



Reaching a compromise between conflicting nuclear and plastid phylogenetic trees: a new classification for the genus *Cattleya* (Epidendreae; Epidendroideae; Orchidaceae)

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Abstract

A new classification for the 114 species *Cattleya* is proposed, based on and compatible with previously published nuclear, plastid and combined phylogenetic trees. *Cattleya* is divided into four subgenera, three sections and five series. A key to the infrageneric categories and a table listing all species and their placement is presented.

Key words: Laeliinae, *Laelia*, *Sophranitis*, infrageneric classification

Introduction

Cattleya Lindley (1824: t. 33) is a Neotropical genus with 114 species of outstanding horticultural importance (van den Berg 2005, 2008). On the basis of molecular phylogenetic results based on nuclear internal transcribed spacer (ITS) and plastid *trnL-F* (intron and intergenic spacer), *matK* and *rbcL* (van den Berg *et al.* 2000, van den Berg 2009, van den Berg *et al.* 2009), *Sophranitis* Lindley (1828a: t. 1147) and all Brazilian species previously included in *Laelia* Lindley (1831a: 115) were transferred to *Cattleya* (van den Berg 2008). In the last paper, the rationale justifying lumping as a better option than splitting *Cattleya* in smaller genera was presented. The alternative option of splitting into several genera would the number of narrowly defined genera and create many thousand nothogenera in horticulture. Therefore, new combinations for species binomials previously placed in *Sophranitis*, *Hoffmannseggella* Jones (1968: 69) and other genera of Chiron & Castro (2002) were made in *Cattleya* (van den Berg 2008 for species, van den Berg 2010 for natural hybrids). As a result, a new classification was clearly needed, especially because part of the rationale for improving nomenclatural stability was to deal with nomenclatural changes from that point onwards without the need for further species transfers. Various classifications have been proposed for *Cattleya* and *Laelia*, partly reviewed in Withner (1988, 1990), where he provided an intricate system of subgenera and sections. However, in most cases, basionyms were not correctly cited, even in amendments made later (Withner 2000), which rendered several transfers invalid.

I propose here a new system of infrageneric taxonomy for *Cattleya* based previous phylogenetic studies (van den Berg 2009, van den Berg *et al.* 2000, 2005, 2009). The figure comparing plastid and plastid+ITS topologies and phylogenetic relationships among groups of *Cattleya*, which was inadvertently excluded from van den Berg (2009), is published here for the first time, providing a framework for the new classification (Fig. 1). Despite being based on several DNA regions, decisions on infrageneric groupings for *Cattleya* were challenging. Some infrageneric groups display conflicting placements between ITS and plastid trees. Also due to differences in rates of molecular evolution, the combination of all eight plastid regions generated a tree that is less resolved than that of just ITS. On the other hand, the content of each infrageneric group, i.e. the sets of species recovered in both topologies is similar and compatible with various previously recognized groups based on their morphology. For example, the set of species that corresponds to the former Brazilian *Laelias* (*Sophranitis* sensu van den Berg & Chase 2000) is recovered as a clade, and the species groups within this follow closely the classification of Schlechter (1917a). In fact the main conflict between the two trees in Fig. 1 lies in relationships between these main groups and can be summarized by three main points: a) subgenus

