieria	Mozambique	Myklebust, Smoley, Beckman
9	*Sansevieria aethiopica*	Sansevieria	South Africa	Silverhill. Arid Lands stock
10	*Sansevieria concinna*	Capitatus	west of Vilanculos, Mozambique (Lavranos and Lubbers 5933)	Myklebust
11	*Sansevieria pinguicula*	Paniculatus	northeastern Kenya	Pima Valley, Plantas del Sol
12	*Sansevieria francisii*	Sansevieria	Coast Province, Kenya (FKH 432)	Grigsby, Smoley
13	*Dracaena aletriformis*	Dracenaceae	South Africa	Lifestyle Seeds
14	*Sansevieria masoniana*	Capitatus	Congo	Pima Valley, Grigsby, Smoley
15	*Sansevieria fischeri*	Capitatus	N of Mangea Hill, Kenya (WY 1068)	Webb-Yocum
16	*Sansevieria hargeisana*	Sansevieria	WSW of Hargeisa, Somalia (Lavranos 7382), Grigsby's clone 1	Grigsby
17	*Sansevieria erythraeae*	Sansevieria	Eritrea, Ethiopia	Grigsby, Smoley
18	*Sansevieria canaliculata (sulcata)*	Capitatus	Mozambique	Myklebust, Turner Greenhouse
19	*Sansevieria kirkii var. kirkii*	Capitatus	Tanzania	Turner Greenhouses
20	*Sansevieria kirkii var. pulchra*	Capitatus	Tanzania	Pima Valley, Grigsby
21	*Sansevieria bagamoyoensis*	Paniculatus	near Bagamoyo, Tanzania	Myklebust
22	*Sansevieria bella*	Sansevieria	Ewaso Ngiro, Kenya; Newton 3945 (type specimen)	Newton
23	*Nolina palmeri var. brandegei*	Nolinaceae	Baja California, Mexico	seed
24	*Sansevieria robusta*	Paniculatus	Mwatate, Kenya (WY 1078)	Webb-Yocum
25	*Sansevieria arborescens*	Paniculatus	Tanzania	Myklebust
26	*Sansevieria dumetescens*	Paniculatus	Sala Gate, Kenya (WY 1067)	Webb-Yocum
27	*Sansevieria stuckyi*	Capitatus	Mozambique	Smoley
28	*Sansevieria gracilis*	Sansevieria	clone 2, Kenya	Torrebundo
29	*Sansevieria sp.*	Capitatus	Igomea, Tanzania; Bhitala 1000	Bhitala
30	*Sansevieria raffillii var. raffillii*	Sansevieria	Wangala Station, Kenya; WY 1076	Webb-Yocum
31	*Sansevieria frequens*	Sansevieria	Lake Baringo, Kenya (WY 1063)	Webb-Yocum
32	*Dracaena serrulata*	Dracenaceae	Audhali Plateau N. of Lawder, Yemen	ISI release
33	*Dracaena cinnabari*	Dracenaceae	Socotra, Yemen	Arid Lands Greenhouses
34	*Sansevieria downsii*	Sansevieria	Malawi (P. Downs, GC 126-78)	ISI release
35	*Sansevieria dumetescens*	Paniculatus	Sala Gate, Kenya (WY 1067)	Webb-Yocum
36	*Sansevieria longiflora*	Sansevieria	Congo	Smoley
37	*Sansevieria abyssinica*	Sansevieria	allegedly the same as S. forskaoliana	Smoley
38	*Sansevieria hallii*	Capitatus	Zimbabwe	Ellert
39	*Sansevieria sp. aff. rorida*	Sansevieria	Lav 23154	Exotica
40	*Sansevieria cylindrica var. cylindrica*	Sansevieria	Angola	Smoley
41	*Sansevieria volkensii*	Sansevieria	Same, Tanzania; WY 1049	Webb-Yocum
42	*Sansevieria ebracteata*	Sansevieria	India	Singh
43	*Sansevieria eilensis*	Sansevieria	Eil, Somalia; probably a Lavranos collection	Arid Lands Greenhouses
44	*Sansevieria fasciata*	Sansevieria	Congo	Smoley
45	*Sansevieria sinus-simiorum*	Capitatus	Zimbabwe	Myklebust
46	*Sansevieria cv 'Superclone'*	Capitatus	unknown	Myklebust
47	*Sansevieria roxburghiana*	Sansevieria	India	Singh
48	*Nolina microcarpa*	Nolinaceae	common in southern Arizona and Sonora, Mexico	seed, Mesa Garden
49	*Nolina parvifolia*	Nolinaceae	central Mexico	seed, Mesa Garden
50	*Sansevieria pedicellata*	Sansevieria	Zimbabwe, Chimanimani Mountains	Myklebust
51	*Sansevieria dooneri*	Sansevieria	Kenya	Myklebust
52	*Sansevieria burmanica*	Sansevieria	Burma, type locality	Torrebundo through Myklebust
53	*Sansevieria hargeisana*	Sansevieria	WSW of Hargeisa, Somalia (Lavranos 7382), Grigsby's clone 2	Grigsby
54	*Dracaena serrulata*	Dracenaceae	Audhali Plateau N. of Lawder, Yemen	ISI release
55	*Sansevieria rhodesiana*	Sansevieria	Zimbabwe	Butler
56	*Sansevieria elliptica 'Horwood'*	Sansevieria	Eastern Kenya, FKH 424	Arid Lands Greenhouses

Table 2. List of *Sansevieria* samples analyzed for this study.

