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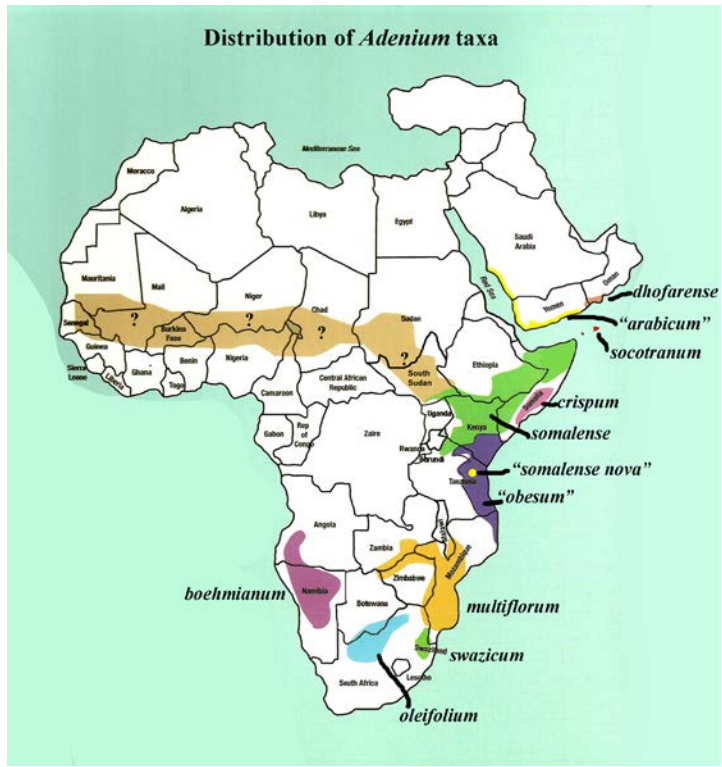
Adenium Taxonomy and Nomenclature:

Progress creates more questions

Introduction

Adenium Roemer and Schultes is a small genus of succulent plants in the dogbane family Apocynaceae. Almost unknown in cultivation before about 1990, they have since then become extremely popular, especially in tropical climates. The two most common English names are desert rose and adenium. I (Dimmitt) dislike the name desert rose, because the plants and flowers bear no resemblance to roses, and most species do not grow in deserts. I prefer to call them by their generic name. When used as a common name, adenium is neither capitalized nor italicized.

In nature adenium populations are widely scattered in semiarid habitats throughout Africa and along the southern edge of the Arabian Peninsula (Fig. 1). Most taxonomists recognize several species, but the exact number is still unresolved (Hargreaves 2002; this study). There is also a nomenclatural problem; *Adenium "obesum"* and *A. "arabicum"* are not legitimate names (Dimmitt et al. 2009), as will be explained later. Their uncertain status will be highlighted in this article by enclosing them in double quotation marks. This article addresses three topics: 1) confirmation of seven well-defined species; 2) discussion of a confusing complex of at least three taxa that was not resolved by the DNA analysis; and 3) description of the problems inhibiting the resolution of the taxonomic and nomenclatural issues. A more comprehensive DNA analysis could potentially resolve some of the remaining questions.



1. Approximate known distributions of *Adenium* taxa. The map was drawn from a rough sketch by John Lavranos, based on about 120 European herbarium records and his extensive field observations.

The DNA Study

Taylor Edwards (Associate Staff Scientist, University of Arizona Genetics Core) extracted DNA from 48 *Adenium* specimens of 11 taxa provided by Dimmitt and other adenium collectors, plus *Pachypodium rosulatum* as an outgroup. Most of the plants are from known wild localities or seedlings from controlled crosses of wild parents. The sample set represents all of the ten putative species recognized by Dimmitt *et al.* (2009) plus an undescribed form known in cultivation as *A.* "somalense nova". A few specimens of hybrids and unidentified cultivars were also sequenced. We could locate no specimens of one or more taxa described in the vast Sahel region from South Sudan to Senegal. We sequenced 5 different genes, or "loci", representing different locations in the adenium genome; 1 mitochondrial, 3 chloroplast, and 1 nuclear. We reconstructed phylogenetic trees for each of the loci and we performed a multi-locus analysis combining data from each of the individual trees into a species tree. A technical publication is in preparation.