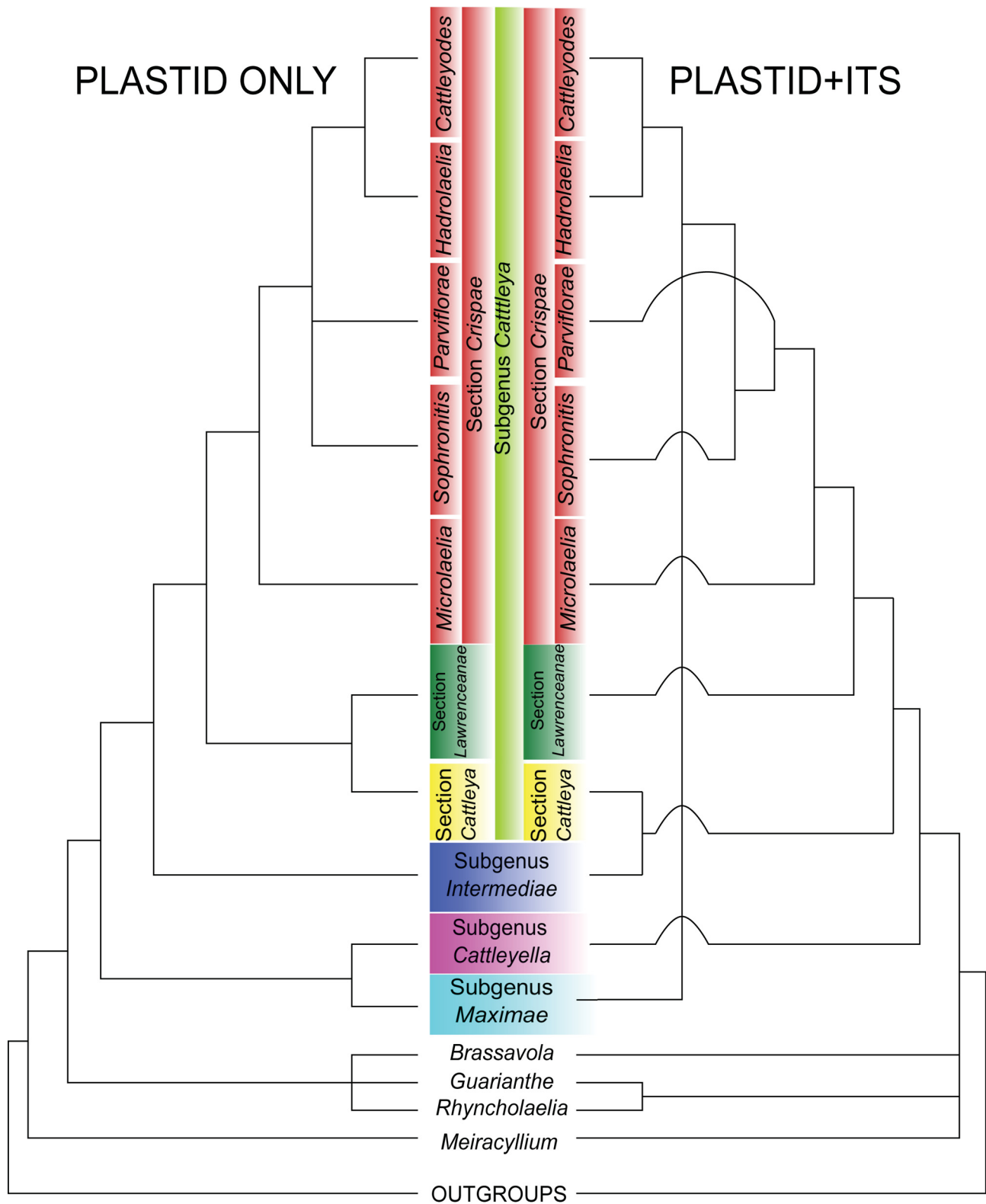


FIGURE 1. A comparison of the phylogenetic relationships between subgroups of *Cattleya* and related genera based on a Bayesian analyses of plastid and ITS sequence data (details of the data collection and analyses presented in van den Berg, 2009). Plastid regions: *matK*, *trnL* intron, *trnL-F* spacer, *rps16*, both introns of *trnK*, and *atpB-rbcL* and *psbA-trnH* spacers. Nuclear region: ITS.

Maximae is sister to subgenus *Cattleyella* in plastid DNA-based trees but sister to ser. *Cattleyodes*+*Hadrolaelia* of sect. *Crispae* in the ITS tree; b) section *Lawrenceanae* is sister to sect. *Cattleya* in plastid trees but sister to sect. *Crispae* in the ITS tree and; c) subgenus *Intermediae* is sister to all other groups of *Cattleya* except subgenera *Maximae* and *Cattleyella* in plastid trees but sister only to sect. *Cattleya* in ITS results. These patterns were considered by van den Berg *et al.* (2000) to be peculiar, and because of this they performed extensive cloning of the ITS region for species

in subgenus *Maximae* and sect. *Lawrenceanae* during the data gathering for van den Berg *et al.* (2009) to determine if copies agreeing with plastid DNA could be recovered. Despite this effort, no evidence for other copies of ITS was found, indicating that these differences could be better explained only by invoking hybridization (known to be common in the genus) or lineage-sorting. In either case, there is no obvious solution for these topological conflicts (which cannot be therefore improved simply by increasing the number of characters for either nuclear or plastid regions). Nevertheless, establishment of a classification for *Cattleya* is necessary for horticultural purposes, and here I develop a compromise by designing a classification that is compatible with both tree topologies. A much more thorough study with 15 DNA regions restricted to *Cattleya* subgenus *Intermediae* (Santos 2011, Santos & van den Berg unpubl.) indicated that within the latter subgenus, hybridization between plants of different groups appears to be important for speciation. Considering the stereotypical generalized deceit pollination system found in *Cattleya* (Smidt *et al.* 2006, Silva-Pereira *et al.* 2007), hybridization is also likely to be important in other subgenera and might even be involved in the origin of some infrageneric taxa (van den Berg 2013). At least 34 naturally occurring hybrids between sections of *Cattleya* are listed (more than 60 including natural hybrids within the infrageneric taxa).

This classification of *Cattleya* is similar to the previous morphological understanding of these groups of species previously placed in *Cattleya*, *Laelia* and *Sophranitis*. It seems likely that the subgenera *Maximae* and *Cattleyella* (both monotypic) and all of sect. *Lawrenceanae* are candidates for origin through ancient hybridization, a result backed not only by phylogenetic patterns, but also their mosaic of morphological traits. According to Santos (2011), subgenus *Cattleyella* (which had been segregated as a monotypic genus by van den Berg & Chase 2004) might have originated by ancient hybridization between *Cattleya* and *Brassavola* Brown (1813: 216). This ancient event cannot be linked to parentage by extant species in *Cattleya* or *Brassavola*. Since the overall morphology of this species is closer to *Cattleya*, I decided to classify this plant as a monospecific subgenus in *Cattleya*. This type of decision is similar to the treatments of hybrid taxa in the infrageneric classification of *Nicotiana* (Solanaceae; Knapp *et al.* 2004). Groups that have arisen by hybridization are here recognized as subgenera (*Cattleyella* and *Maximae*), and sect. *Lawrenceanae* is included in subgenus *Cattleya* because the conflicting positions are both within the subgenus, a position that is supported as well by overall morphology.

