Chapter 3

TOTAL EVIDENCE PHYLOGENY OF COELOGYNE AND ALLIED GENERA (COELOGYNINAE, EPIDENDROIDEAE, ORCHIDACEAE) BASED ON MORPHOLOGICAL, ANATOMICAL AND MOLECULAR CHARACTERS

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SUMMARY

A phylogenetic analysis of subtribe Coelogyninae (Epidendroideae, Orchidaceae) is performed based on 41 macromorphological and 4 anatomical characters scored from 43 taxa in Coelogyninae (27 *Coelogyne* species and 13 representatives of other genera) and three outgroups from Bletiinae and Thuniinae. The results from this analysis are analysed together with an earlier constructed molecular data set for the same species. All datasets confirm the monophyly of the Coelogyninae. *Coelogyne* appears to be polyphyletic, with species falling in at least two different clades. Key characters for generic and sectional delimitation were mapped on the total evidence tree and a comparison of their states within the various groups in Coelogyninae is used for a discussion of evolutionary polarity. Trichome type, presence of stegmata, inflorescence type, number of flowers per inflorescence, persistence of floral bracts, presence of sterile bracts on the rhachis, ovary indumentum, petal shape, presence and shape of lateral lobes of hypochile, number of keels on the epichile and presence of a fimbriate margin on the epichile appear to be good characters for defining major clades in Coelogyninae. The number of leaves per pseudobulb, size of the flowers, shape of the lip base and petals and presence of stelidia and calli show many reversals. The total evidence phylogeny is compared with traditional classifications of *Coelogyne* and Coelogyninae.

Key words: Orchidaceae, Coelogyninae, *Coelogyne*, phylogeny, morphology, leaf anatomy.

INTRODUCTION

Coelogyne is one of the 16 orchid genera in subtribe Coelogyninae (tribe Coelogyneae, subfamily Epidendroideae) with approximately 200 species occurring from central Asia southward through Malaysia and Indonesia into the Indopacific region (Pedersen et al., 1997). All genera in the subtribe are characterized by a sympodial growth, pseudobulbs of one internode, terminal inflorescences, a winged column and massive caudicles (Dressler, 1981; De Vogel, 1986; Butzin, 1992b). According to a molecular phylogeny based on plastid RFLPs, *matK* and nuclear rDNA ITS sequences, the subtribe is monophyletic (Gravendeel et al., in prep.). The main characters used for generic delimitation in the subtribe are the number of leaves per pseudobulb, number and size of the flowers, shape of the base, lateral lobes and calli of the lip, shape of the petals and sepals, shape of the column and presence of stelidia and stipes (Butzin, 1992b; Pedersen et al., 1997). Many of these characters intergrade among the genera of the subtribe. For example, a lip with small, inconspicuous lateral lobes characterizes both *Chelonistele* Pfitzer and *Panisea* (Lindl.) Steud. (De Vogel, 1986; Lund, 1987). Lateral sepals with a saccate base are present in *Neogyna* Rchb.f. and *Bracisepalum* J.J. Sm. (De Vogel, 1986; Butzin, 1992b).

Coelogyne Lindl. is defined merely by the absence of a saccate lip base, which is present in all other genera of the subtribe (Butzin, 1992a). Lindley subdivided *Coelogyne* into five sections in 1854, when only few species of large and diverse groups were known for comparison. As more and more new species were described, which could not be assigned to one of those sections, Pfitzer & Kraenzlin published an entirely new classification of 14 sections in 1907. Many later authors used this classification, and the same key characters, with minor changes, until De Vogel (1994) and Clayton (in press) came up with 23 sections / subgenera (11 new ones in addition to 12 of the sections of Pfitzer & Kraenzlin). The main characters used for subgeneric and sectional delimitation in *Coelogyne* are the number of leaves per pseudobulb, presence/absence of sterile bracts on the scape and / or rhachis, diameter of the internodes of the rhachis, inflorescence type (either heteranthous, proteranthous, synanthous or hysteranthous and erect or pendulous), simultaneous or successive flowering, presence / absence of hairs on the ovary, flower size and colour, shape of the petals, number and morphology of the keels and presence of a fimbriate margin on the lip (Pfitzer & Kraenzlin, 1907d; De Vogel, 1994; Clayton, in press). Many of these characters intergrade among the species of different sections. For instance, both sect. *Coelogyne* and *Ocellatae* are defined by white flowers with yellow keels.

