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The Genera *Cattleyopsis* Lem., *Laeliopsis* Lindl. and *Broughtonia* R. Br. Reestablished

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ABSTRACT

The genera *Cattleyopsis* Lem. and *Laeliopsis* Lindl. are reestablished. The characters that clearly separate the genera including the cDNA data are given. The expansion or redefinition of the genus *Broughtonia* R. Br. to include the characters of *Cattleyopsis* and *Laeliopsis* is rejected.

There have been several differences of opinion considering the three genera *Broughtonia* R. Br., *Cattleyopsis* Lem. and *Laeliopsis* Lindl. Three taxonomic approaches to the classification of these genera have been proposed. Several authors have considered the three genera as distinct (Correll, 1941; Leon, 1946; Dietrich, 1984; Sauleda & Adams, 1984; Withner, 1996), others have considered only two genera incorporating *Laeliopsis* into *Broughtonia* and only recognizing *Broughtonia* and *Cattleyopsis* (Rofle, 1889; Cogniaux, 1910; Schlechter, 1915; Acuña, 1939; Fowlie, 1961a and 1961b). The third approach recognizes only the genus *Broughtonia* lumping *Laeliopsis* and *Cattleyopsis* into *Broughtonia* (Fawcett & Rendle, 1910; Dressler, 1966; Loigier, 1969; Adams, 1970 and 1971; Diaz Dumas, 1996; Nir, 2000; Diaz Dumas, 2014; Mújica *et al.*, 2015; Mújica & González, 2015).

Dressler (1966) united the species of *Cattleyopsis* with *Broughtonia* because of "the very close floral resemblances between *Broughtonia sanguinea* (Sw.) R. Br. and *Cattleyopsis ortgiesiana* (Rchb. f.) Cogn. and between *Broughtonia domingensis* (Lindl.) Rolfe and *Cattleyopsis lindenii* (Lindl.) Cogn., as well as the vegetative resemblances between *B. domingensis* and *C. lindenii*".

Dressler states that the only distinction between *Broughtonia* and *Cattleyopsis* is the number of pollinia; *Cattleyopsis* has eight pollinia and *Broughtonia* have four

pollinia and "those that consider the number of pollinia to be an inviolable generic feature will, of course, maintain *Cattleyopsis* as a distinct genus". He adds that "the distinction drawn by Lindley (1853) between *Broughtonia* and *Laeliopsis* was based on a morphological misconception (the external adnate spur of *Broughtonia*), that has been quite untenable when the plants of extreme western Jamaica are considered (*Broughtonia negrilensis* Fowlie)". In addition, Dressler confused *Epidendrum cubense* Lindl. (*Cattleyopsis cubense* (Lindl.) Sauleda & Adams) with *Barkeria chinensis* (Lindl.) L. B. Thien. He stated that after examining the type specimen of *E. cubense* he agreed with the conclusion previously reached by him and L. B. Thien that it is *B. chinensis* and added that he doubted the Cuban origin of the plant (*E. cubense*).

Sauleda & Adams (1984) published a comprehensive and detailed monograph of the three genera. They addressed most of Dressler's misconceptions and added several important features of the three genera, which were unknown to Dressler. Each genus is restricted to a separate island. *Laeliopsis* occurs only in Hispanola, *Broughtonia* only occurs in Jamaica and *Cattleyopsis* is restricted to Cuba and the Bahama Islands. The Bahamian occurrence is not unusual since most if not all of the species in the Bahama Islands. The geographic isolation of the genera is a character that cannot be ignored. The distinctive distributional patterns suggest evolutionary divergence as a function of isolation (Dobzhansky, 1940).

Dressler also gave the floral similarity as a reason for uniting *B. sanguinea* and *C. ortgiesiana* and giving the same reason for uniting *B. domingensis* and *C. lindenii*. This similarity is due to convergent evolution on a pollination system. *Broughtonia sanguinea* and *C ortgiesiana* have been observed being visited by hummingbirds and *B. domingensis* and *C. lindenii* have been observed being visited by visited by bees. The floral differences of the species within the genera *Broughtonia* and *Cattleyopsis* are due to the adaptive nature of floral traits due to pollinator-mediated microevolution (Harder & Johnson, 2009). Shifts in pollination systems result in correlated shifts in floral traits and speciation within a genus (Forest *et al.*, 2014; Van der Niet *et al.*, 2014).