Identification key for infrageneric taxa within genus *Cattleya*

1. Pollinia 8.....2
- Pollinia 4.....6
2. Leaves 2, terete.....series *Microlaelia*
- Leaves mostly 1, or 2 not terete.....3
3. Spathaceous bract subtending the inflorescence absent.....4
- Spathaceous bract subtending the inflorescence present.....5
4. Flowers red, orange or yellow, or pink (in this case pseudobulbs <2 cm long and leaves <4 cm long, more or less flat). series *Sophranitis*
- Flowers pink, purple or mauve, plants with conduplicate leaves >4 cm long.....series *Hadrolaelia*
5. Plants epiphytic with more or less clavate pseudobulbs and flowers generally larger than 6 cm.....series *Cattleyodes*
- Plants mostly rupicolous or terrestrial with cylindrical or subcylindrical pseudobulbs or epiphytic plants with long, slender pseudobulbs and flowers generally less than 6 cm.....series *Parviflorae*
6. Leaves 2 or 3.....subgenus *Intermediae*
- Leaf solitary.....7
7. Column tip with unciform projections around the sides of the anther.....subgenus *Cattleyella*
- Column tip without unciform projections.....8
8. Pseudobulbs subcylindrical or slender and cylindrical; flowers pink to purple, Peru and Ecuador.....subgenus *Maximae*
- Pseudobulbs more or less clavate or fusiform, flowers not pink to purple if from Peru and Ecuador.....9
9. Plants from mountain regions (>600m) [Peru, Ecuador, Colombia and Venezuela, or eastern Brazil].....section *Cattleya*
- Plants from low elevation in the Amazon (<400) [northern Brazil and Venezuela], or from lowland, dry habitats [Lara, Yaracuy, Carabobo, Vargas, Aragua States, and Distrito Federal, Venezuela].....subgenus *Lawrenceanae*

Taxonomy

A general classification for *Cattleya* and total numbers of species is presented in Table 1. The following pages deal with the new combinations required and synonymy, whereas the species membership for each infrageneric group is given in Table 2 to avoid excessive cluttering of the protologues. In the taxonomic paragraphs, names that are homotypic have all synonyms clustered in the same paragraph to avoid repetition of the type in each name, except when a typification is needed. Similarly, all names for which a typification later or here is not indicated have been typified by the original author or were automatically typified by having just a single species.

TABLE 1. Outline of the taxonomic arrangement of sections and subgenera in *Cattleya* as proposed here with the number of species in each group.

Taxon	Species number
1. <i>Cattleya</i> subgenus <i>Cattleya</i>	91
1.1. section <i>Cattleya</i>	17
1.2. section <i>Crispae</i> (Pfitzer) Van den Berg	71
1.2.1. series <i>Cattleyodes</i> (Schltr.) Van den Berg	8
1.2.2. series <i>Hadrolaelia</i> (Schltr.) Van den Berg	6
1.2.3. series <i>Microlaelia</i> (Schltr.) Van den Berg	1
1.2.4. series <i>Parviflorae</i> (Lindl.) Van den Berg	47
1.2.5. series <i>Sophronitis</i> (Lindl.) Van den Berg	9
1.3. section <i>Lawrenceanae</i> Van den Berg	3
2. <i>Cattleya</i> subgenus <i>Cattleyella</i> (Van den Berg & M.W.Chase) Van den Berg	1
3. <i>Cattleya</i> subgenus <i>Intermediae</i> (Cogn.) Withner	21
4. <i>Cattleya</i> subgenus <i>Maximae</i> (Withner) Van den Berg	1
Total	114

Cattleya Lindley (1824: t. 33). Type species: *Cattleya labiata* Lindley (1824 t. 33)

Brasilaelia Campacci & Gutfreund (2006: 99). *Chironiella* Braem (2006: 110). Type species: *Cattleya crispa* Lindley (1828c: t. 1172). *Cattleyella* van den Berg & Chase (2004: 100). *Schluckebieria* Braem (2004: 49). Type species: *Cattleya araguaiensis* Pabst (1967: 9). *Dungisia* Chiron & Castro (2002:11). Type species: *Cattleya harpophylla* (Reichenbach 1873: 542) Van den Berg (2008: 7). *Hadrolaelia* (Schlechter 1917a: 88) Chiron & V.P. Castro (2002: 11). Type (chosen by Withner 1990: 18): *Cattleya pumila* Hooker (1838: t. 3656). *Hoffmannseggella* Jones (1968: 69). Type species: *Cattleya cinnabarina* (Bateman ex Lindley 1839a: t. 28) Van den Berg (2008: 6). *Maelenia* Dumortier (1834: 13, t. 10). Type species: *Cattleya forbesii* Lindley (1825: t. 37) [as *Maelenia paradoxa* Dumortier (1834: 13, t. 10)]. *Microlaelia* (Schlechter 1917: 88) Chiron & Castro (2002:11). Type (chosen by Withner 1990:17): *Cattleya lundii* (Reichenbach & Warming 1881: 92) Van den Berg (2008: 9). *Sophronitis* Lindley (1828a: t. 1147). Type species: *Cattleya cernua* (Lindley 1828b: t. 1129) Van den Berg (2010: 13).

1. *Cattleya* subgenus *Cattleya*

1.1. ***Cattleya*** section ***Cattleya***. Type species: *C. labiata* Lindley (1824: t. 33). *Cattleya* ser. *Monophyllae* Barbosa Rodrigues (1882: 156). Type (designated here): *Cattleya labiata* Lindley (1824: t. 33). *Cattleya* sect. *Mossiae* (Pfitzer 1889: 146). Type (designated here): *C. labiata* Lindley (1824: t. 33).

Cattleya subg. *Stellatae* Withner (1988: 21). Type species: *C. luteola* Lindley (1853: 774)
Cattleya sect. *Xantheae* Withner (1988: 21). Type species: *C. dowiana* Bateman (1866: 922).

The species in this section (Table 2) are the species complex around *C. labiata*, and species placed by Withner (1988) in *Cattleya* subg. *Stellatae*: *Cattleya iricolor* Reichenbach (1874: 162), *C. luteola* and *C. mooreana* Withner, Allison & Guenard in Withner (1988: 95). These three species have much smaller flowers with narrow sepals and petals and could be recognized as a separate group, but we feel that it would be a small group and the vegetative morphology of all species in sect. *Cattleya* is so consistent that this would not be necessary. This is also true for some species with small flowers that were included in *Cattleya* ser. *Cattleyodes*.