Until now, there has been no explicit morphological cladistic analysis of *Coelogyne* and the Coelogyninae. We believe that such an analysis would be useful for evaluating previous systems of classification. It provides a concrete, explicit set of character data and codings, in contrast with previous classifications based on informal phenetic comparisons and allows the evaluation of traditionally emphasized characters. Moreover, combined with earlier collected molecular data sets for the Coelogyninae (Gravendeel et al., in prep.) the morphological data of this study are used in a total evidence analysis.

Important arguments against combining data in a total evidence approach are that gene trees can deviate from species trees because of paralogy, lineage sorting, ancestral polymorphisms, long branch attraction or lateral gene transfer (Huelsenbeck et al., 1996), and morphological data can be swamped by DNA sequence data because of the much lower number of characters (Bull et al., 1993). However, we choose to analyse different data sets in a total evidence approach because we believe that historical patterns in different categories of data are strengthened by congruence (Wiens, 1998), starting trees tend to be much closer to the ultimate shortest trees in such analyses (Chase & Cox, 1998), and smaller data sets can have a significant impact on the outcome of analyses, too (De Queiroz et al., 1995).

The aims of the present study are to use phylogenetic analyses of morphological and anatomical data (separately and combined with earlier collected molecular data sets) to

1) discuss trends in character evolution with respect to the key characters used for (sub)generic and sectional delimitation in the Coelogyninae and *Coelogyne* and
2) compare the total evidence phylogeny with traditional classifications.

MATERIALS AND METHODS

Sampling

In total, 43 taxa were analysed. The sampling includes 17 of the 23 sections/subgenera currently recognised within *Coelogyne* and 10 of the 16 genera of Coelogyninae. Morphologically uniform sections/(sub)genera are represented by a single species only, whereas larger, more variable groups are represented by several species. Not included were six small sections of *Coelogyne* (sect. *Ancipites* Pfitzer, *Fuscescentes* Pfitzer & Kraenzl., sect. *Lawrenceanae* Clayton, *Micranthae* Pradhan, *Ocellatae* Pfitzer and *Proliferae* Lindl.) and six mostly monotypic genera (*Bulleya* Schltr., *Dickasonia* L.O. Williams, *Gynoglottis* J.J. Sm., *Ischnogyne* Schltr., *Otochilus* Lindl. and *Panisea* (Lindl.) Steud., which were not available. Outgroups were sampled from tribe Arethuseae, based on the placement of representatives of these subtribes as sister taxa to *Coelogyne* using morphological data (Burns-Balogh & Funk, 1986), *ndhF* (Neyland & Urbatsch, 1996), *rbcL* (Cameron et al., 1999) *nad1* b–c (Freudenstein et al., 2000) and *matK* evidence (Gravendeel et al., in prep.; Chase et al., unpubl.). Voucher specimens are listed in Table 3.1 and deposited at K or L.

Characters

In total, 45 multi-state and binary characters were scored from living and/or preserved specimens. Of these 45 characters, 9 relate to vegetative and 36 to reproductive features. Variation in characters for the taxa examined was scored from at least 5 different collections, whenever no recent taxonomic treatment was available. Leaf anatomical characters were scored from a subset of 20 taxa (see Table 3.2) and from Møller & Rasmussen (1984). Transverse leaf sections were prepared on a sledge microtome and mounted without staining. They were also observed under polarised light, in order to observe crystals. Cuticular macerations were prepared by incubating the samples overnight in a mixture of equal volumes of glacial acetic acid and 30% hydrogen peroxide and staining the remaining cuticles with Sudan IV. The following characters and character states were used.

1. Rhizome: 1 = present; 2 = absent.
2. Pseudobulbs: 1 = present; 2 = absent.
3. Pseudobulbs, lifetime: 1 = less than one year; 2 = more than one year.
4. Pseudobulbs, number of internodes: 1 = one; 2 = more than one.
5. Pseudobulbs, number of leaves: 1 = one; 2 = two or more.
6. Inflorescence, type: 1 = heteranthous; 2 = proteranthous; 3 = synanthous; 4 = hysteranthous.
7. Inflorescence, position: 1 = (sub)erect; 2 = pendulous.
8. Inflorescence, number of flowers: 1 = up to 15; 2 = more than 15.
9. Scape, sterile bracts on base: 1 = present; 2 = absent.
10. Scape, shape in cross section: 1 = laterally flattened; 2 = terete.
11. Rhachis, sterile bracts on base: 1 = present; 2 = absent.
12. Rhachis, sterile bracts on base: 1 = imbricate; 2 = not imbricate.
13. Rhachis, internodes: 1 = extremely swollen; 2 = not swollen.
14. Floral bract: 1 = caducous; 2 = persistent.