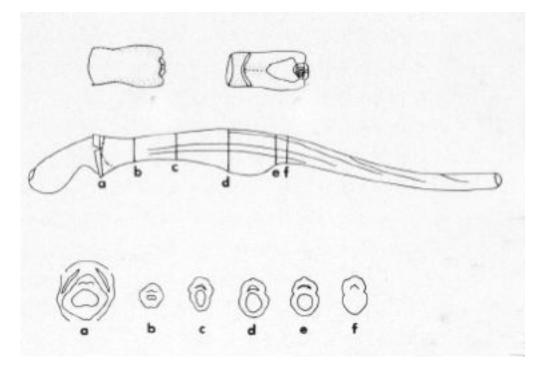
Lindley (1853) gave the distinction between *Broughtonia* and *Laeliopsis* as an "external adnate spur". Dressler says this is a "morphological misconception, and has proven to be quite untenable when the plants of extreme western Jamaica are considered" in reference to *B. negrilensis*. Sauleda & Adams (1984) have demonstrated in clear drawings of cross-sectional dissections of living flowers that the plants of western Jamaica (*B. negrilensis*) do have this structure and what

Lindley considered an external adnate spur is actually a well-defined swollen nectary embedded within the ovary. In *Cattleyopsis* and *Laeliopsis* the nectary lumen is wide at its distal opening gradually narrowing proximally, this is not so in *Broughtonia* where the proximal end of the nectary lumen swells to a nectarfilled chamber. This externally visible proximal swelling has been confused with a spur or sepaline tube. Arditti (1969) and Arditti and Fisch (1977) were the only researchers to recognize the true nature of the prominent proximal nectary chamber present only in *Broughtonia*. The presence of the nectary and the results of pigment analyses led Arditti and Fisch (1977) to question the lumping of *Cattleyopsis* and *Laeliopsis* into *Broughtonia*.

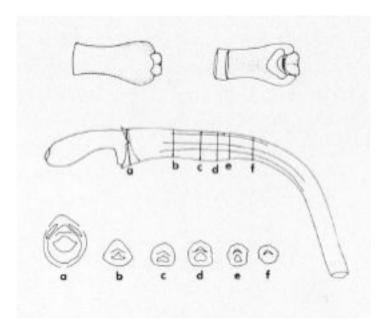
The number of pollinia is an important character, especially when taken in consideration with the other important characters. This did not seem important to Dressler at the time. It is clearly evident that *Cattleyopsis* and *Laeliopsis*, which occur on different islands from Broughtonia, evolved this character independently from *Broughtonia*. *Cattleyopsis* and *Laeliopsis* are more closely related to each other than to *Broughtonia*.

Diaz Dumas (1996) states that *Broughtonia* is a natural group and a separation into multiple genera cannot be done and therefore follows the opinion of Dressler. Diaz Dumas recognizes the geographical isolation of each genus as Sauleda & Adams (1984) demonstrated but ignores all the other characters that clearly separate the three genera. Many authors currently follow Diaz Dumas's treatment reducing *Cattleyopsis* and *Laeliopsis* to *Broughtonia* based on Dressler's treatment (Nir, 2000; Valle *et al.*, 2010; Acevedo-Rodríguez & Strong, 2012; Mújica & González, 2015; Mújica *et al.*, 2015).

The characters that separate the three genera must be revisited. The reproductive isolation of the three genera makes them endemic to their respective islands. The floral similarities among members of each genus are attributable to secondary adaptations to ornithophily or to melittophily (Sauleda & Adams, 1984). This is a good example of convergent evolution. The vegetative similarities of the four species that comprise *Cattleyopsis* and *Laeliopsis* are attributable to secondary adaptation to the xeric habitats in which they occur (Sauleda & Adams, 1984; Lowry *et al.*, 2014). *Laeliopsis* makes vegetative phenotypic adjustments to environmental conditions. Vegetatively *Laeliopsis* resembles *Broughtonia* in mesic habitats and *Cattleyopsis* in xeric habitats (Sauleda & Adams, 1984). In *Cattleyopsis* and *Laeliopsis* the nectary lumen is wide at its distal opening gradually narrowing proximally, this is not so in *Broughtonia* where the proximal end of the nectary lumen swells to a nectar-filled chamber. This externally visible proximal swelling has been confused with a spur or sepaline tube.