1.2. *Cattleya* section ***Crispae*** (Pfitzer) Van den Berg, *comb. nov.*

Basionym: *Laelia* sect. *Crispae* Pfitzer (1889: 147). Type (chosen by Withner 1990: 18): *Cattleya crispa* Lindley (1828c: t. 1172). *Laelia* subg. *Crispae* Withner (1990: 18), *nom. inval.* (missing basionym reference). *Laelia* sect. *Monophyllae* Cogniaux (1901: 273). Type (designated here): *Cattleya crispa* Lindley (1828c: t. 1172).

This section includes all Brazilian species previously assigned to *Laelia* and the expanded concept of *Sophronitis sensu* van den Berg & Chase (2000, 2001). This group has always been recovered as monophyletic (van den Berg 2009, van den Berg *et al.* 2000, 2005, 2009), and for this reason I prefer to recognize it at sectional level, and then establish several series for smaller units such as *Laelia* sect. *Cattleyodes* Schlechter (1917a: 88), sect. *Hadrolaelia* Schlechter (1917a: 88), and sect. *Microlaelia* Schlechter (1917a: 89), as well as sect. *Parviflorae* Lindley (1842a t. 62) while keeping the same component species.

1.2.1. *Cattleya* series *Cattleyodes* (Schltr.) Van den Berg, *comb. et stat. nov.*

Basionym: *Laelia* sect. *Cattleyodes* Schlechter (1917a: 88). Type (designated here): *Cattleya crispa* Lindley (1828c: t. 1172) Campacci & Gutfreund (2006: 99). *Chironiella* Braem (2006: 110).

Laelia subsect. *Lobatae* Cogniaux (1901: 283). Type (designated here): *Cattleya lobata* Lindley (1848: 403).

Laelia sect. *Perrinae* Withner (1990:18). Type : *Cattleya perrinii* Lindley (1838: t. 2). *Hadrolaelia* sect. *Perrinae* (Withner) Chiron & Castro (2002: 17). *Chironiella* sect. *Perrinae* (Withner) Braem (2006: 110).

Hadrolaelia sect. *Fidelensis* Chiron & Castro (2002: 17). Type : *Cattleya ×fidelensis* (Pabst 1967: 11) Van den Berg (2008: 7). *Chironiella* sect. *Fidelensis* (Chiron & Castro 2002: 17) Braem (2006: 109).

Hadrolaelia sect. *Virens* Chiron & Castro, (2002: 17). Type species: *Cattleya virens* (Lindley 1844: misc. 1) Van den Berg (2008: 11). *Chironiella* sect. *Virens* (Chiron & Castro 2002: 17) Braem (2006: 110).

Cattleya ser. *Cattleyodes* includes some of the showiest species in the genus, along with sect. *Cattleya*. The vegetative morphology is similar to that of *C.* sect. *Cattleya*, but the flowers are reminiscent of *C.* subg. *Maximae*. This group retains eight species (Table 2), since *Cattleya ×fidelensis* was found to be a natural hybrid by Fraga *et al.* (2008).

TABLE 2. Species placement in different infrageneric taxa within *Cattleya* Lindl.

Infrageneric taxon	Member species
1.1. <i>Cattleya</i> section <i>Cattleya</i>	1.1.1. <i>C. aurea</i> Linden
	1.1.2. <i>C. dowiana</i> Bateman & Rchb.f.
	1.1.3. <i>C. gaskelliana</i> (N.E.Br.) B.S.Williams
	1.1.4. <i>C. iricolor</i> Rchb.f.
	1.1.5. <i>C. jenmanii</i> Rolfe
	1.1.6. <i>C. labiata</i> Lindl.
	1.1.7. <i>C. luteola</i> Lindl.
	1.1.8. <i>C. mendelii</i> Dombrain
	1.1.9. <i>C. mooreana</i> Withner, Allison & Guenard
	1.1.10. <i>C. mossiae</i> C.Parker ex Hook.
	1.1.11. <i>C. percivaliana</i> (Rchb.f.) O'Brien
	1.1.12. <i>C. quadricolor</i> Lindl.
	1.1.13. <i>C. rex</i> O'Brien
	1.1.14. <i>C. schroederae</i> (Rchb.f.) Sander
	1.1.15. <i>C. trianae</i> Linden & Rchb.f.
	1.1.16. <i>C. warneri</i> T.Moore ex R.Warner
	1.1.17. <i>C. warscewiczii</i> Rchb.f.
1.2.1. <i>Cattleya</i> series <i>Cattleyodes</i>	1.2.1.1. <i>C. crispa</i> Lindl.
	1.2.1.2. <i>C. grandis</i> (Lindl.) A.A.Chadwick
	1.2.1.3. <i>C. lobata</i> Lindl.
	1.2.1.4. <i>C. perrinii</i> Lindl.
	1.2.1.5. <i>C. purpurata</i> (Lindl. & Paxton) Van den Berg
	1.2.1.6. <i>C. tenebrosa</i> (Rolfe) A.A.Chadwick
	1.2.1.7. <i>C. virens</i> (Lindl.) Van den Berg
	1.2.1.8. <i>C. xanthina</i> (Lindl.) Van den Berg

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TABLE 2. (Continued)

