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Pollination Biology and Taxonomy of the Genera *Tolumnia* Raf. and *Oncidium* Sw. (Orchidaceae) in South Florida: *Tolumnia bahamensis* (Nash ex Britton & Millspaugh) Braem, *Oncidium floridanum* Ames, *Oncidium undulatum* (Sw.) Salisb. (*Lophiaris maculata* (Aubl.) Ackerman).

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Pollination Biology and Taxonomy of the Genera *Tolumnia* Raf. and *Oncidium* Sw. (Orchidaceae) in South Florida: *Tolumnia bahamensis* (Nash ex Britton & Millspaugh) Braem, *Oncidium floridanum* Ames, *Oncidium undulatum* (Sw.) Salisb. (*Lophiaris maculata* (Aubl.) Ackerman)

Ruben P. Sauleda¹

22585 S. W. 187 Avenue, Miami, FL 33170

Recent estimates indicate that approximately 87% of flowering plants are dependent on animals for reproduction (Ollerton *et al.* 2011). Many animals receive their nutrition from flowers. Others like bees have life histories based on floral resources (Kevan and Baker 1983) and are the most common pollinators of terrestrial plants (Kearns *et al.* 1998, Kevan & Imperatriz-Fonseca 2002).

An important association of bees with plants is with oil producing flowers. Oil-collecting bees are a part of a specialized type of pollination system known as the “oil flower pollination syndrome” (Vogel 1974). This type of specialized pollination system is mainly found in the Malpighiaceae (Buchmann 1987, Renner & Schaefer 2010, Gaglianone *et al.* 2011). The Malpighiaceae produce floral oils as a reward to attract pollinators (Simpson & Neff 1983, Buchmann 1987). Oils are produced in specialized glands known as elaiophores located on the floral sepals, underneath the floral whorl (Vogel 1974).

Centris errans Fox (Apinae: Centridini) is one of the bee species known to collect floral oils in South Florida (Neff & Simpson 1981, Michener 2000, Alves-dos-Santos *et al.* 2007, Renner & Schaefer 2010, Gaglianone *et al.* 2011). These oil-collecting bees are solitary, and nest in pre-existing wood cavities or in the ground. Female *C. errans* visit the oil-reward flowers to obtain oils for their brood. Several orchids in South Florida mimic the oil-reward flowers to attract *C. errans* to pollinate the flowers. However, the orchid flowers do not produce oil.

Brysonima lucida (Mill.) DC, an understory shrub found in the in pinelands or along hammock edges, is the main oil-rewards plant found in South Florida. Several orchids mimic the flowers of *B. lucida* to attract *C. errans*.



Brysonima lucida (Mill.) DC. Photograph reproduced from Natives For Your Neighborhood. <http://www.regionalconservation.org>.

In the early 1970's a series of studies was initiated to determine the pollinators of several Florida orchids.

The first study was to determine the pollinator of *Tolumnia bahamensis* (Nash ex Britton & Millspaugh) Braem. *Tolumnia bahamensis* was abundant in Martin County, Florida along County Line Road around the Jupiter cemetery (Saulea 1966). The area was a pristine white sand scrub habitat that had not been disturbed. At present almost the entire area where *T. bahamensis* was found has been destroyed by development and only isolated pockets in residential lots remain.

In 1966 a relocation project was undertaken to ensure the survival of the *T. bahamensis* since it was obvious that development would soon wipe out the majority of the population (Sauleda 1966). Almost 1000 plants were collected in less than an hour, attesting to the abundance of plants, and were relocated to Jonathan Dickinson State Park in Martin County, Florida. The plants were planted in three remote locations within the park. Recent reports of *T. bahamensis* being found in Jonathan Dickinson State Park indicate that the relocated plants survived.