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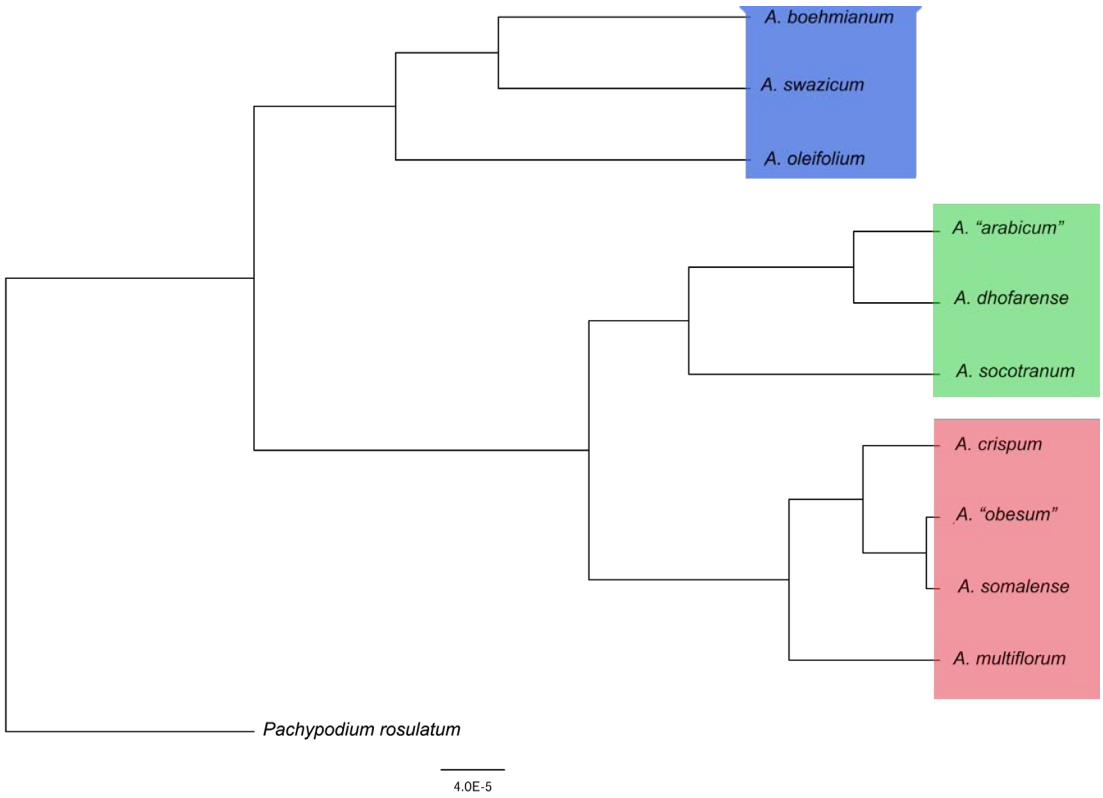


2. Phylogenetic tree generated with combined data from five loci. It shows three major clades in the genus *Adenium*. The lengths of the horizontal lines in the tree roughly correlate with the degrees of genetic differences among taxa.

Results and Discussion

Among the individual genetic loci, each of the individual gene trees exhibited high concordance and the multilocus analysis species tree identified three major clades; sister clades East African and Arabian rooted by the Southern African clade. In the resulting phylogenetic tree (species tree) (Fig. 2), the horizontal lines roughly approximate the evolutionary relationships among taxa. The longer the line after a bifurcation, the greater the genetic divergence. The tree substantially agrees with current taxonomic classifications based on morphology. The location of the *Pachypodium rosulatum* branch far from the *Adenium* branch verifies that *Adenium* is a natural group of species that is distinct from the related genus *Pachypodium*. The phenotypic variation observed among all of these taxa likely represent true, evolutionary relationships.

It is clear that there are three major clades (natural groups), defined here as the Southern African, East African, and Arabian clades (colored boxes in Fig. 2).