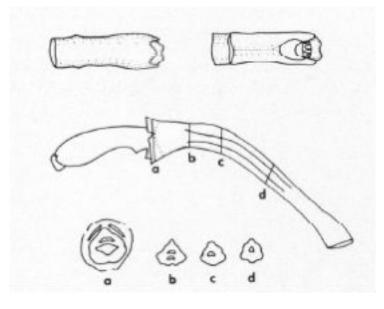


Broughtonia sanguinea (Sw.) R. Br. Column and ovary, lateral view and serial cross-sections showing swollen nectary lumen. From Sauleda & Adams (1984).

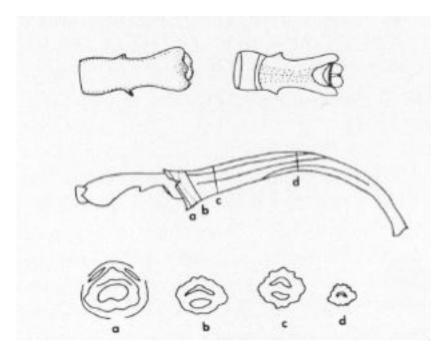


Broughtonia negrilensis Fowlie. Column and ovary, lateral view and serial cross-sections showing swollen nectary lumen. From Sauleda & Adams (1984).

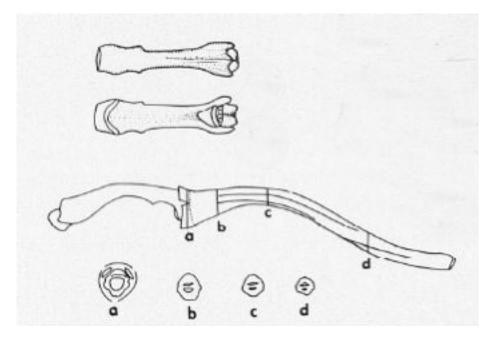
The columns of the three genera are distinctively different. The column of *Cattleyopsis* has two auricle-like appendages near the base and is narrowly winged towards the apex. *Broughtonia* have a short blunt column with thick and short wings near the apex. In *Laeliopsis* the column is elongate, clavate and narrowly winged towards apex.



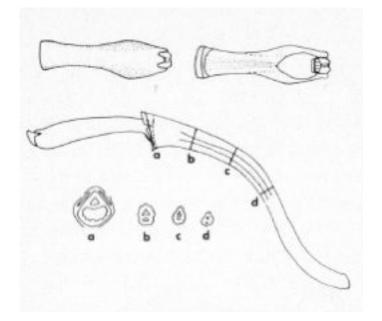
Cattleyopsis cubensis (Lindl.) Sauleda & Adams. Column and ovary, lateral view and serial cross-sections showing nectary lumen. From Sauleda & Adams (1984).



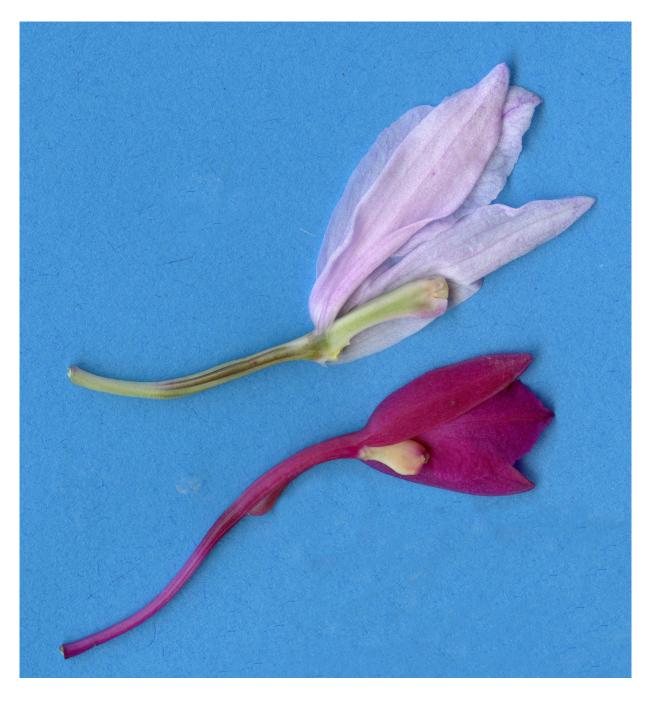
Cattleyopsis ortgiesiana (Rchb. f.) Cogn. Column and ovary, lateral view and serial cross-sections showing nectary lumen. From Sauleda & Adams (1984).



Cattleyopsis lindenii (Lindl.) Cogn. Column and ovary, lateral view and serial cross-sections showing nectary lumen. From Sauleda & Adams (1984).