Samples colored gray are discussed in the phylogeny trees and the text; the other samples are yet to be analyzed.

| Sample Number	Species	Group	Data	Source
57	*Sansevieria rorida*	Sansevieria	Somalia, Lav 23319	Myklebust
58	*Sansevieria patens*	Sansevieria	purportedly a hybrid	Grigsby's
59	*Sansevieria sp. (flat leaf)*	Sansevieria	Eil, Somalia; no number, probably Lav	Exotica
60	*Sansevieria sp. aff. rorida*	Sansevieria	Lav 23395, Eil Pass, GC-85-10	Myklebust
61	*Sansevieria nitida*	Sansevieria	Chahinian plant he descibed	Myklebust
62	*Sansevieria raffillii var. glauca*	Sansevieria	Kenya	Butler
63	*Sansevieria subtilis*	Sansevieria	Uganda	Butler
64	*Sansevieria arborescens*	Paniculatus	Lav 23151, Somalia	Myklebust
65	*Sansevieria zeylanica*	Sansevieria	India, Sri Lanka, small leaf data plant	Myklebust
66	*Sansevieria sp.*	Sansevieria	N of Arusha, Tanzania (WY 1056)	Webb-Yocum
67	*Sansevieria pearsonii*	Sansevieria	Transvaal, South Africa	Myklebust
68	*Sansevieria powellii 'Pfennig'*	Paniculatus	Pfennig form, uncertain origin	Dirty Louie
70	*Sansevieria trifasciata* var. *laurentii*	Sansevieria	common in the trade	unknown
71	*Sansevieria grandicuspis*	Sansevieria	supposedly from the Congo, could be a hybrid	Myklebust
72	*Sansevieria forskaoliana*	Sansevieria	Yemen 2W203	Butler
73	*Sansevieria raffillii var. raffillii*	Sansevieria	Mwembeni Station, Kenya; WY 1168	Webb-Yocum
74	*Sansevieria conspicua*	Sansevieria	Kenya	Myklebust
75	*Sansevieria sp.*	Sansevieria	Mwatati, Tanzania; Bhitala 1004	Bhitala
76	*Sansevieria cylindrica var. patula*	Sansevieria	Angola	Pima Valley
77	*Dracaena draco*	Dracenaceae	Canary Islands	seed
78	*Nolina parryi var. wolfii*	Nolinaceae	common in southern California mountains	seed, Mesa Garden
79	*Sansevieria pearsonii*	Sansevieria	Transvaal Form, RSA	Myklebust
80	*Sansevieria dawei*	Sansevieria	Uganda	Smoley
81	*Dracaena fragrans*	Dracenaceae	probably West Africa	Arid Lands Greenhouses
82	*Sansevieria canaliculata (sulcata)*	Capitatus	Mozambique	Myklebust, Turner Greenhouse
83	*Sansevieria hyacinthoides (macrophylla)*	Sansevieria	South Africa	Myklebust
84	*Sansevieria canaliculata*	Capitatus	Somalia (very controversial)	Turner Greenhouses
85	*Sansevieria gracillima*	Sansevieria	Sansevieria gracillima (Chahinian)	Myklebust (Chahinian)
86	*Sansevieria scimitariformis*	Capitatus	Zimbabwe; Richards 995	Myklebust
87	*Sansevieria burdettii*	Sansevieria	Malawi	Myklebust
88	*Sansevieria volkensii*	Sansevieria	Same, Tanzania; WY 1049	Webb-Yocum