The most confident conclusion is that the three taxa of the Southern African clade are distinct species. The DNA data strongly support the current taxonomy that is based on their separate geographic distributions and their very different phenotypic traits. All three are allopatric; i.e., their geographic ranges do not overlap. *Adenium oleifolium* (Fig. 3) is a dwarf shrub that is rarely over 30 cm (one foot) tall. *Adenium swazicum* (Fig. 4) and *A. boehmianum* (Fig. 5) occur on opposite sides of the continent. The former is a small shrub to 30–60 cm (one to two feet) tall with subterranean caudexes. The latter is an upright shrub or small tree to about two meters (six feet) tall with a succulent trunk. The species tree shows that these two are more closely related to each other than they are to *A. oleifolium*, which occurs between them in central southern Africa. Both of them have very similar flowers that are distinctive in the genus: round with overlapping, solid-colored white to pink petals (no fading from margin to throat as in the other taxa), and very short anther tails deep in the dark colored throat. *Adenium oleifolium* has tiny, star-shaped, light pink to dark red flowers with long anther tails that usually protrude from the throat.

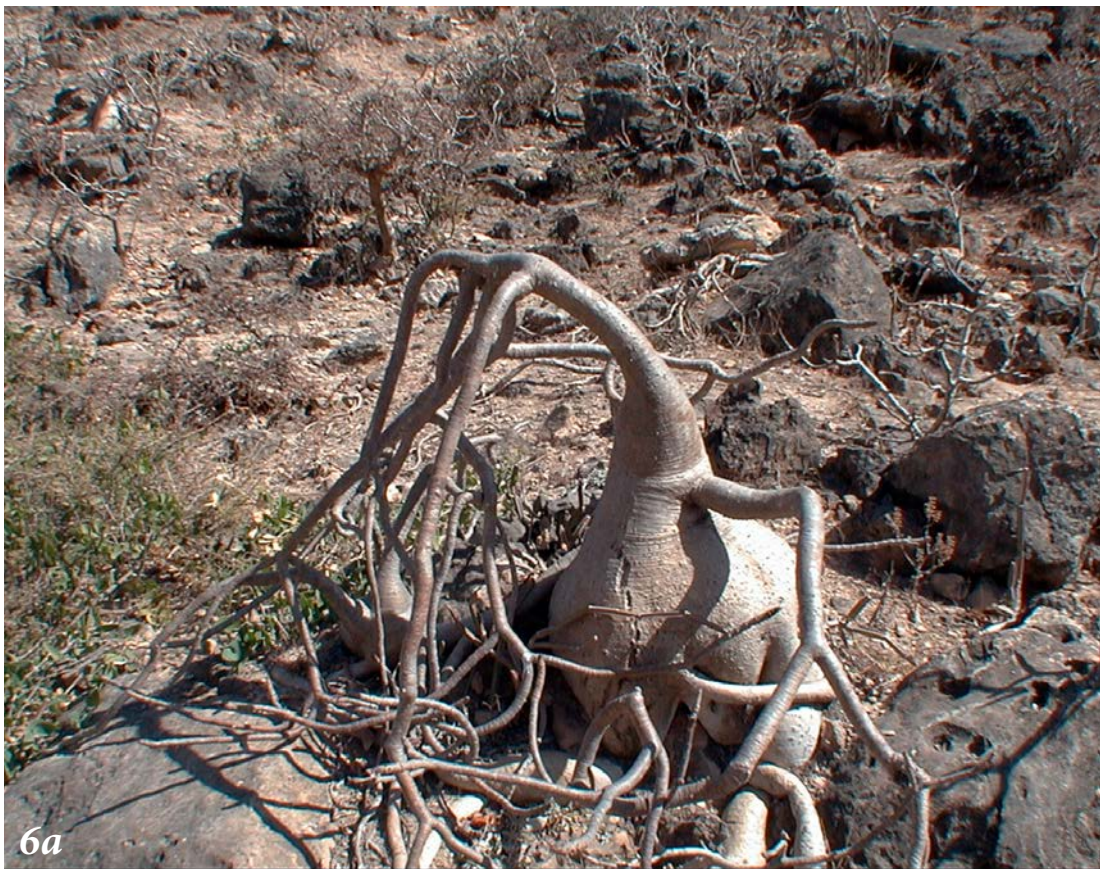
The three taxa in the Arabian group are less genetically differentiated, but the data tend to support the

3a. *Adenium oleifolium* near Upington, South Africa. **3b.** Flowers from several plants showing variability in size, shape, and color in a single population. The anther tails also vary in length. Photos: Dawie Human.