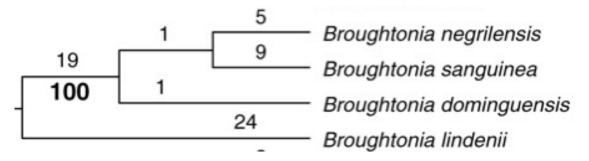


Laeliopsis domingensis (Lindl.) Lindl. Column and ovary, lateral view and serial cross-sections showing nectary lumen. From Sauleda & Adams (1984).



Comparison of live material of *Cattleyopsis lindenii* (Top) and *Broughtonia sanguinea* (Bottom) demonstrating the diagnostic characters of each.

Several authors continue to include the species of *Cattleyopsis* and *Laeliopsis* in *Broughtonia* based in part on the results of plastid DNA sequences (van den Berg *et al.*, 2009). However, the same cDNA results (van den Berg *et al.*, 2009) can be used to conclude that only two species belong in *Broughtonia* and that the species of *Laeliopsis* and *Cattleyopsis* are distinct.



cDNA results from van den Berg *et al.*, 2009, indicating that *Broughtonia negrilensis* and *Broughtonia sanguinea* belong in the same genus and that *Cattleyopsis* and *Laeliopsis* are separate genera.

There is a disturbing trend to modify and expand the concept or definition of a genus to accommodate the plastid DNA results (Sauleda, 2016). The lumping of the genera *Sophronitis* Lindl. and *Laelia* Lindl. into the genus *Cattleya* Lindl. (van den Berg, 2008) and the lumping of the species that belong in the genera *Anacheilium* Hoffmanns, *Pollardia* Withner & Harding, *Euchile* Withner and *Panarica* Withner & Harding into *Prosthechea* Knowles & Westc. (Higgins, 1997) based solely on molecular analysis and totally ignoring the morphology are prime examples of expanding the generic descriptions.

By including the species of *Cattleyopsis* and *Laeliopsis* in *Broughtonia* the concept of the genus has to be greatly expanded from the original description. The characters used to expand the generic concept of *Broughtonia* include changes in geographical distribution, structure of the column and vegetative characters. To the description of the column as a short blunt column as originally described in *Broughtonia* now must be added a narrow slender column as found in *Laeliopsis* and with basal auricle-like appendages as found in *Cattleyopsis*. The number of pollinia, the presence of eight must now be added to the original description of four. To the vegetative description of *Broughtonia* of a broad coriaceous leaf with entire margin and ellipsoid to ovoid pseudobulbs now must be added narrow fleshy-rigid leaves with erose margin and cylindrical pseudobulbs. Diaz Dumas (2014) made these additions to the concept of *Broughtonia* in the treatment of *Broughtonia* in Orchid flora of the Greater Antilles.

Considering the extensive changes that have to be made to the generic concept of *Broughtonia* as described by Robert Brown, Diaz Dumas' treatment of the genus *Broughtonia* although not illegal under the International Code of Nomenclature is an affront and demonstrates a lack of respect for the work of Robert Brown and other previous authors.

According to article 47A.1. of the International Code of Nomenclature "when an alteration ….. has been considerable, the nature of the change may be indicated by adding ….. abbreviated where suitable, "emendavit" (emend.) followed by the name of the author responsible for the change. *Broughtonia* as revised by Diaz Dumas differs from the genus as originally circumscribed by Robert Brown, but the generic name remains *Broughtonia R. Br.* since the type of the name is still included in the genus but should be cited as *Broughtonia R. Br.* emend. Diaz Dumas.

The distributional data, morphological data, results of pigment analyses and cDNA data are extensive enough to substantiate that *Broughtonia, Cattleyopsis* and *Laeliopsis* should be maintained as separate genera as Sauleda and Adams (1984) suggested. The concept of the genus *Broughtonia* should not be modified to include characters of two other genera.



This photograph is from William Osment's personal collection of photographs taken in Cuba. It represents the first plant of *Cattleyopsis cubensis* he brought to the United States in the 1950's.



These are pictures of the result of the self-pollination of a plant of *Cattleyopsis cubensis* collected by William Osment in Prov. de Pinar del Rio, Cuba in July 1959. The original plant was self-compatible as are the resulting seedlings.



Results of self-pollinating a seedling of *Cattleyopsis cubensis* from the original plant collected by William Osment (F2).



This photograph is from William Osment's personal collection of photographs taken in Cuba. It represents the first plant of *Cattleyopsis ortgiesiana* he brought to the United States in the 1950's.

ACKNOWLEDGMENT

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