89	*Sansevieria humiflora*	Capitatus	Zimbabwe	Myklebust
90	*Sansevieria ehrenbergii*	Paniculatus	Lav 24977 Somalia	Myklebust
91	*Sansevieria aethiopica*	Sansevieria	van Jaarsveld 14969, Polokwane, Chunies Poort	Kirstenbosch
92	*Sansevieria ehrenbergii*	Paniculatus	Omani form 02-522-01	Dimmitt (Butler)
93	*Sansevieria frequens*	Sansevieria	Lake Baringo, Kenya WY1146	Webb-Yocum
94	*Sansevieria volkensii*	Sansevieria	Wangela Station, Kenya	Webb-Yocum
95	*Sansevieria metallica*	Sansevieria	van Jaarsveld et al 87, Tembe Elephant Park, RSA	Kirstenbosch
96	*Sansevieria frequens*	Sansevieria	Tony Dyer Farm, type locality (WY 1007)	Webb-Yocum
97	*Sansevieria aethiopica*	Sansevieria	van Jaarsveld 11172, Graaff-Renet, RSA	Kirstenbosch
98	*Sansevieria cylindrica var. cylindrica*	Sansevieria	van Jaarsveld 22665, Lobito to Huambo, Angola	Kirstenbosch
99	*Sansevieria elliptica*	Sansevieria	NW Buchuma Road, Kenya (WY 1031)	Webb-Yocum
100	*Sansevieria fischeri*	Capitatus	Tana River, Kenya (Thick leaf)	Powys
101	*Sansevieria phillipsiae*	Sansevieria	Somalia (KEW 410-74-03700)	Myklebust
102	*Sansevieria 'Superclone'*	Capitatus	unknown	Myklebust
103	*Dracaena ellenbeckii*	Dracenaceae	from Ann Powys' yard, Laikipia Plateau, Kenya	nd
104	*Sansevieria ascendens*	Paniculatus	type plant from Len Newton	Newton
105	*Sansevieria dawei*	Sansevieria	from type locality, W of Entebbe, Uganda	WY 1001
106	*Sansevieria lineata*	Sansevieria	from type locality, Tom Forest	Forest
107	*Sansevieria 'marsabitensis'*	Paniculatus	N of Marsabit, Kenya	WY 1186
108	*Sansevieria 'marsabitensis' 2*	Paniculatus	N of Marsabit, Kenya	WY 1188
109	*Sansevieria nilotica*	Sansevieria	from type locality for S. nilotica var. obscura, N Entebbe, Uganda	WY 1000
110	*Sansevieria perrotii*	Paniculatus	from type locality, E of Lindi, Tanzania	Bhitala 1034
111	*Sansevieria pfennigii*	Capitatus	from type locality, W of Lindi, Tanzania	Bhitala 1031
112	*Sansevieria powysii*	Paniculatus	type plant from Gilfrid Powys	Powys
113	*Sansevieria sp.*	Sansevieria	Ngare Nanyuki, Tanzania	WY 1194
114	*Sansevieria arborescens*	Paniculatus	Tarasa, Kenya	Bhitala 1017
115	*Sansevieria pfisteri*	Sansevieria	Namibe, Angola	van Jaarsveld et al 22985
116	*Sansevieria pearsonii*	Sansevieria	E of Benguela, Angola	van Jaarsveld 226600
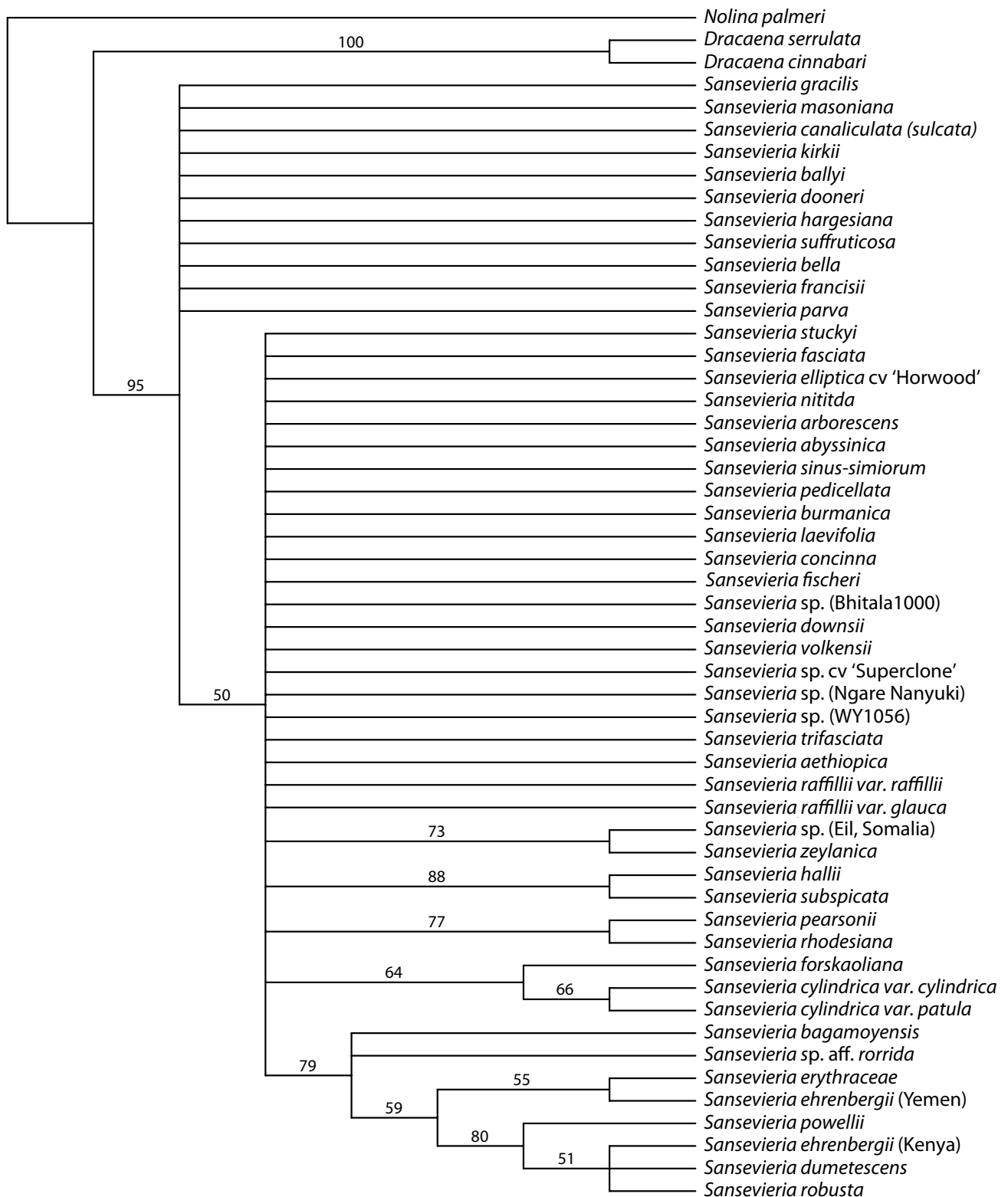
Fig. 2 - Phylogenetic reconstruction of Dracaenoid species using maximum parsimony.
Numbers on branches represent statistical bootstrap values. Values of 80 or higher are equivalent to 95% significance.

