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A Biosystematic Study and Taxonomic Appraisal of *Anacheilium cochleatum* (L.) Hoffmanns. And *Anacheilium cochleatum* var. *triandrum* (Ames) Sauleda, Wunderlin & Hansen

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ABSTRACT

The Florida population of *Anacheilium cochleatum* (L.) Hoffmanns. was recognized as a distinct variety by Ames in 1904 on the basis of its triandrous habit. Systematic analysis reveals other slight morphological differences correlated to the evolutionary history of the population.

INTRODUCTION

The identification and classification of organisms are the most intricate problems in biosystematics. The problems arise from defining and delimiting the species as an evolutionary unit and identifying a group of individuals as belonging to a particular species.

Traditionally a series of correlated characters of the phenotype, pertaining to the exterior morphology, have been used to define a species (Solbrig, 1970). Evolutionary theory has shown the importance of genetic relationships between members of a breeding population (Solbrig, 1970). This has led to a redefinition of the species concept: "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from each other as groups." This definition, called "the biological species concept", was first introduced by Dobzhansky and Mayr (in Solbrig, 1970). According to this concept, species are classified solely on reproductive isolation.

Most species, whether they are related or not, are morphologically distinct and reproductively isolated; but related species may not be genetically isolated. Grant (in Solbrig, 1970) has shown that populations exist which are genetically isolated but are morphologically identical; proving there is no absolute correlation between morphological differences and reproductive isolation. Therefore, before classifying groups of organisms, a determination must be made

if speciation, in the groups being observed, has progressed sufficiently to consider them different evolutionary units. A classification of the organisms can then be made based on morphological observations and measurements, results of genetic isolation tests and evaluation of all the physiological and ecological data obtainable. Prior to collecting data to classify a group, an understanding of the evolutionary processes, which have led to speciation in the group, is necessary. Unfortunately, many of the classifications being made today totally ignore the basic principles. The classifications are based solely on DNA analysis of ancestral DNA that does not reflect reality.

In flowering plants there are many examples of self-pollinating (autogamous) plants, which have different patterns of variation from out-crossing (allogamous) plants (Briggs and Walters, 1969). Muller (1932) postulates that in an autogamous population a new mutation can produce only one new genotype and consequently, an increase in genetic variability must be very slow. In an allogamous population a new mutation can, after a few generations of out-crossing, give rise to hundreds or thousands of new genotypes.

The isolation of one or a few individuals from the gene flow of a large population and the enforced inbreeding in the following generations of the new isolated population has drastic genetic effects on the population (Grant, 1963). The organisms will be converted from a state of genetic heterozygosity to one of genetic homozygosity (Grant, 1963).

Baker (1955) postulates that the establishment of self-compatibility is a result of "long distance dispersal" and further suggests that accidental long distance dispersal of a single propagule can lead to the establishment of a colony only if the propagule is capable of self-fertilization. If the type established is well adapted; it can spread throughout the area, even though its capacity for genetic variability is much reduced (Ehrendorfer, 1965). A high selective advantage is given to a genetic type, which can quickly build up populations of well-adapted individuals as the progeny of one or more initial colonizers (Stebbins, 1950). This ability depends not only on a high reproductive capacity, but also on the assurance that the progeny will be equally well adaptive to these same conditions (Ehrendorfer, 1965). Only a homozygous self-pollinating colonizer will have these advantages. Haskell (1953) found that indeed from a single self-pollinating homozygous individual a large population could be established which would maintain itself in a homozygous state, maintaining its adaptive advantage.

Wright (1931) found that in self-pollinating species a mutation was quickly manifested into a new biotype and that most long established self-pollinating populations, consisted of a number of homozygous biotypes each genetically isolated and distinct. Wright (1931) postulated this type of population was well adapted for continuous evolution in a stable or varying environment, through simple mutation and possible rare, chance out-crossing.