4a. *Adenium swazicum* in the Hlane Game Reserve, northeastern Eswatini (formerly Swaziland). This specimen was recently either burned in a grass fire or grazed by impala. Plants regrow quickly from the subterranean caudex. Photo: James Culverwell. **4b.** Typical flower. Diagnostic traits include broad petals of uniform color and dark throats. The anther tails are deeply included in the throat. The flowers of *A. boehmianum* are almost identical, and no other *Adenium* has this combination.

5a. *Adenium boehmianum* (with *Aloe kaokoensis*) at Otjihipa, northwestern Namibia. Note the very large leaves, second in size only to those of *A. dhofarensis*. Photo: Ernst Van Jaarsveld. **5b** and **c.** Flowers share with those of *A. swazicum* the broad petals of uniform color, dark throats, and deeply included anther tails.

current taxonomy that is based on phenotypic traits. The recently described *Adenium dhofarense* (Rzepecky 2015, Fig. 6) is almost identical to *A. "arabicum"* at the loci sequenced. However, it is isolated from *A. "arabicum"* by a hundred-kilometer (60 mile) gap where no *Adenium* species occurs (John Lavranos, personal communication). *Adenium dhofarense* is also phenotypically very different from *A. "arabicum"*, reflecting its unique habitat. The monsoon season brings little rain, only three months of warm mist. As an adaptation to the dark, humid weather during the growing season, this species has the largest leaves in the genus.

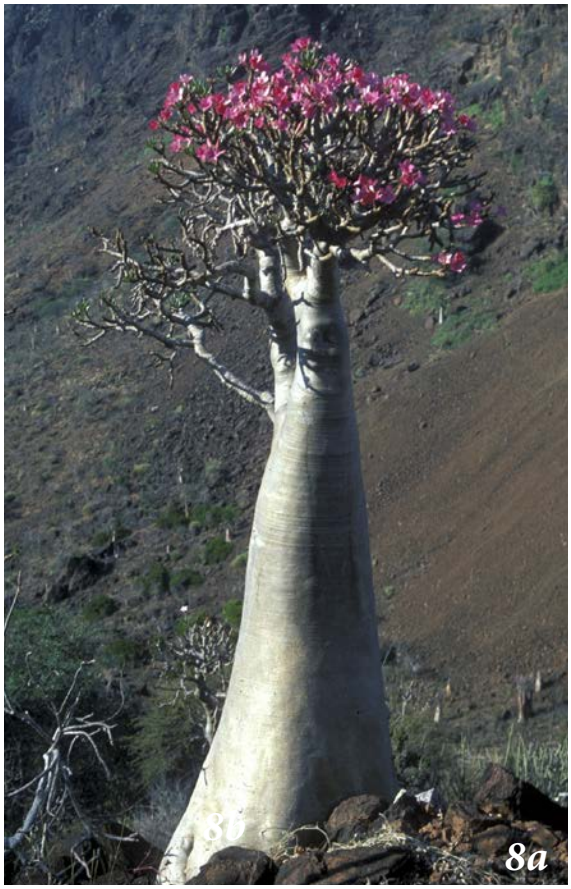


6a. *Adenium dhofarensis* near Mugsayl, Oman. The drooping stems are characteristic, although erect-stemmed plants also exist. Where the stems touch the ground, they may root and form new caudexes. Photo: Robert H. Webb. **6b** and **c.** Flowers of two clones.

Its flowers are small (ca. 2 inches, 5 cm wide) and usually light pink. *Adenium "arabicum"* (Fig. 7) populations are quite variable. Plants range from dwarf shrubs with squat caudexes only 30 cm (a foot) high to trees with massive succulent trunks to 3 meters (10 feet) tall. The flowers are also variable in both shape and size. They range from round to star-shaped, and are pink to light red at the edges and fade toward the throat. Furthermore, it's a tetraploid species (contains four copies of each chromosome instead of the usual two, aka 4n; Richard J. "Jake" Henny, unpublished data); it will rarely hybridize with any other taxon in