ally easier because of their more predictable DNA sequences.

Once large data sets of DNA sequence data are generated, the analysis is quite computer-intensive involving sophisticated statistical analyses. Those species that share the same DNA 'letter' sequence for any given region of the gene are assumed to have inherited that sequence from a common ancestor. Maximum parsimony (MP) and maximum likelihood (ML) are two of the more popular statistical approaches for data analysis. MP operates under the assumption that the simplest answer, meaning the phylogenetic tree with the fewest number of evolutionary steps, is preferred over more complicated hypotheses. ML takes into account 'biases' within the data
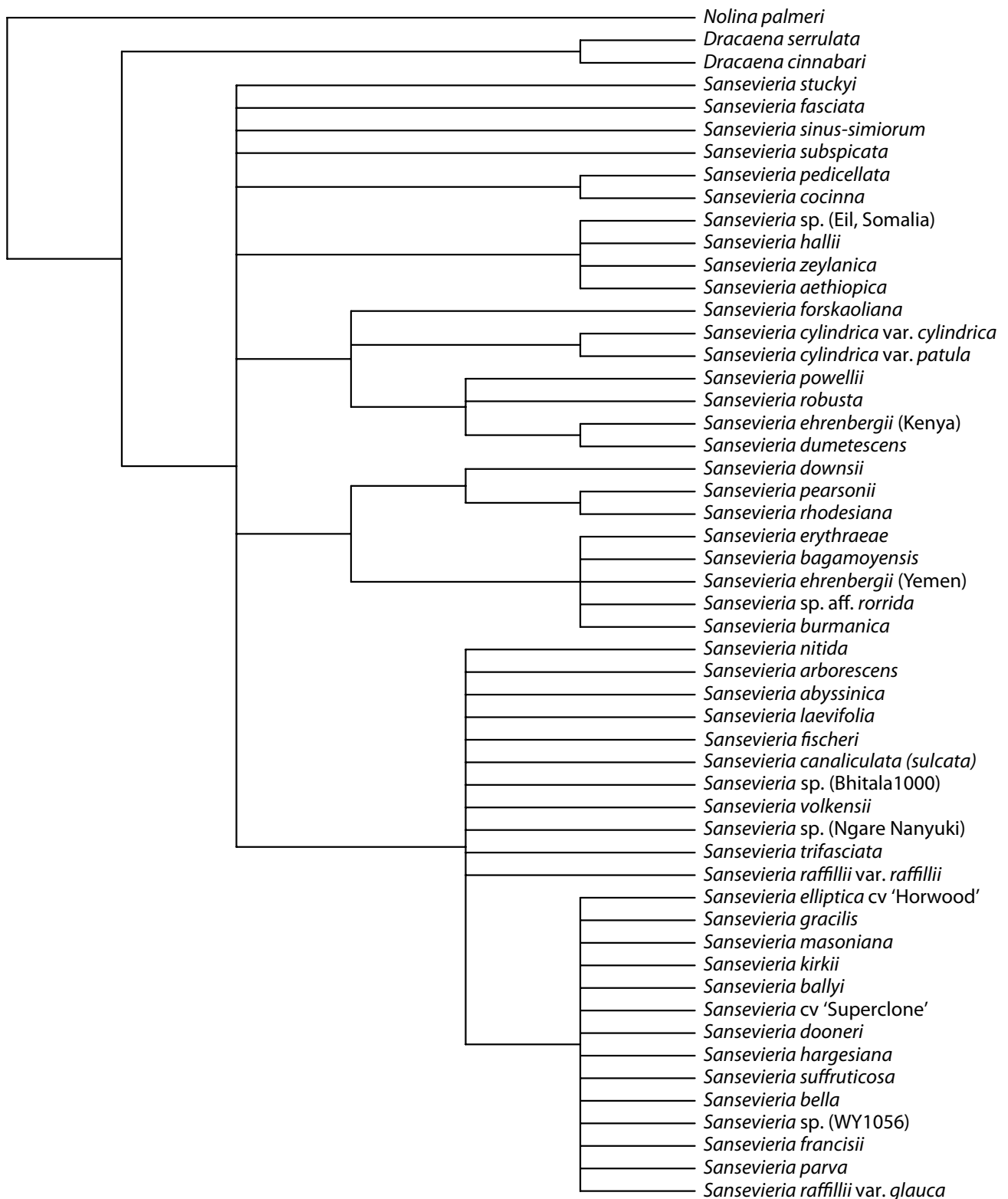
Fig. 3 - Phylogenetic structure of sampled Dracaenoid species
using maximum-likelihood analysis.

set and generates a mathematical model that weights the information. In other words, not all differences within the genes may be equal as some mutations may be more rare (and be more important) than others. MP treats all data equally.