Infrageneric taxon	Member species
1.2.2. <i>Cattleya</i> series <i>Hadrolaelia</i>	1.2.2.1. <i>C. alaoarii</i> (Brieger & Bicalho) Van den Berg 1.2.2.2. <i>C. bicalhoi</i> Van den Berg 1.2.2.3. <i>C. jongheana</i> (Rchb.f.) Van den Berg 1.2.2.4. <i>C. praestans</i> (Rchb.f.) Van den Berg 1.2.2.5. <i>C. pumila</i> Hook. 1.2.2.6. <i>C. sincorana</i> (Schltr.) Van den Berg
1.2.3. <i>Cattleya</i> series <i>Microlaelia</i>	1.2.3.1. <i>C. lundii</i> (Rchb.f. & Warm.) Van den Berg
1.2.4. <i>Cattleya</i> series <i>Parviflorae</i>	1.2.4.1. <i>C. alvarenguensis</i> (Campacci) Van den Berg 1.2.4.2. <i>C. alvaroana</i> (F.E.L.Miranda) Van den Berg 1.2.4.3. <i>C. angereri</i> (Pabst) Van den Berg 1.2.4.4. <i>C. blumenscheinii</i> (Pabst) Van den Berg 1.2.4.5. <i>C. bradei</i> (Pabst) Van den Berg 1.2.4.6. <i>C. briegei</i> (Blumensch. ex Pabst) Van den Berg 1.2.4.7. <i>C. caulescens</i> (Lindl.) Van den Berg 1.2.4.8. <i>C. cinnabarina</i> (Bateman ex Lindl.) Van den Berg 1.2.4.9. <i>C. colnagoi</i> (Chiron & V.P.Castro) Van den Berg 1.2.4.10. <i>C. concepcionensis</i> (V.P.Castro & Chiron) Van den Berg 1.2.4.11. <i>C. crispata</i> (Thunb.) Van den Berg 1.2.4.12. <i>C. endsfeldzii</i> (Pabst) Van den Berg 1.2.4.13. <i>C. esalqueana</i> (Blumensch. ex Pabst) Van den Berg 1.2.4.14. <i>C. flavasulina</i> (F.E.L.Miranda & K.G.Lacerda) Van den Berg 1.2.4.15. <i>C. fournieri</i> (Cogn.) Van den Berg 1.2.4.16. <i>C. ghillanyi</i> (Pabst) Van den Berg 1.2.4.17. <i>C. gloedeniana</i> (Hoehne) Van den Berg 1.2.4.18. <i>C. guanhanensis</i> (Campacci) Van den Berg 1.2.4.19. <i>C. harpophylla</i> (Rchb.f.) Van den Berg 1.2.4.20. <i>C. hatae</i> (V.P.Castro & K.G.Lacerda) Van den Berg 1.2.4.21. <i>C. hegeriana</i> (Campacci) Van den Berg 1.2.4.22. <i>C. hoehnei</i> Van den Berg, 1.2.4.23. <i>C. itambana</i> (Pabst) Van den Berg 1.2.4.24. <i>C. kautskyana</i> (V.P.Castro & Chiron) Van den Berg 1.2.4.25. <i>C. kettieana</i> (Pabst) Van den Berg 1.2.4.26. <i>C. kleberi</i> (F.E.L.Miranda) Van den Berg 1.2.4.27. <i>C. liliputana</i> (Pabst) Van den Berg 1.2.4.28. <i>C. longipes</i> (Rchb.f.) Van den Berg 1.2.4.29. <i>C. luetzelburgii</i> Van den Berg 1.2.4.30. <i>C. macrobulbosa</i> (Pabst) Van den Berg 1.2.4.31. <i>C. marcaliana</i> (Campacci & Chiron) Van den Berg 1.2.4.32. <i>C. milleri</i> Blumensch. ex Pabst) Van den Berg 1.2.4.33. <i>C. mirandae</i> (K.G.Lacerda & V.P.Castro) Van den Berg 1.2.4.34. <i>C. munchowiana</i> (F.E.L.Miranda) Van den Berg 1.2.4.35. <i>C. neokautskyi</i> Van den Berg 1.2.4.36. <i>C. pabstii</i> (F.E.L.Miranda & K.G.Lacerda) Van den Berg 1.2.4.37. <i>C. pendula</i> (R.C.Mota, P.L.Viana & K.G.Lacerda) Van den Berg 1.2.4.38. <i>C. pfisteri</i> (Pabst & Senghas) Van den Berg 1.2.4.39. <i>C. presidentensis</i> (Campacci) Van den Berg 1.2.4.40. <i>C. reginae</i> (Pabst) Van den Berg 1.2.4.41. <i>C. rupestris</i> (Lindl.) Van den Berg 1.2.4.42. <i>C. sanguiloba</i> (Withner) Van den Berg 1.2.4.43. <i>C. tereticaulis</i> (Hoehne) Van den Berg 1.2.4.44. <i>C. vandenberghii</i> Fraga & Borges 1.2.4.45. <i>C. vasconcelosiana</i> (Campacci) Van den Berg 1.2.4.46. <i>C. verboonenii</i> (F.E.L.Miranda) Van den Berg 1.2.4.47. <i>C. viridiflora</i> (Verola & Semir) Van den Berg

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TABLE 2. (Continued)