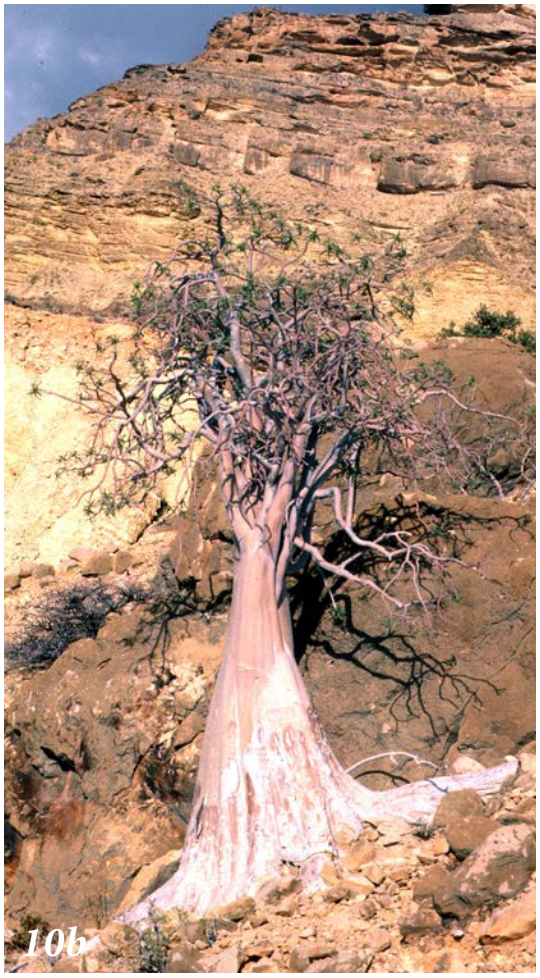
7a. Arborescent form of *Adenium "arabicum"* between Muhayl and Ad Darb, Saudi Arabia. Photo: Sheila Collenette. **7b.** Toni Yocum next to a shrubby form of *A.* "*arabicum*" near Manakhah, Yemen. Photo: Robert H. Webb. These growth forms seem to be largely genetic. Seeds from arborescent and squat plants usually grow true to the parent plant (author, unpublished data), even though both forms grow in close proximity (Sheila Collenette and Tom McCoy, personal communication). **7c, d** and **e.** Flowers of *A. "arabicum"* are highly variable in shape and size; these photos show a small sample of the variation among populations.

cultivation (Dimmitt, unpublished data). (Das et al. 1999 reported that *A. swazicum* is tetraploid, but several specimens examined by Henny were all diploid.) *Adenium socotranum* (Fig. 8) is isolated on a remote island. It's the giant of the genus, with trunks that can grow to two and a half meters (eight feet) wide and almost twice as tall. Therefore, despite the genetic similarities, it is reasonable to regard this clade as containing three good species. The DNA also firmly establishes that *A. socotranum* is most closely related to *A.* "*arabicum*", not to the phenotypically similar and geographically close *A. somalense*.



8a. *Adenium socotranum* with darker than average flowers. Photo: Dylan Hannon. ***8b.*** Greg Corman under one of the biggest specimens. Photo: Greg Corman. ***8c.*** Typical flower of *A. socotranum*. Photo: Robert H. Webb.

9a. *Adenium* "*obesum*" on the Nairobi-Mombasa road near Voi, Kenya. Photo: Gaetano Moschetti. **9b.** Plant in western Samburu, Kenya. The flower is unusually dark and sharply contrasted. A bit of the large caudex is exposed. The plant must be very old; cultivated *A. "obesum"* from Kenya rarely grow significant caudexes even in 20 years. Photo: Robert H. Webb. **9c** and **d.** Typical flowers of *A. "obesum"* are pink- to red-edged, fading toward the throat. The throat may or may not have nectar guides.



10a. *Adenium somalense* near Lake Baringo, Kenya. Photo: Gaetano Moschetti. **10b.** Near Bargal, Somalia. Photo: Myron Kimnach. **10c.** Typical flowers are narrow-petaled with red-edges that fade toward the throat. Bold nectar guides often extend partway onto the petals.

If only all data could be as clearly interpreted as for the above six species. The status of three of the four currently recognized taxa in the East African group is still unresolved for three reasons:

1) Genetic: The DNA data revealed very small differences between *Adenium "obesum"* (Fig. 9) and *A. somalense* (Fig. 10), while *A. crispum* (Fig. 11) is only slightly more different. In cultivation plants of these three taxa interbreed freely and produce viable and fertile offspring.