The goal of the statistical analyses is the construction of a "tree" that shows the amount of similarity in genetic data among the species that are included in the analysis. This could be viewed as similar to classical taxonomic trees, where a family has genera, which are separated into species, some of which are separated into subspecies or varieties (e.g., family Asparagaceae>genus *Sansevieria*>group Sansevieria>species *kirkii*>variety *pulchra*). The trees built using molecular data are based

on statistical modeling, which has good and bad aspects: good that it is objective analysis, bad that it is dependent upon the amount of data, the variability (or lack of) of the data, if that variability represents "junk" or real plant characteristics, and number of samples (species) that are included.

A brief interlude here on probability and statistics may be warranted. Consider a coin flip: the probability of getting a "heads" is 50%, or 1:2, and is the same as the probability of getting a "tails." This probability, by the way, is one measure of the concept of "by chance alone:" if you flip a coin, the probability of getting a heads is 50% by chance alone. This simple binary example is useful, but the understanding curve goes up dramatically as you get into data that involves lots of information. You never get a probability of 100% in the statistics game, because there is by definition a built-in uncertainty, and this is why the most definite conclusions that are obtained using statistics tend to refer to probability > 95% that a result obtained is different than by chance along. With the types of statistical analyses that are used in molecular biology, the higher the probability, the more certain the conclusion, but the conclusions are never ever 100% certain.

For additional statistical support of these tree-building analyses (both MP and ML), there is a method called bootstrapping. Essentially, this is a resampling-subsampling method where phylogenies are continually constructed but from subsets of the data. In other words, if you have 100 pieces of data, you can analyze 50-60 pieces randomly 1000 times and then average the conclusions from those 1000 analyses (also called realizations). If the same relationship is recovered multiple times from different realizations, then it means that relationship is not based on a single (or a few) unique pieces of information. Obviously, the higher the bootstrap value, the better the support for the tree that gets constructed. Felsenstein (1985) indicated that a bootstrap value of 80 was equivalent to science's 95% statistical standard of 'not due to chance alone.'

The benefit of molecular data is that either there is a "G' in that specific nucleotide position which is shared among multiple taxa, or there isn't a G in that position. There is no ambiguity here as there potentially is in coding morphological data. For instance, coding a certain species' leaf as cylindrical, broad, flat, or any one of the infinite intermediate values that might be defined could influence the way a researcher would reconstruct historical relationships. On the other hand, there is so much molecular information, and in some loci too little variation, to allow conclusions with any certainty unless a whole lot of base pairs are involved as well as a whole lot of species. To get better results, and to minimize the prominence of "non-coding" or "junk" sequences, the more the merrier: questions involving inter-generic relationships benefit from including all recognized species, or at least as many as can be analyzed given the rather prosaic limitations of funding and time.

Some Research Questions

This study is not the first to use molecular data to attempt to resolve relationships involving the genus *Sansevieria*. Lu and Morden (2014) used cpDNA to resolve the relationships among Dracaenoid genera, which included 34 species of *Sansevieria*, but their emphasis was not within the genus *Sansevieria*. Instead, they were attempting to elucidate relationships among the related genera *Sansevieria*, *Dracaena*, and *Pleomele* within the family Asparagaceae, which is where current thinking places these genera. In a conclusion similar to that of Bos (1984), who based his conclusions on the similarity of flowers and fruit, Lu and Morden (2014) concluded that the species of *Sansevieria* fell within the genus *Dracaena* and therefore the two genera should be merged into *Dracaena*. Pay attention now: Lu and Morden (2014) based their conclusions on cpDNA data alone using 34 species of *Sansevieria*. Using the same type of cpDNA data, albeit from different loci, with more species, can we add to this discussion about whether the related genera of *Sansevieria* and *Dracaena* should be merged?

Following Jankalski (2009), Mansfeld (2013) divided many of the species of *Sansevieria* into three sections on the basis of characters, mostly inflorescence structure. As shown in Table 1, we continue to use the groups originally defined by Pfennig (1977), and these map exactly into the sections proposed by Jankalski (2009). Mansfeld (2013) takes this even farther as he defines subsections within section *Sansevieria* and includes additional characters, such as vegetative propagation via stolons or rhizomes (see additional discussion within Webb and Newton, this volume). Can molecular data help to support this proposed scheme of sections, or would additional data "muddy the waters" and call any inter-generic classification scheme into question?