Van der Fijji and Dodson (1966), Levine (1972), Briggs and Walters (1969) and others, postulate that although autogamy is considered dangerous to evolution and a blind alley leading to rapid speciation which sacrifices the future for survival in the present, a group of plants can travel down the blind alley for a long way, evolving new variations which ultimately become new groups. The evolution of autogamy does not always eventually lead

to evolutionary extinction, since many autogamous groups have outlasted their allogamous ancestors (Stebbins, 1957).

Van der Fijji and Dodson (1966) estimate approximately two hundred species of the Orchidaceae are autogamous. Species of the Orchidaceae, which are autogamous, and sometimes cleistogamous have been found to produce viable seed when out-crossed (Sauleda, in prep.). Sauleda (in prep.) found that the physical condition of a plant was a factor in the degree of autogamy the plant exhibits. A higher percentage of autogamous capsules are produced when the plant is experiencing environmental or physical stress. Knudsen (1956) and Harlon (1945) found the temperature and humidity of the environment and the frequency of watering of cultivated autogamous plants to change the degree of autogamy exhibited by the plants. Sauleda (in prep.) also noted that in large plants producing multiple inflorescences during the blooming period; the first inflorescences produced, exhibited a higher percentage of autogamous capsules, than inflorescences produced later during the blooming period. After a number of autogamous seed capsules are formed the autogamous mechanism appears to turn off and later inflorescences produce no autogamous capsules. The flowers remain open and unpollinated, due to the absence of a pollination vector. If a pollination vector becomes available, the plant will still have the autogamous mechanism and could also be allogamous. This system allows for chance out-crossing which Wright (1931) postulated would make the population well adapted for continuous evolution in a stable or changing environment.

The purpose of this paper is to document as extensively as possible the differences between two reproductively isolated populations of *Anacheilium cochleatum* (L.) Hoffmanns (Orchidaceae). One of the populations, *A. cochleatum*, is an allogamous monandrous species from Andros Island in the Bahamas; the other population, *Anacheilium cochleatum* var. *triandrum* (Ames) Sauleda, Wunderlin & Hansen, is an autogamous triandrous species from Florida. Morphological measurements, reproductive isolation tests, and statistical analysis will be used to evaluate the rank previously assigned the populations.

MATERIALS AND METHODS

Plants of *A. cochleatum* var. *triandrum* were examined in the Fahkahatchee Strand in the Big Cypress area of Collier County, Florida. Mature plants of *Anacheilium cochleatum* cultivated in Miami-Dade County from seeds originally from Andros Island were examined

Extensive measurements were made of the floral and vegetative parts. Scatter diagrams were generated using the measurements and ratios calculated from the measurements. The mean, standard deviation, and coefficient of variability were determined for each measured character in each population. Plants from Andros Island and in the Fahkahatchee Strand were observed to determine if visitors or pollinators were present. Plants from the two populations were artificially self-pollinated and out-crossed to determine if any obligatory

reproductive or self-incompatibility system occurs. Plants from the different populations were also inter-bred to determine if genetic isolation exists between the populations. The relative amount of viable seed produced by each capsule was determined after fertilization by dissecting the capsules and microscopically examining the contents for viable zygotes. Observations were made on the number of autogamous seed capsules set per inflorescence on Florida plants and period of fragrance production in both populations.

RESULTS

Extensive measurements were taken from the plants in both populations. In Florida measurements were made in different locations in a variety of environmental conditions, to remove any morphological differences resulting from different environmental stress exerted on each population. The morphological differences measured are a combination of genetic differences and can be used for accurate morphological comparisons.