Infrageneric taxon	Member species
1.2.5. <i>Cattleya</i> series <i>Sophronitis</i>	1.2.5.1. <i>C. acuensis</i> (Fowlie) Van den Berg 1.2.5.2. <i>C. alagoensis</i> (V.P.Castro & Chiron) Van den Berg 1.2.5.3. <i>C. brevipedunculata</i> (Cogn.) Van den Berg 1.2.5.4. <i>C. cernua</i> (Lindl.) Van den Berg 1.2.5.5. <i>C. coccinea</i> Lindl. 1.2.5.6. <i>C. dichroma</i> Van den Berg 1.2.5.7. <i>C. mantiqueirae</i> (Fowlie) Van den Berg 1.2.5.8. <i>C. pygmaea</i> (Pabst) Van den Berg 1.2.5.9. <i>C. wittigiana</i> (Barb.Rodr.) Van den Berg
1.3. <i>Cattleya</i> section <i>Lawrenceanae</i>	1.3.1. <i>C. lawrenceana</i> Rchb.f. 1.3.2. <i>C. lueddemanniana</i> Rchb.f. 1.3.3. <i>C. wallisii</i> (Linden) Rollison
2. <i>Cattleya</i> subgenus <i>Cattleyella</i>	2.1. <i>C. araguaiensis</i> Pabst
3. <i>Cattleya</i> subgenus <i>Intermediae</i>	3.1. <i>C. aelandiae</i> Lindl. 3.2. <i>C. amethystoglossa</i> Linden & Rchb.f. 3.3. <i>C. bicolor</i> Lindl. 3.4. <i>C. dormiana</i> (Rchb.f.) Rchb.f. 3.5. <i>C. elongata</i> Barb.Rodr., 3.6. <i>C. forbesii</i> Lindl. 3.7. <i>C. granulosa</i> Lindl. 3.8. <i>C. guttata</i> Lindl. 3.9. <i>C. harrisoniana</i> Bateman ex Lindl. 3.10. <i>C. intermedia</i> Graham ex Lindl. 3.11. <i>C. kerrii</i> Brieger & Bicalho 3.12. <i>C. loddigesii</i> Lindl. 3.13. <i>C. nobilior</i> Rchb.f. 3.14. <i>C. porphyroglossa</i> Rchb.f. 3.15. <i>C. schilleriana</i> Rchb.f. 3.16. <i>C. schofieldiana</i> Rchb.f. 3.17. <i>C. tenuis</i> Campacci & Vedovello 3.18. <i>C. tigrina</i> A.Rich. 3.19. <i>C. velutina</i> Rchb.f. 3.20. <i>C. violacea</i> (Kunth) Rolfe 3.21. <i>C. walkeriana</i> Gardner
4. <i>Cattleya</i> subgenus <i>Maximae</i>	4.1. <i>C. maxima</i> Lindl.

1.2.2. *Cattleya* series ***Hadrolaelia*** (Schltr.) Van den Berg, *comb. et stat. nov.*

Basionym: *Laelia* sect. *Hadrolaelia* Schlechter (1917a: 88). Type (chosen by Withner 1990: 18): *C. pumila* Hooker (1838: t. 3656). *Hadrolaelia* (Schltr.) Chiron & Castro (2002:11), *pro parte*.

Laelia sect. *Sincoranae* [as *Sinocoranae*] Withner (1990: 18). Type species: *Cattleya sincorana* (Schlechter 1917b: 72) Van den Berg (2008: 11).

This section is maintained with the same component species previously assigned to *Laelia* sect. *Hadrolaelia* by Schlechter (1917a) and not including the additional *Sophronitis* species placed there by Chiron & Castro (2002).

1.2.3. *Cattleya* series ***Microlaelia*** (Schltr.) Van den Berg, *comb. et stat. nov.*

Basionym: *Laelia* sect. *Microlaelia* Schlechter (1917a: 89). Type (chosen by Withner 1990: 18): *Cattleya lundii* (Reichenbach & Warming 1881: 92) Van den Berg (2008: 9). *Laelia* subg. *Microlaelia* Withner (1990: 18), *nom. nud.* *Microlaelia* (Schltr.) Chiron & Castro (2002: 11).

Laelia sect. *Diphyllae* Cogniaux (1901: 299). Type (designated here): *Cattleya lundii* (Reichenbach & Warming 1881: 92) Van den Berg (2008: 9).

This monotypic taxon has been recognized in many classifications for *Laelia* and segregated genera (Schlechter, 1917a; Withner, 1990; Chiron & Castro 2002). It is sister to the rest of the taxa in sect. *Crispae* (van den Berg 2009, van den Berg *et al.* 2000, 2009). It is peculiar morphologically, especially by the bifoliate pseudobulbs with terete leaves.

1.2.4. *Cattleya* series ***Parviflorae*** (Lindl.) Van den Berg, *comb. et stat. nov.*

Basionym: *Laelia* sect. *Parviflorae* Lindley (1842a: sub t. 62). Type (chosen by Withner 1990: 18): *Cattleya crispata* (Thunberg 1818: 18) Van den Berg (2008: 6) [as *Laelia flava* Lindley (1839b: misc. 88)]. *Laelia* subg. *Parviflorae* (Lindley 1842a: sub t. 62) Withner (1990: 18), *nom. inval.* (missing basionym reference).

Laelia subsect. *Crispatae* Cogniaux (1901: 273). Type (here designated): *Cattleya crispata* (Thunberg 1818: 18) Van den Berg (2008: 6). *Laelia* sect. *Rupestres* Withner (1990: 18).

Laelia sect. *Cyrtolaelia* Schlechter (1917a: 89). Type (designated here): *Cattleya cinnabarina* (Bateman ex Lindley: 1839a: t. 28) Van den Berg (2008: 6). *Hoffmannseggella* Jones (1968: 69).

Laelia sect. *Harpophyllae* Withner (1990:18). Type species: *Cattleya harpophylla* (Reichenbach 1873: 542) Van den Berg (2008: 7). *Dungesia* Chiron & Castro (2002: 11).

Laelia sect. *Esalqueanae* Withner (1990: 18). Type species: *Cattleya esalqueana* (Blumenschein ex Pabst 1973a: 367) Van den Berg (2008: 7).

Laelia sect. *Liliputanae* Withner (1990:18). Type species: *Cattleya liliputana* (Pabst 1973b: 334) Van den Berg (2008: 9).

This series, previously termed the ‘rupicolous laelias’, or *Laelia* sect. *Parviflorae*, is the largest infrageneric group within *Cattleya* (47 species, Table 2). Some epiphytic species, such as *C. harpophylla*, *C. marcaliana* (Campacci 2002: 77) Van den Berg (2008: 9), and *C. neokautskyi* Van den Berg (2008: 10) are also placed here, and constitute a small clade sister to the remaining rupicolous species. They have slightly different habit, but their flower morphology is similar to some typically rupicolous species such as *C. cinnabarina* and relatives, and they putatively may represent the plesiomorphic morphology from which the rupicolous condition evolved.