A large population growing at the base of the native rosemary (*Ceratiola ericoides* Michx.) was chosen for observation. In a short time, *Centris errans*, at the time indentified as *Centris versicolor* (F), began visiting the flowers. A male bee would line up with a flower and fly into the flower bumping it at just the right point to have a pair of pollinia attach to the front of its head. It would then backup and bump the next flower with its head, usually depositing a pair of pollinia on the stigma and removing a new pair. Not all of the visits resulted in a pair of pollinia being deposited on the stigma and the bee would have multiple pairs of pollinia attached to its head. It would continue this behavior until most of the flowers had been visited. Although *T. bahamensis* mimics *B. lucida*, an oil producing flower, the behavior of *C. errans* in respect to the flowers of *T. bahamensis* appears to be pseudoantagonism (Dodson & Frymire 1961) or pseudoterritoriality (Jolivet 1998). Dressler (personal communication) observed flowers of several oncidiums being attacked by a species of *Centris* in Ecuador. The bees would set up a territory and rest on a twig waiting to attack and drive out any other insect that entered their territory. When the oncidiums flowered the bees perceived them as invaders and would attack them. The behavior of *C. errans* was not the behavior of an oil-collecting bee, but of a bee defending its territory. Several bees with the pollinia attached were collected and voucher specimens were deposited at Florida Atlantic University².

Centris errans has been observed pollinating *T. bahamensis* on Andros Island and Abaco Island in the Bahama Islands. The bee exhibited the same behavior as the bees in South Florida.

The next species studied was *Oncidium undulatum* (Sw.) Salisb. A number of plants in flower were observed near Seven Palm Lake in the Everglades National Park. At the time motorized boats were allowed into the lake and there was a campground at the mouth of McCormick Creek where several interesting nights with mosquitoes and strange noises were spent. Two plants in flower were observed for several days, but the weather was cloudy and windy and the pollinator did not appear. On the fourth day the pollinator appeared, *Centris errans*, the same pollinator of *T. bahamensis*, except that only female bees visited the flowers. The bee would land for a few seconds, probe around the crest of the flower and quickly leave. Each time removing a pair of pollinia and most of the time on the visit to another flower would deposit the pollinia on the stigma. The behavior was different from the behavior with *T. bahamensis*. The behavior was typical of oil collecting bees. Bees were not collected, only observations were made. At a later date bees were collected with pollinia attached at a site in Miami, Florida, from plants of *O. undulatum* imported from Jamaica. *Oncidium undulatum* is native to Florida, Cuba and Jamaica. Voucher specimens of the bees with pollinia attached were made and deposited at Florida Atlantic University².

The study was made in the early 1970's prior to the naturalization of *Centris nitida* Smith (Pemberton & Liu, 2008) in South Florida. *Centris nitida*, also an oil-collecting bee, seems to visit the same flowers and exhibits the same behavior as *C. errans*.

This species was identified as *Oncidium luridum* Lindl. (Correll 1950) in the early literature of the Orchidaceae of Florida. *Oncidium luridum* refers to a Central American species (Sauleda & Adams 1991). Most of the later literature cites this species as *Oncidium undulatum* (Sw.) Salisb. (Small 1933, Nir 2000). *Epidendrum maculatum* Aubl. (Hist. Pl. Guiane 2: 825. 1775.), refers to this species and predates *Epidendrum undulatum* Sw. (Sw. Prodr. 122. 1788.) which also refers to this species. However, at the time of the transfer by Urban of *E. maculatum* to *Oncidium* the name already existed in *Oncidium - Oncidium maculatum* (Lindl.) Lindl. The next available name that could be used in *Oncidium* was *Epidendrum undulatum* Sw. Salisbury made the transfer to *Oncidium - Oncidium undulatum* (Sw.) Salisb.

Oncidium maculatum was transferred into the genus *Trichocentrum* Poepp. & Endl. by Chase & Williams (2001) - *Trichocentrum maculatum* (Aubl.) M. W. Chase. However *maculatum* already existed in the genus *Trichocentrum - Trichocentrum maculatum* Lindl. The next available name that could be used in *Trichocentrum* was *E. undulatum*. *Trichocentrum undulatum* (Sw.) Ackerman & M. W. Chase is the name being used in the literature. It is obvious that this species does not belong in the genus *Trichocentrum*. The long spur of the labellum and the lack of a crest on the labellum are just two characters among many that easily distinguish *Trichocentrum* from the mule-eared oncidiums. In addition, the pollination system is different for the two groups. The mule-eared *Oncidium* mimic oil-producing flowers to attract oil-collecting bees and the *Trichocentrum* are pollinated by fragrance collecting bees in the genera *Eulaema* and *Euglossa* (van der Pijl & Dodson 1966). The conclusion to place *O. undulatum* in *Trichocentrum* resulted from sequencing ancestral (mainly from plastid region) DNA that does not reflect reality. Plastid DNA has very little bearing on the morphology of the plant. The morphology of the two groups could not have been taken into consideration when the decision was made to include the mule-eared *Oncidium* and rat-tailed *Oncidium* in *Trichocentrum*. The DNA data demonstrates that the mule-eared and rat-tailed *Oncidium* are related to *Trichocentrum*. Using the same data the reverse can be true; *Trichocentrum* can be placed in the genus *Oncidium*. The DNA data is indicating that the genera are related; that does not imply that all related genera should be combined. The definition of a genus is a group of similar species, not groups of similar species. If a change need to be made it would be more reasonable to place this species in the genus *Lophiaris* Raf. (*Lophiaris maculata* (Aubl.) Ackerman).