11a. *Adenium crispum* (*A. somalense* var. *crispum*) near Warsheikh, Somalia. Photo: Myron Kimnach. ***11b.*** Flower selected in cultivation showing the most diagnostic traits: narrow quilled petals, bold nectar guides extending to petal tips, and long-exserted anther tails. Throat color is unstable; it varies from yellow to white on the same plant at different times. Note also the linear, crisped leaves with whitish veins. The last trait is also diagnostic of *A. somalense*. ***11c, d,*** and ***e.*** The degree of petal quilling and length of nectar guides varies substantially, and occasional red-flowered plants exist in the wild. Photo 11e: John Lavranos.

12a. *Adenium multiflorum* in Kruger National Park, South Africa (transplanted at the Kruger Gate). Photo: Sheryl Hayes. **12b** and **c.** The flowers are always white with sharp red margins, and almost all are star-shaped.

Adenium multiflorum (Fig. 12) sorts with the East African clade, although it is genetically more different from the other three taxa. It hybridizes readily with *A. "obesum"* in cultivation; crosses between it and the other East African taxa are unreported. *Adenium multiflorum* is well supported as a distinct species.

2) Geographic: *Adenium multiflorum* is clearly related to the other three in this clade even though it's geographically distant from them. As far as is currently known, there is a large gap in central Mozambique where no *Adenium* occurs.

According to numerous field observers (including John Lavranos, Chuck Hanson, and Robert Webb; all personal communication), *Adenium "obesum"*, *A. somalense*, and *A. crispum* occur as numerous isolated populations throughout the group's large geographic range from Senegal near the west coast of Africa eastward to Somalia and south to Tanzania. There are very few herbarium specimens and no known living plants in cultivation of *Adenium* from west of South Sudan.

The few photos found of plants in the western Sahel (Fig. 13), are of succulent trees to about three meters (10 feet) tall with conical trunks. Their growth form closely resembles that of plants called *A. somalense* in East Africa. However, the western Sahel plants and *A. somalense* are separated by the shrubby *A. "obesum"* in Kenya and Tanzania. Because we couldn't find any Sahel specimens to sequence, we don't know if these populations fit within the East African clade.

3) Phenotypes: East African taxa are fairly distinct in growth and flower traits. *Adenium "obesum"* plants in Kenya and Tanzania vary from scrawny shrubs with

13a. *Adenium* sp. near Benoue National Park, Cameroon. Photo: Joel Peterson. ***13b*** and ***c.*** *Adenium* sp. near Tintane, Mauritania. Photo: Helene Jousse (via Jan Schlogl). These Sahel plants have been published as *A. honghel*, which some authors have lumped into *A. "obesum"*. There are no known plants from this region in cultivation, which prevents further study at this time.

14a. *Adenium "somalense nova"* near Same, Tanzania. There is a large subterranean caudex. **14b.** Flowers. The plants and flowers in this small isolated location look like intermediates between *A. somalense* and *A. crispum*, but they are surrounded by populations of *A. "obesum"*. Photos: Robert H. Webb.

poorly developed caudexes to large shrubs to a couple of meters tall with big subterranean or exposed caudexes. The flowers are less variable; most have round-tipped petals that are pink on the margins and fade to near white at the throat. The pale throats may have nectar guides, which do not extend onto the petals.

On rocky terrain *Adenium somalense* occurs as trees up to three or more meters tall with massive, conical, succulent trunks, but in sandy soils the plants are medium-sized shrubs with underground caudexes (Robert H. Webb, personal communication). The star-shaped flowers are deep pink to red on the margins and fade toward the throat. Strong nectar guides in the throat often extend somewhat onto the petals.

Adenium crispum plants are dwarf shrubs with subterranean caudexes and above ground stems that are rarely more than 30 cm (a foot) tall. The star-shaped flowers have narrow, pointed petals that are usually quilled (curled lengthwise), and the nectar guides often extend nearly or completely to the petal tips. Adding to the confusion, though, is a photo from Ethiopia (by J & R Esterle) of a large arborescent plant resembling *A. somalense* but with the foliage and flowers of *A. crispum*, indicating that these taxa may intergrade in nature. This taxon has not been published as a full species, but only as *A. somalense* var. *crispum* Chiov. Add that fact to the confusion that plagues this clade.