Morphologically the two populations are very similar. The only observable differences without measuring the floral and vegetative parts is in the number of anthers. The Andros plants have one anther; the Florida plants have one main anther and two smaller anthers, which appear to be functional. Measurements of floral and vegetative parts reveal distinct differences. The Florida plants have fewer flowers per inflorescence, smaller floral parts, and smaller vegetative parts than the Andros Island plants. Scatter diagrams of measurements of morphological characters and ratios of measurements of morphological characters demonstrate a distinct clustering for each population and a clear separation between the two populations. The scatter diagrams indicated no overlap of the two populations but occasionally an individual from the Andros population fell within the limits of the Florida population. The coefficient of variability for each character proves the Andros Island population to be considerably more variable than the Florida population. The Andros Island population was more variable for seventeen of the twenty-six characters observed; equal in eight characters and less variable than the Florida population for only one character. The Florida population was demonstrated to be autogamous and also the mechanism to turn off the autogamy process described by Saulea (in preparation) was found to be operating. After a number of autogamous capsules had formed on an inflorescence the remaining flowers on that inflorescence and flowers on subsequent inflorescences did not form autogamous capsules. The average inflorescence produced sixty-two percent autogamous capsules. The Andros Island population produced no autogamous capsule. No pollinator or visitor was observed for the Andros Island plants in Florida. A species of wasp was found visiting a flower of a Florida plant. A different wasp has been found to be the pollinator for the Andros population in its natural habitat (Adams, personal communication).

The production of floral fragrance by the Andros Island population was noticeably higher than the Florida population. The floral fragrance of the two populations was similar but a slight difference could be detected.

Artificial pollination showed the Andros Island population to out-cross and be self-compatible, excluding the possibility of an obligatory reproductive system. The Florida population also out-crosses and is self-compatible. Although geographical location and the

autogamous system of the Florida population maintain reproductive isolation: genetic isolation does not exist. A test cross between the Andros Island population and the Florida population was easily made and contained viable seed.

DISCUSSION

Anacheilium cochleatum (L.) Hoffmanns. Was first described by Linnaeus in 1753 as *Epidendrum cochleatum*. Hoffmannsegg in 1842 established the genus *Anacheilium* based on *Epidendrum cochleatum* L. Dressler in 1961 transferred most of the epidendrums with pseudobulbs, including *E. cochleatum* to the genus *Encyclia* Hooker. Higgins in 1998 transferred *E. cochleatum* to the genus *Prosthechea*. In 2004 Withner & Harding restored the genus *Anacheilium*, including *E. cochleatum* in the genus.

In 1877 A. L. Garber first collected Florida plants in a hammock near Miami, Miami-Dade County, Florida (Luer, 1972). The differences between the Florida population and the rest of the populations distributed throughout the Caribbean islands and from Mexico to Colombia were not noticed until Oakes Ames described the Florida population in 1904 as a variety of *Epidendrum cochleatum* L. Ames recognized the only difference between the populations to be the presence of three anthers in the Florida population.

Without measurement and statistical analysis, the triandrous habit of the Florida population is the only observable taxonomically significant difference. Measurement and statistical analysis reveals slight differences correlated to the evolutionary history of the population. The Florida plants have fewer flowers per inflorescence, which is related to the reproductive mechanism of the population. Populations with autogamous reproductive mechanisms tend towards a reduction in the number of flowers. However, populations, which are insect, pollinated benefit by increased numbers of flowers to attract the insects. Autogamous plants also tend towards a reduction in size of floral parts.

The scatter diagrams show a distinct difference between the populations. No overlap of the clusters occurred, but an individual from the Andros population was found to be similar to the Florida population. This may indicate the Florida population was derived from one or more introductions from the Bahamas islands or other neighboring Caribbean islands. The morphology of the orchid seed makes it ideal for long distance dispersal and many introductions may have occurred, but only the autogamous individuals produced offspring, since no pollination vector was available in Florida. The Andros Island population was considerably more genetically variable than the Florida population. Allogamous, out-crossing, populations are more variable since mutations and other genetic changes occurring within the gene pool can flow freely. In an autogamous population gene flow does not occur throughout the population. It is also possible that in the past there was a monandrous allogamous population in Florida. A climatic change of only a few degrees can cause the extinction of a pollinator. As a result only autogamous individuals would produce viable offspring. The Florida population would be a relic population. Plants from the Florida population appear to have a mechanism to turn off autogamy after a certain number of autogamous capsules are formed. An inflorescence can turn off the production of autogamous capsules after approximately six to ten capsules are formed. The remaining

flowers on the inflorescence stay open and unpollinated. Plants with multiple inflorescences turn off the autogamy system after approximately two inflorescences produce eight to ten autogamous capsules each. The flowers on the remaining inflorescences open and remain unpollinated. A visitor similar to the pollinator for the Andros Island population was found visiting flowers of the Florida population. No pollination was observed but the possibility exists that this visitor could pollinate the open non-autogamous flowers. The pollinator was physically well suited to pollinate the flowers.