Oncidium undulatum (Sw.) Salisb. in the Everglades National Park.



Trichocentrum species from Colombia demonstrating the long spur not found in any of the mule-eared oncidiums and lacking the crest characteristic of the mule-eared oncidiums.

The last species studied was *Oncidium floridanum* Ames, In the area of Monument Road in Collier County prior to the area being established as the Big Cypress National Preserve (established 11 October 1974), hundreds of plants of *O. floridanum* could be observed in the center of Cypress domes. The domes provided a sanctuary from fires due to the standing water in the center of the domes. The fires would go around the domes and never penetrate the interior of the domes. However, due to political mismanagement of the water levels in the Big Cypress, fires would sweep through the domes killing all of the orchids that were not fire resistant. Most of the plants of *Oncidium floridanum*, *Anacheilium cochleatum* var *triandrum* (Ames) Sauleda, Wunderlin & Hansen, *Epidendrum floridense* Hagsater, *Epidendrum nocturnum* Jacq., *Dendrophylax lindenii* (Lindl.) Benth. Ex Rolfe, *Epidendrum anceps* Jacq. and *Polystachya concreta* (Jacq.) Garay & Sweet which were very common are now gone. In the Big Cypress *O. floridanum* grew just above the water line on stumps of cypress that had been logged earlier. In a single day a dozen female *C. errans* with pollinia were collected and deposited at Florida Atlantic University². The behavior of the bees was very similar to the oil collecting behavior on *O. maculatum*.

Luer (1972) proposed that *O. floridanum* is conspecific with the Guatemalan species, *Oncidium ensatum* Lindl. An examination of a photograph of the holotype of *O. ensatum* at Kew revealed that both species are vegetatively very similar but exhibit many distinct floral differences which are difficult to see in a dried specimen (Sauleda & Adams 1991). The differences are evident when comparing live material of both species.



Oncidium ensatum Lindl. from Guatemala.



Oncidium floridanum Ames in the Big Cypress National Preserve.

In areas of the Everglades Nation Park, *O. undulatum* and *O. floridanum* grow sympatrically and flower concurrent, but a natural hybrid has never been found. It is possible that *C. errans* could visit both species while carrying pollinia. After over 200 reciprocal cross attempts were made between *O. undulatum* and *O. floridanum*, the conclusion was reached that there is a genetic barrier preventing the production of a natural or man made hybrid. Both species readily produce seed capsules with viable seeds from both selfing and sib crosses.

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¹In 1969 after graduating from Miami-Dade Community College with an Associates Degree and being accepted to the Bachelor's Degree program at Florida Atlantic University as a pre-med student, I met Dr. Ralph Adams and my pre-med plans quickly changed. Dr. Adams had heard about my orchid background and was eager for me to work with him on the pollination biology of the orchids of Florida and the Bahama Islands.

Dr. Adams had been a student of Dr. Callaway Dodson at the University of Miami, a pioneer in pollination biology. We began a series of studies to determine the pollinators of the Florida orchids.

²At the present time all of the voucher specimens deposited at Florida Atlantic University are missing and their whereabouts is unknown. The missing vouchers included the pollinator of *Dendrophylax lindenii*, *Epidendrum anceps*, *Epidendrum difforme*, *Cyrtopodium punctatum*, *Polystachya concreta*, *Encyclia gracilis (correllii)* and *Encyclia altissima*.