Adenium multiflorum is phenotypically distinct from the other three taxa in its clade in that it blooms during winter. (Other *Adenium* species may produce flowers during winter, at least in cultivation, but their main bloom is during the warmer months.) It is also obligately winter-deciduous in contrast to the other three. We are confident that *A. multiflorum* is a valid species.

There is a small population of adeniums in Tanzania that are known in horticulture as *Adenium* "*somalense nova*" (Fig. 14); the taxon has not been formally described. The medium-sized shrubs with globular subterranean caudexes resemble intergrades between *A. somalense* and *A. crispum*. They have narrowly linear leaves with whitish veins, sometimes with somewhat crisped margins. The flowers are small like those of *A. crispum*, with narrow non-overlapping petals that are pink or white with narrow red margins. The flowers have bold nectar guides; on some plants they have faint extensions onto the petals. This isolated population near Same is surrounded by populations of *A. "obesum"*. The loci sequenced located these plants closer to the *somalense* specimens than the "*obesum*" ones. This result conflicts with the geographic distribution; the nearest known *A. somalense* population is at least 320 kilometers (200 miles) away.

It appears to us that *Adenium "obesum"*, *A. somalense,* and *A. crispum* are either a single extremely variable species, or perhaps a complex of numerous closely related species. More extensive field observations as well as DNA analysis of more specimens are needed to clear up this mess. Even then it will be difficult, because taxonomists are far from achieving consensus on a precise definition of a species (Queiroz 2005), and plant taxonomy is particularly fractious (Duminil and Michele 2009). In simpler language, taxonomy is as much professional opinion as it is science.

The DNA data helped to solve a couple of mysteries. They indicate the identities of two old adenium cultivars of uncertain origin:

15a. *Adenium* 'Singapore' is the oldest known named cultivar, introduced in the 1970s. It has a substantial caudex (this is a 4-year-old cutting), and large flowers up to 100 mm (4 inches) wide. ***15b.*** Flower. DNA analysis indicates that it is intermediate between *A. somalense* and *A. "obesum"*.

The oldest known named *Adenium* cultivar is 'Singapore' (Fig. 15), for where it first appeared in cultivation in the 1970s. The nurseryman Albert Chan who introduced it said that he obtained it in Saudi Arabia, so Dimmitt assumed that it is *A. "arabicum"*. It loosely fit that taxon in having a relatively large caudex and very big leaves. It also has very large flowers, which is atypical but not unknown for Arabian plants. However, in cultivation it does not cross with *A. "arabicum"* but does cross with *A.* "*obesum*". Thus it is probably diploid, not tetraploid as *A. "arabicum"* is. The nuclear locus tree indicates that it is in the *Adenium "obesum"-somalense* clade; *A.* "*obesum*" often has large flowers that can exceed three inches in spread (four inches in cultivars), and *A. somalense* has large caudexes. So the PHYA tree appears to have solved the mystery: the cultivar 'Singapore' looks like an *"obesum"-somalense* intergrade from nature (in East Africa) or perhaps a horticultural hybrid. This inference is bolstered by the fact that 'Singapore' has also been called *A. coetanum*, which was described from East Africa although the status of this taxon is unresolved.

The oldest *Adenium* clone in cultivation known to us is an *A. "arabicum"* that has been grown in India since at least the 1930s (Ashish Hansoti. pers. comm.). Dimmitt obtained a cutting in 1999 and named it 'Hansoti Dwarf' (Fig. 16) because of its compact growth habit. Its most likely origin is the port of Aden, because India was trading extensively with Yemen in the early 20th century. This supposition is supported by another specimen collected in Aden by John Lavranos (Lavranos no. 1694); it sorted on the tree immediately adjacent to 'Hansoti Dwarf'.

The Nomenclatural Mess

There are at least two nomenclatural errors in the genus, but they can't be corrected until the taxonomic status of the East African clade and the Sahel populations is resolved.

1. *Adenium "arabicum"* is not the correct name for the plants in Saudi Arabia and Yemen. The type specimen for the genus is a plant from Yemen originally published as *Nerium obesum* Forssk. in 1775 and later amended to *Adenium obesum* Roem. & Schult. in 1819. *Adenium arabicum* Balf. f. was described later from Jabal Shamsan on the Aden Peninsula of Yemen. The DNA results indicate that all Yemeni and Saudi Arabian adeniums belong to the same species. The first-published name has priority; therefore *A. obesum* is the correct name for the plants on the Arabian Peninsula (except *Adenium dhofarense*) but this nomenclatural correction can't be published until the next dilemma is unraveled.