Approach

We have assembled samples of many species, varieties, and undescribed species from the living collection housed at Arid Lands Greenhouses (see Myklebust and Webb, this volume). This sample set includes leaves of 116 plants (Table 2), most with locality data. Our preliminary analysis uses only 53 of these taxa (colored gray in Table 2), and these are displayed in our preliminary phylogeny diagrams. Many plants were ob-

tained from collectors within the United States (notably Alan Myklebust, see Myklebust and Webb, this volume), from nurseries (notably the Lavranos plants primarily from Grigsby's Cactus Gardens), from field settings under permit from the Kenyan government in 2003 and the Tanzanian government in 2009-2013, and from Kirstenbosch Gardens in Cape Town (Ernst van Jaarsveld). Undescribed species include several potential new species from Kenya (e.g., *Sansevieria laevifolia*, Webb and Newton, this volume) and as many as eight undescribed species from Tanzania collected by Bhwire Bhitala of Arusha, Tanzania. For a variety of reasons, not all taxa available are included in our preliminary data.

We also included what are known as "outgroups," or taxa either from different families (*Nolina*) or from genera that may or may not be the same as *Sansevieria* (*Dracaena*). We expect these taxa we to be different than our ingroup (*Sansevieria*), and lets us see the bigger family tree perspective. In our preliminary analysis, we include one *Nolina* (*N. parryi*) and two *Dracaena* (*D. cinnabari* and *D. serrulata*) and have other members of these genera awaiting future analysis (Table 2). Just for the heck of it, for future analyses we'll probably go to the local grocery and throw in a sample of asparagus as well.

We obtained genomic DNA from freshly sampled and immediately frozen leaf tips using standard molecular protocols. We initially obtained chloroplast DNA sequences using universal primers described by Taberlet et al. (1991) and following their PCR protocols. These data were analyzed using MP and ML phylogenetic analyses in MEGA 6.0 (Tamura et al., 2013) and PAUP* (Swofford, 2002). Additional sequence data from another source within the cells of *Sansevieria* other than the chloroplasts will likely increase phylogenetic resolution (Baldwin and Webb, preliminary and unpublished data).

Some Preliminary Results

We first wish to offer some guidance (and caveats) in interpreting phylogenies statistically inferred from molecular data. First and foremost, these are preliminary data that neither involve the full number of species in the genus (Table 2) nor sufficient DNA base pairs; in other words, consider this as a progress report. We hope that more definitive information comes when additional species are analyzed and additional loci for analysis of base pairs are examined.

The lengths of the horizontal branches in the phylogeny reflect the degree of genetic variation from neighboring branches. When you see what is termed a polytomy, which is a list of names gathered to the right of a vertical bar, it indicates that those taxa have no genetic differ-

ences among them given the base-pair data analyzed, and the proper conclusion is that their ordering within the phylogenetic tree is random. In other words, those taxa can be rearranged in any order to the right of that bar, and we purposefully left them out of alphabetical order to emphasize their random relationship to one another. However, you must recognize that the species aggregated to the right of each bar have at least some genetic distinction from all other aggregations. With the low genetic information recovered from the genes we have analyzed so far, the bootstrapping analysis collapses all aggregations without strong statistical support into a much larger polytomy (Fig. 2). The reader should remember that only bootstrap values of 80 or higher are statistically significant at the 95% confidence level (Felsenstein,1985), and other relationships, either tantalizing or confounding, are inconclusive.

Our preliminary results come from analysis of 994 base pairs within the chloroplast DNA sequence. Only 8.25% of these base pairs offer unique phylogenetic information, with a maximum of 11.3% difference among species of *Sansevieria*, 17.0% between *Sansevieria* and *Dracaena*, 18.2 % between *Sansevieria* and *Nolina.* Our limited data suggest a significant separation at the >95% level between *Sansevieria* and two prominent species of tree *Dracaena* (Fig. 1). We would like to preliminarily reject the assertion of Bos (1984), who suggested combining the two genera, but we use far fewer specimens of *Dracaena* than Lu and Morden (2014) and cannot reject their conclusions. It may seem like a cliché, but "more study is needed" to really test the results of Lu and Morden (2014), and those tests would likely involve more than cpDNA molecular data along with more species of *Sansevieria* and *Dracaena*.

We digress now to consider how resolution of the question of whether *Dracaena* and *Sansevieria* should be merged is to the further subdivision of *Sansevieria* (or combined genus *Dracaena*). If a merger were supported, the combined genus *Dracaena* would have at least the subgenera of *Dracaena* and *Sansevieria*; if they remain separated, the genus *Sansevieria* currently has no subgenera, only the proposed sections of Jankalski (2009) or groups of Pfennig (1977). If these sections or groups are sustained by further research, shouldn't the information be raised a rank into subgenera, leaving open the possibilities raised by Mansfeld (2013) for further subdividing the genus? Taking this even further, is there any real basis beyond opinions on physical differences that support subdivision between genera and species (e.g., sections)?

Our initial results give some hints as to where this subdivision might go (Fig. 2). As discussed in Webb and Newton (this volume), Mansfeld (2013) erected

subsection *Stolonifera* to include a number of East African species that produce stolons. Much of that subsection, including *S. ballyi*, *S. bella*, *S. francisii*, *S. gracilis*, *S. hargeisana*, and *S. suffructicosa*, appear together in an aggregation high in the tree (Fig. 2). And while that might seem to be a good thing, that aggregation includes other species with seemingly no connection in terms of physical characteristics, including *S. dooneri* and *S. parva* (which we suspect could be one species variable in size), *S. masoniana*, *S. kirkii*, and *S. canaliculata*, which on the physical face of it have nothing whatsoever in common with one exception: they belong to the group or section called *Sansevieria*.