If a system evolved, in an established autogamous population allowing out-crossing, the genetic variability and adaptability of the allogamous individuals would result in selection favoring the allogamous individuals. The new allogamous individuals would out-compete the autogamous forms and greatly restrict the growth of the autogamous population and eventually replace the autogamous forms from the geographical area.

The Andros Island plants are self-compatible. A necessary step towards the production of autogamous propagules suited for long distance dispersal. Test crosses between the Florida and Andros Island plants produced viable offspring, excluding the possibility of genetic isolation and demonstrating a close affinity between the populations.

The rank of variety was given by Ames to the Florida population based on the triandrous characteristic. Systematic analysis of the population shows the rank of subspecies could not be used. A subspecies must be a major morphological variant of a species occupying a different geographical area and not have differences only determinable by experimental technique (Lawrence, 1951). Forma could not be used since its use is restricted to trivial variations occurring among individuals of a population (Lawrence, 1951). The variation between the two populations is not major or trivial, making the rank of variety for the Florida population the logical choice.

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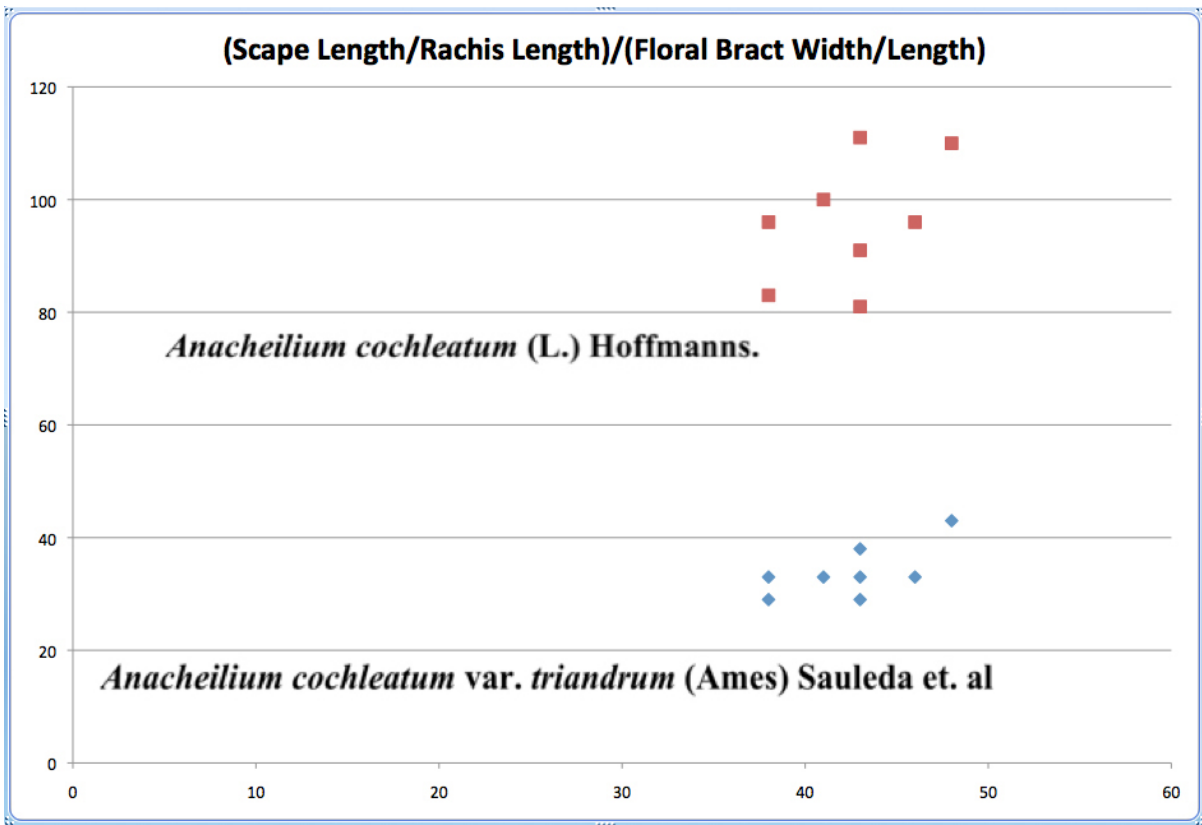
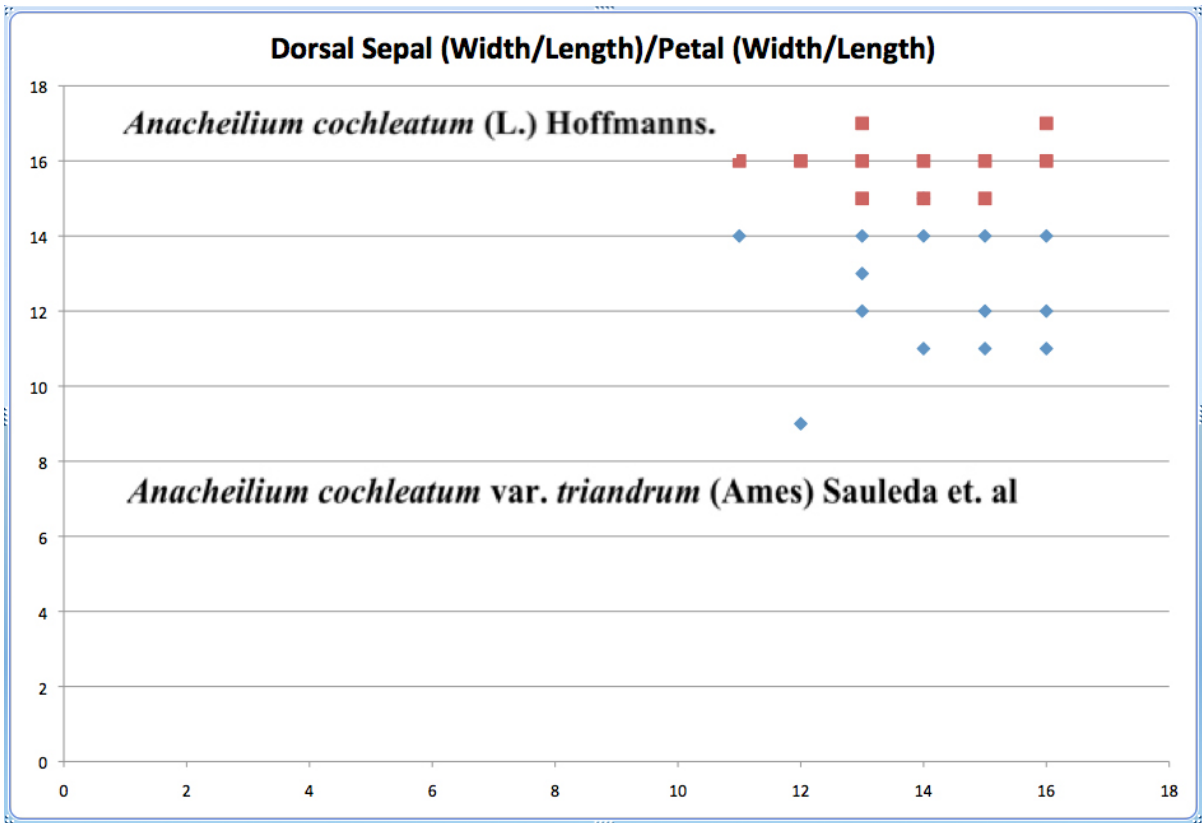
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Examples of Scatter Diagrams



Anacheilium cochleatum (L.) Hoffmanns.



Anacheilium cochleatum var. *triandrum* (Ames) Saulea, Wunderlin & Hansen



Anacheilium cochleatum (L.) Hoffmanns.



Anacheilium cochleatum var. *triandrum* (Ames) Sauleda, Wunderlin & Hansen