1.2.5. *Cattleya* series ***Sophronitis*** (Lindl.) van den Berg, *comb. et stat. nov.*

Basionym: *Sophronitis* Lindley (1828a: t. 1147). Type species: *Cattleya cernua* (Lindley 1828b: t. 1129) van den Berg (2010: 13). *Hadrolaelia* sect. *Sophronitis* Chiron & Castro (2002:11). Type species: *Cattleya coccinea* Lindley (1836: sub. t. 1919).

This series corresponds to the traditional concept of *Sophronitis* used before the molecular study of Van den Berg *et al.* (2000). It comprises most species related and similar to *C. coccinea* Lindley (1836: sub t. 1919), whereas *C. cernua* and *C. alagoensis* (Castro & Chiron 203: 101) Van den Berg (2008: 4) have much smaller flowers with distinct morphology. Section *Sophronitis* in *Hadrolaelia* is actually based on *C. coccinea* (not the type of the genus *Sophronitis*, which is *C. cernua*), since Chiron & Castro (2002) considered only some species originally placed in *Sophronitis* as belonging to *Hadrolaelia*.

1.3. *Cattleya* section ***Lawrenceanae*** Van den Berg, *sect. nov.*

Similar to section *Cattleya* at first sight, but the species are native to warmer areas. Species in this section also present anomalous morphologies in relation to section *Cattleya*: *Cattleya lueddemanniana* differs from section *Cattleya* by the conspicuous unciform projections in the column apex, *C. lawrenceana* by the flowers and column smaller, resembling *Guarianthe*, and *C. wallisii* and *C. lueddemanniana* in its narrow pseudobulbs and frequently suberect leaves that are narrow at the base.

Type species: *C. lawrenceana* Reichenbach (1885: 338)

This new section includes plants at first sight similar to the *C. labiata* complex. However, they occupy lowland, warmer habitats and bear morphological peculiarities not seen anywhere else in the genus. Flowers of *C. lawrenceana* have a tubular lip and very small column like species now assigned to *Guarianthe* Dressler & Higgins (2003: 37) e.g. *G. skinneri* (Bateman 1839: t. 13) Dressler & Higgins (2003: 38). *Cattleya lueddemanniana* Reichenbach (1858: 29) and *C. wallisii* (Linden 1865: 102) Rollison (1875: 11) are smaller plants than in sect. *Cattleya*, and the leaves are more erect and

slightly elongated at the base. *Cattleya lueddemanniana* has unusual projections at the tip of the anther, a character also present in *C. maxima* Lindley (1833: 116) and *C. iricolor*. This character is of doubtful homology, or it might represent a plesiomorphic state conserved in early divergent branches within sections *Cattleya*, *Lawrenceanae* and *Maximae*.

2. *Cattleya* subgenus *Cattleyella* (Van den Berg & M.W.Chase) Van den Berg, *comb. et stat. nov.*

Basionym: *Cattleyella* Van den Berg & Chase (2004: 100). Type species: *Cattleya araguaiensis* Pabst (1967: 9). *Schluckebieria* Braem (2004: 49)

The sole species of this subgenus is distinct in habit and floral characters, and its placement elsewhere in *Cattleya* would be problematic from a morphological standpoint. Molecular results also placed it in an isolated position sister to the remainder of the genus or as sister to *C. maxima*, to which it bears no similarity. Initially, we segregated this species in a separate genus (van den Berg & Chase 2004b), a classification given up by van den Berg (2008) and here in order to be able to keep *C. maxima* Lindley (1833: t. 116) in *Cattleya*. Floral morphology, especially apex of the column, and molecular results (Santos & van den Berg unpubl..) suggest that this taxon most likely originated as a hybrid between *Cattleya* and *Brassavola* Brown (1813: 216). Its overall morphology supports its retention in *Cattleya*.

3. *Cattleya* subgenus *Intermediae* (Cogniaux 1901: 191, 216) Withner (2000: 168) Type (chosen by Withner 1988): *Cattleya forbesii* Lindley (1825: t. 37). *Cattleya* ser. *Intermediae* Cogniaux (1901: 191, 216). *Cattleya* subg. *Intermediae* [as *Intermedia*] (Cogn.) Withner (1988: 21), *nom. inval.* (missing basionym reference). *Cattleya* sect. *Cryptochila* Barbosa Rodrigues (1882: 156). Type (designated here): *Cattleya forbesii* Lindley (1825: t. 37).

Cattleya sect. *Acklandia* (Pfitzer 1889: 146). Type (chosen by Withner 1988: 21): *Cattleya aelandiae* Lindley (1840: t. 48). *Cattleya* subg. *Acklandia* Withner (1988: 21), *nom. inval.* *Cattleya* subsect. *Acranthemum* Cogniaux (1898: 194). Type (designated here): *Cattleya aelandiae* Lindley (1840: t. 48). *Cattleya* subsect. *Diphyllae* Barbosa Rodrigues (1882: 156). Type (designated here): *Cattleya aelandiae* Lindley (1840: t. 48)

Cattleya subg. *Schomburgkoidea* Withner (1988: 21). Type species: *Cattleya violacea* Kunth (1816: 341) Rolfe (1889: 802).

Cattleya sect. *Bicolores* (Pfitzer 1889: 146). Type species: *Cattleya bicolor* Lindley (1836: sub. t. 1919). *Cattleya* subg. *Bicolores* [as *Bicolorea*] (Pfitzer) Withner (2000: 168).