15. Flowers: 1 = opening in succession; 2 = opening (almost) simultaneously.
16. Ovary: 1 = glabrous; 2 = hairy.
17. Petals: 1 = linear; 2 = ovate-oblong.
18. Sepals, base: 1 = saccate; 2 = flat.
19. Sepals, indumentum: 1 = glabrous; 2 = hairy.
20. Lateral sepals: 1 = connate; 2 = free.
21. Lip, base: 1 = sigmoid; 2 = flat.
22. Lip, length: 1 = smaller than 10 mm; 2 = between 10 and 30 mm; 3 = larger than 30 mm.
23. Hypochile, base: 1 = rounded; 2 = saccate; 3 = spurred.
24. Hypochile, lateral lobes size: 1 = narrow; 2 = broad; 3 = absent.
25. Hypochile, lateral lobes: 1 = continuing towards the base; 2 = not continuing towards the base.
26. Hypochile, lateral lobes position: 1 = erect; 2 = spreading.
27. Hypochile, keels number: 1 = 0; 2 = 2–3; 3 = more than 3.
28. Hypochile, keels shape: 1 = decurrent plate-like projections with undulating crest; 2 = more or less fused irregular rounded warts; 3 = elongate plate-like projections with glabrous apices; 4 = decurrent plate-like projections with fimbriate margin; 5 = elongate plate-like projections with stellately arranged hairs at the apices.
29. Hypochile, callus: 1 = present; 2 = absent.
30. Epichile, lateral lobes: 1 = absent; 2 = present.
31. Epichile, lateral lobes shape: 1 = semi-orbicular, widely retuse; 3 = not orbicular, only slightly retuse.
32. Epichile, number of keels: 1 = 0–3; 2 = more than 3.
33. Epichile, apex margin: 1 = fimbriate; 2 = glabrous.
34. Column, length: 1 = short; 2 = long.
35. Column, connected to lip: 1 = up to middle; 2 = only at the base.
36. Column, stelidia: 1 = present; 2 = absent.
37. Column, wing: 1 = present over total length; 2 = present only at the apex.
38. Column, apex: 1 = with small wings; 2 = with large wings.
39. Pollinia, number: 1 = 4; 2 = 8.
40. Stipes: 1 = present; 2 = absent.
41. Pollinia, caudicle: 1 = large; 2 = small.
42. Trichomes on leaf surface: 1 = elongate, with acute top; 2 = short, with broadly rounded top; 3 = short, with acute top.
43. Stomata: 1 = subsidiary cells not clearly different from unspecialised epidermal cells; 2 = subsidiary cells different from unspecialised epidermal cells, but not largely submerged below guard cells; 3 = subsidiary cells different from unspecialised epidermal cells and almost fully submerged below guard cells.
44. Epidermal crystals: 1 = present; 2 = absent.
45. Stegmata in sclerenchymatous tissues: 1 = present; 2 = absent.

Some of the character codings need justification. These cases are briefly discussed below.

Table 3.1. List of species analysed. Arranged by (sub)tribe, (sub)genus and section according to Dressler (1990), Butzin (1992), De Vogel (1994) and Clayton (in press).