One subdivision seems to be supported: the group Paniculatus is largely set apart from the remainder of the species at the bottom of Fig. 2. With a bootstrap value of 79, close to the 80 required for >95% confidence, *S. ehrenbergii* (two geographic forms) clusters with species that include *S. dumetescens*, *S. robusta*, and *S. bagamoyensis*, all belonging to the Paniculatus group. On the other hand, *S. arborescens* clusters with species within the Sansevieria group, and *S. erythraeae* clusters with those species in the Paniculatus group. Our preliminary data is tending to support previously suggested subgeneric groupings, but we need to get more data and more species to attempt to gain a statistically significant result.

Suspension of disbelief would be required for some relationships: anyone believe the close relationship between *S. hallii* and *S. subspicata*, or between the little undescribed flat-leaf species from Eil, Somalia, and *S. zeylanica* from Sri Lanka? These aggregations, and some of the larger ones, underscore the preliminary nature of our data. Among the seemingly incongruent relationships suggested by this preliminary data, some little nuggets appear that might be suggestive of real relationships. Could *S. rhodesiana* be a form of *S. pearsonii*? – they cluster together with nearly a >95% confidence level in Fig. 2. Similarly, *S. cylindrica* varieties *cylindrica* and *patula* cluster together, albeit with less confidence, and it is possible that the varieties of *cylindrica* could be eliminated.

The maximum-likelihood analysis (Fig. 3) doesn't add that much to the discussion, but it does show how volatile the relationships are using different statistical analyses. This, of course, results from the high variability inherent in this preliminary data and underscores how little separates the species within our target group. Although *Sansevieria subspicata* no longer clusters with *S. hallii*, as it did in the parsimony analysis (Fig. 2), *S. hallii* now appears with *S. zeylanica* and the undescribed flat-leaf species from Eil, Somalia. Neither of the two statistical techniques are able to mine real nuggets from this limited dataset.

Discussion

We don't have many Damned Nasty Answers from our work so far, and perhaps the jury verdict will be a mistrial, but we do have some insights as to where all this might lead. Our guess is that the question of whether *Sansevieria* belongs within *Dracaena* (Lu and Morden, 2014) might lead to *Dracaena* being split into two genera, one involving trees and the other involving smaller life forms; these two genera might bookend the genus *Sansevieria* within an evolutionary framework.

Within what is currently conceived as the genus *Sansevieria*, separation could well be warranted at the subgenus level, and the genus is likely to be split into several subgenera as a result of combining molecular data and morphological characteristics of its 73 species (Table 1). Although our vision is clouded by a noisy, messy dataset at present, we think we can see molecular support for at least one of those subgenera, which we've referred to here as the group Paniculatus. But one of those Damned Nasty Answers could arise if *Sansevieria arborescens* is excluded and *S. erythraeae* is included. You guessed it, "more research is needed" to address that question.

As the science of molecular biology progresses and the description of new species of *Sansevieria* continues, we will build upon this preliminary data set by including additional species not analyzed yet (see Table 2) and DNA sequences from more variable, or "hot," loci. The goal is to resolve intrageneric relationships with greater statistical support and hopefully better address the many biogeographic, evolutionary, hybrid, and taxonomic questions that currently remain. As an example of one potential direction, we obtained a partial mitochondrial genome from *Sansevieria trifasciata* from an unrelated study (Steele et al., 2012), and we are constructing an additional mitochondrial DNA sequence data set using custom amplification primers to complement our existing chloroplast data. Our first attempts at this did not add to the discussion; the mitochondrial DNA data showed little variation. This type of customization may be what is needed to potentially document differences among species in a rapidly evolving genus such as *Sansevieria*.

A significant research question concerns whether phenotypic variation (e.g., leaf morphology of cylindrical versus flat) results from phylogenetic inheritance, ecological adaptation, or both. Our preliminary data does not support any separation along the lines of leaf morphology. Finally, if we can attain sufficient molecular resolution, it is possible to resolve certain questions among species groups, including whether *S. powellii* is a hybrid (Newton, this volume), whether *S. bella* and *S. laevifolia* should be reduced under *S. suffruticosa* (Webb

and Newton, this volume), and the relationship between *S. perrotii* and *S. ehrenbergii* in East Africa and whether what is now called *S. ehrenbergii* in Oman, Yemen, the Sudan, Somalia, and Kenya is really one species or another complex along the lines of the allies of *S. suffruticosa* (Webb and Newton, this volume). We offer no insights as to whether molecular data can address these questions.

The genus *Sansevieria* is in need of a significant revision, in part because the only comprehensive monograph on the genus is Brown (1915). Many new species have been described since Brown, and whether these plants warrant species, subspecies, or variety rank are open taxonomic questions. Just getting the infra-generic structure established would be a fine result of our work, but full-genomic evaluations could take things much further with less opinion and more data. Our hope is that this work could potentially establish a basis for the first revision of the genus since Brown (1915), or at least spur someone else to do this.