Cattleya subg. *Falcatae* [as *Falcata*] Withner (1988: 21). Type species: *Cattleya guttata* Lindley (1831b: t. 1406). *Cattleya* ser. *Guttatae* Cogniaux (1898: 200). Type (chosen by Withner 1988): *Cattleya guttata* Lindley (1831b: t. 1406). *Cattleya* sect. *Guttatae* (Cogn.) Withner (1988: 21) *nom. inval.* (missing basionym with reference). *Cattleya* sect. *Leopoldia* (Pfitzer 1889: 146). Type (designated here): *Cattleya guttata* Lindley (1831b: t. 1406). *Cattleya* subg. *Leopoldia* (Pfitzer) Withner (2000: 168).

Cattleya sect. *Granulosae* Withner (1988: 21). Type species: *Cattleya granulosa* Lindley (1842b: t. 1). *Cattleya* subsect. *Granulosae* Fowlie (1977: 11), *nom. inval.* (without Latin diagnosis).

Cattleya sect. *Gymnochila* Barbosa Rodrigues (1882: 156) [as *gymnoschila*]. Type (designated here): *Cattleya walkeriana* Gardner (1843: 663). *Cattleya* subsect. *Rhizanthemum* Cogniaux (1898: 192). Type (chosen by Withner 1988): *Cattleya walkeriana* Gardner (1843: 663). *Cattleya* subg. *Rhizanthemum* (Cogn.) Withner (1988: 21) [as *Rhizantha*], *nom. inval.* (missing basionym). *Cattleya* subg. *Rhizanthemum* (Cogn.) Withner (2000: 168).

Cattleya subg. *Laeliodea* Withner (1988: 21). Type species: *Cattleya dormaniana* (Reichenbach 1880: 168) Reichenbach (1882: 216). *Cattleya* sect. *Laelioides* Fowlie (1977: 11), *nom. nud.*

This subgenus has previously been recognized as the “bifoliate cattleyas”. However, at least *C. walkeriana* and most plants of *C. kerrii* Brieger & Bicalho (1976: 61) are unifoliate; in all other characters, these species are typical of the subgenus. Molecular results indicate that this subgenus is not so closely related to sect. *Cattleya*, with which it has been placed for nearly two centuries. Great confusion over subgenera, sections, subsections and series derives from unranked infrageneric names by Barbosa Rodrigues (1882) and partially ranked ones by Cogniaux (1901). Withner (1988) tried to make new combinations for many of these and those of Pfitzer (1889), but he did not cite the correct basionyms, rendering many combinations invalid. Because he provided a Latin diagnosis for each of the names, in some cases (when he used a different epithet) this can be considered as a newly described infrageneric binomial (e.g. *Schomburgkoidea*), but in other cases he used the same epithet as previous authors. In this case if interpreted as a combination, the name is invalid because it lacks the basionym literature reference, and if considered a new description, it would be an illegitimate later homonym according to article 21.1 of the *International code of nomenclature* (McNeill *et al.* 2012). Despite this, Withner (1988) assigned type species for all his names, which can

be interpreted as designation of types for several earlier names. He later corrected some of these errors (Withner 2000). In the case of subg. *Bicolores* Withner (2000: 168) the type indicated (*C. violacea*) is against Article 10.2 of the *Code* because this species was not listed by Pfitzer (1889) among the members of the section. In fact Pfitzer (1889) mentioned only *C. bicolor*, which makes it automatically the type species for the section. To avoid further confusion, we provide types and ranking for all names still lacking them, and types were chosen in a manner to cluster the names as much as possible around fewer type species, considering that they are all synonyms of *C. subg. Intermediae*.

4. *Cattleya* subgenus *Maximae* (Withner) Van den Berg, *stat. nov.*

Basionym: *Cattleya* section *Maximae* Withner (1988: 21). Type species: *Cattleya maxima* Lindley (1833: t. 116).

Cattleya maxima is generally considered a relative of the *C. labiata* complex, but phylogenetic trees based on ITS only (van den Berg *et al.* 2000), embedded it in *C. sect. Crispae*. In contrast, plastid analyses indicated a position as sister group of all remaining species of *Cattleya* (van den Berg *et al.* 2009). Its subcylindrical pseudobulbs are anomalous for *C. subg. Cattleya*, despite having unifoliate leaves. The coastal form of *C. maxima* has tall, cylindrical pseudobulbs that resemble *C. subg. Intermediae*. The flowers have narrower petals and sepals than the *C. labiata* complex and are similar to those of species in *C. ser. Cattleyodes* such as *C. purpurata* (Lindley & Paxton 1852: 111) Van den Berg (2008: 10) or *C. lobata* Lindley (1848: 403) but with 4 pollinia. The mosaic of morphological characters with *C. sect. Cattleya* and *C. ser. Cattleyodes* might suggest a hybrid origin for this species, which might then also explain the highly discordant placement in plastid and nuclear topologies.

New combinations

Cattleya alvarenguensis (Campacci) Van den Berg, *comb. nov.*

Basionym: *Hoffmannseggella alvarenguensis* Campacci (2014: 382)

Cattleya guanhanensis (Campacci) Van den Berg, *comb. nov.*

Basionym: *Hoffmannseggella alvarenguensis* Campacci (2014: 386)

Cattleya vasconcelosiana (Campacci) Van den Berg, *comb. nov.*

Basionym: *Hoffmannseggella alvarenguensis* Campacci (2014: 390)

These new combinations are necessary to complete the checklist in Table 2, with the correct accounting and listing of species within ser. *Parviflorae*.

Acknowledgements

I would like to acknowledge Phillip Cribb and Thiago E.C. Meneguzzo for suggestions to this manuscript and Jefferson Prado for nomenclatural advice. The present work includes financial support of the REFLORA program (CNPq project 563556/2010-2), and the Swiss Orchid Foundation at the Naturhistorisches Museum, Wien. I also thank the curators Andre Schuiteman and Ernst Vitek for access to the collections at K and W, respectively.

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