2. Because this DNA study firmly establishes that the plants in Africa are distinct species and in a different clade from those in Arabia, *A. "obesum"* is an invalid name for the African plants in Kenya and Tanzania. But the DNA could not establish the taxonomic ranks of the numerous populations in the East African region, especially of those in the western two-thirds of the area where there were no specimens available to sequence. Consequently the African *A. "obesum"* can't be renamed until this mess is cleared up.

It gets worse. In addition to the four taxa in this clade mentioned so far, there are several more in the literature. Their status is also unresolved until far more genetic analysis has been conducted:

16a. *Adenium "arabicum"* 'Hansoti Dwarf' is the oldest known adenium clone in cultivation. Shown is a 5-year-old cutting from the original plant that has been grown in India since at least the 1930s. The DNA analysis indicates that it originated on the Aden Peninsula in Yemen. ***16b.*** The flowers of 'Hansoti' Dwarf' are rounder and darker than is typical of the species.

1. *Adenium honghel* A.DC. 1844 is described from far western Africa. If all the plants in the Sahel are the same species and different from those in East Africa, then this is their correct name.

2. *Adenium speciosum* Fenzl, 1865, in Sudan. If the Sahel populations are of different species, then the eastern arborescent ones are either *A. speciosum* or may be combined with *A. somalense*.

3. *Adenium coetanum* Stapf, 1902, from central Tanzania to northern Kenya. This area covers parts of the ranges of *A. "obesum"* and *A. somalense*. Considering the contrast between their different physical traits and the nearly identical DNA sequences, it will take much more research to tease out an acceptable conclusion.

A Final Word

Better resolution of *Adenium* taxonomy and nomenclature requires phenotypical, geographical, and molecular data of many more specimens. It is deeply frustrating that the taxa in need of the most study occur in Sahel nations that are, to put it mildly, experiencing political unrest. Completion of this project will depend on a future generation of researchers.

Acknowledgements

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References

Das, A.B., S. Mohanty, and P. Das. 1999. Chromosome number, karyotype, and nuclear DNA content in some *Adenium* species of the family Apocynaceae. Cytobios 98 (388): 95–104.

Dimmitt, Mark A., Gene Joseph, and David Palzkill. 2009. Adenium: *Sculptural Elegance, Floral Extravagance.* Scathingly Brilliant Idea, Tucson. 153 pp.

Duminil, J. and M. Di Michele. 2009. Plant species delimitation: A comparison of morphological and molecular markers. *Plant Biosystems.* 143: 528–542, doi:10.1080/11263500902722964

Forster, Paul I. 1998. Correct names for some cultivated species of *Adenium* (Apocynaceae). *Cactus and Succulent J. (U.S.)* 70(4): 199–200.

Hargreaves, Bruce J. 2002. How many species of *Adenium* are there? *Asklepios* 85:4–6.

Lavranos, J. 1966. On the occurrence and taxonomy of *Adenium* in tropical Arabia and on Socotra (Soqotra). *Cac. Succ. J. (US)* 38(1):19–23.

Plaizier, A. C. 1980. A revision of *Adenium* Roem. & Schult. and of *Diplorhynchus* Welw. ex Fic. & Hiern (Apocynaceae). Mededelingen Landbouwhogeschool, Wageninger, Netherlands. 80(12):1–40.

Queiroz, K. de. 2005. Ernst Mayr and the modern concept of species. *PNAS* 102: 6600–6607.

Rambaut, A. 2006–2012. FigTree; tree Fig. drawing tool. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, United Kingdom.

Rzepecky, A. 2015. *Adenium dhofarense*. A long overlooked species from the central-southern part of the Arabian Peninsula. *Cact. Succ. J. (U.S.)* 87(3):129–135.

Thistleton-Dyer, W.T. 1904. Vol. IV. Section 1. Oleaceae to Gentianeae. Pp. 226–230. In *Flora of Tropical Africa*. www.biodiversitylibrary.org/item/60245. Holding institution: NCSU Libraries (archive.org).