If there is to be a conclusion from this preliminary data, it is to add more species and more base pairs from different loci to attempt to gain a greater amount of resolution among these species. Given their obvious physical differences, it is equally obvious that a loci is in the *Sansevieria* genome that creates these differences, and while it may become the proverbial search for the needle in the haystack to find that loci, it should be worth the effort.

Acknowledgments

References

Binojkumar, M.S. (2002). A study on the genus *Sansevieria* Thunb. (*Dracaenaceae*) in India. *Journal of Economic and Taxonomic Botany* 26(2): 455–463.

Bos, J.J. (1984). *Dracaena* in West Africa. Agricultural University Wageningen, Paper 84-1: 126.

Brown, N. E. (1915). *Sansevieria*. A monograph of all known species. *Bull. Misc. Inform. Kew* 1915(5): 185–261.

Chahinian, B. J. (2005). *The splendid Sansevieria*. Buenos Aires (AR): Published by the author.

Felsenstein, J. (1985). Phylogenies and the Comparative Method. *American Naturalist* 125(1): 1-15.

Jankalski, S. (2009). The *Sansevieria* inflorescence and new sections proposed. *Sansevieria* 19: 8–10.

la Croix, I. (2010). *Dracaenaceae*. In: Timberlake, J. R. & Martins, E. S. (eds.): *Flora Zambesiaca*, vol. 13, part 2, pp. 13–35. Richmond (GB): Royal Botanic Gardens, Kew.

Lu, P., & Morden, C.W. (2014). Phylogenetic relationships among Dracaenoid genera (Asparagaceae: Nolinoideae) inferred from chloroplast DNA loci. *Systematic Botany* 39(1): 90–104.

Mansfeld, P.A. (2013). Neugliederung der Gattung *Sansevieria* (Asparagaceae). *Kakteen und andere Sukkulenten* 62: 35–38.

Mbugua, P. K. (2007). *Sansevieria*. In: Beentje, H. J. & Ghazanfar, S. A. (eds.): *Flora of Tropical East Africa*: *Dracaenaceae*; pp. 10–41. Richmond (GB): Royal Botanical Gardens, Kew.

Newton, L. E. (1994). Observations on flowering of *Sansevieria robusta* in Kenya. *E. Afr. Nat. Hist. Soc. Bull.* 24(1): 8–11.

Newton, L. E. (2003). *Sansevieria dooneri* and *S. parva*. *Sansevieria* 7: 10–11.

Newton, L. E. (2005a). Horst Pfennig (1933 - 1994). *Sansevieria* 11: 7–8.

Newton, L.E. (2001). *Sansevieria*. *In* Illustrated Handbook of Succulent Plants, Springer-Verlag Publishers.

Obermeyer, A. A. (1992). *Dracaenaceae*: *Sansevieria*. In: Leistner, O. A. (ed.): *Flora of Southern Africa*, Vol. 5, part 3. Pretoria (ZA): National Botanic Institute.

Perrier, H. (1938). 40e famille. Liliacées (*Liliaceae*). In: Humbert, H. (ed.): *Flore de Madagascar*. Tananarive (Madagascar): Imprimerie Officielle.

Pfennig, H. (1977). Rasenbildend bis baumartig: Die Sansevierien. *Gartenpraxis* 1977: 506–511.

Rulkens, A. J. H. & Baptista, O. J. (2009). Field observations and local uses of the poorly known *Sansevieria pedicellata* from Manica province in Mozambique. *Sansevieria* 20: 2–7.

Rulkens, A. J. H. & Baptista, O. J. (2013). Notes on the distribution of *Sansevieria burdettii* Chahinian. *Sansevieria* 29: 14–16.

Sebsebe, D., & Nordal, I. (2010). *Aloes and other lilies of Ethiopia and Eritrea*. Shama Books, Ethiopia. ISBN 978-99944-0-042-3. 349 s.

Steele, P.R., Hertweck, K. L., Mayfield, D., McKain, M.R., Leebens-Mack, J., & Pires, J. C. (2012). Quality and quantity of data recovered from massively parallel sequencing: Examples in Asparagales and Poaceae. *American Journal of Botany*. 99(2): 330-348.

Swofford, D. (2002). PAUP*. Phylogenetic Analyses Using Parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland, Mass.

Taberlet P., Gielly L, Pautou G, Bouvet J. (1991). Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17(5): 1105-9.

Tamura, K., Stecher, G., Peterson, D., Filipski, A., & Kumar, S. (2013). MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. *Molecular Biology and Evolution* 30: 2725-2729.

Teketay, D. (1995). The genus *Sansevieria* Thunb. in Ethiopia. A contribution to the flora of Ethiopia. *Sansevieria Journal* 4(2): 43–58.

Thiede, J. (1993). Notes on the *Sansevieria* species of Malawi. *Sansevieria Journal* 2(2): 27–34, (3): 51–52.

Thulin, M. (ed.) (1995). *Flora of Somalia*. Volume 4. *Angiospermae* (*Hydrocharitaceae – Pandanaceae*). Richmond (GB): Royal Botanic Gardens Kew.

van Jaarsveld, E. J. (1994). The *Sansevieria* species of South Africa and Namibia. *Aloe* 31(1): 11–15.

Vrskovy, B. P. (2009). A brief account of the Sansevierias of Yemen. *Sansevieria* 20: 11–14.