Tribe	Subtribe	Genus and species	Section / subgenus	Geographic origin	Voucher
Arethuseae	Bletiinae	*Arundina graminifolia* (D. Don) Hochr.		unknown	*Chase 395* (K)
Arethuseae	Bletiinae	*Bletia purpurea* (Lam.) DC		Mexico	*Chase 581* (K)
Arethuseae	Thuniinae	*Thunia alba* (Lindl.) Rchb.f.		Nepal	*Chase 589* (K)
Coelogyneae	Coelogyninae	*Bracisepalum selebicum* J.J. Sm.		Sulawesi	*Leiden cult. 20446* (L)
		Chelonistele amplissima Ames & C. Schweinf.		Brunei	*Leiden cult. 26834* (L)
		Chelonistele sulphurea (Blume) Pfitzer		unknown	*Leiden cult. 21528* (L)
		Dendrochilum glumaceum Lindl.		unknown	*Leiden cult. 950648* (L)
		Dendrochilum longifolium Rchb.f.		PNG	*Leiden cult. 32110* (L)
		Entomophobia kinabaluensis (Ames) de Vogel		Sarawak	*Leiden cult. 970404* (L)
		Geesinkorchis phaiostele (Ridl.) de Vogel		Borneo	*Leiden cult. 30700* (L)
		Nabaluia angustifolia de Vogel		Sabah	*Leiden cult. 26217* (L)
		Neogyna gardneriana (Lindl.) Rchb.f.		unknown	*Leiden cult. 970729* (L)
		Pholidota carnea (Blume) Lindl.		Sumatra	*Leiden cult. 25469* (L)
		Pholidota imbricata Hook.		unknown	*Leiden cult. 21540* (L)
		Pleione bulbocodioides (Franch.) Rolfe		unknown	*Leiden cult. 990010* (L)
		Pleione formosana Hayata		unknown	*Leiden cult. 91051* (L)
		Coelogyne bicamerata J.J. Sm.	*Bicellae*	Sulawesi	*Leiden cult. 931067* (L)
		Coelogyne virescens Rolfe	*Brachypterae*	unkown	*Clayton cult. s.n.* (L)
		Coelogyne cristata Lindl.	*Coelogyne*	unknown	*Leiden cult. 2214* (L)
		Coelogyne foerstermannii Rchb.f.	*Coelogyne*	Sarawak	*Leiden cult. 970591*(L)
		Coelogyne sanderiana Rchb.f.	*Coelogyne*	unknown	*Leiden cult. 30765* (L)
		Coelogyne multiflora Schltr.	*Cyathogyne*	Sulawesi	*Leiden cult. 21747* (L)
		Coelogyne barbata Lindl. ex Griff.	*Elatae*	India	*Leiden cult. 990040* (L)
		Coelogyne stricta (D.Don) Schltr.	*Elatae*	unknown	*Leiden cult. 30695* (L)
		Coelogyne flaccida Lindl.	*Flaccidae*	unknown	*Leiden cult. 940707* (L)
		Coelogyne trinervis Lindl.	*Flaccidae*	unknown	*Leiden cult. 26940* (L)
		Coelogyne fimbriata Lindl.	*Fuliginosae*	unknown	*Leiden cult. 30759* (L)
		Coelogyne miniata (Blume) Lindl.	*Hologyne*	Java	*Leiden cult. 990287*(L)
		Coelogyne chloroptera Rchb.f.	*Lentiginosae*	Philippines	*Leiden cult. 23511* (L)
		Coelogyne bilamellata Lindl.	*Longifoliae*	Philippines	*Leiden cult. 25164* (L)
		Coelogyne cuprea H. Wendl. & Kraenzl.	*Longifoliae*	Brunei	*Leiden cult. 914768* (L)
		Coelogyne harana J.J. Sm.	*Moniliformes*	Kalimantan	*Leiden cult. 970290* (L)
		Coelogyne kelamensis J.J. Sm.	*Moniliformes*	Kalimantan	*Leiden cult. 930568* (L)
		Coelogyne flexuosa Rolfe	*Ptychogyne*	unknown	*Leiden cult. 19937* (L)
		Coelogyne plicatissima Ames & C. Schweinf.	*Rigidiformes*	Sarawak	*Leiden cult. 980409* (L)
		Coelogyne beccarii Rchb.f.	*Speciosae*	PNG	*Leiden cult. 32230* (L)
		Coelogyne macdonaldii F. Muell. & Kraenzl.	*Speciosae*	Vanuatu	*Leiden cult. 25836* (L)
		Coelogyne dayana Rchb.f.	*Tomentosae*	unknown	*Leiden cult. 20247* (L)
		Coelogyne rhabdobulbon Schltr.	*Tomentosae*	Sabah	*Leiden cult. 26597* (L)
		Coelogyne velutina de Vogel	*Tomentosae*	Peninsular Malaysia	*Leiden cult. 25835* (L)
		Coelogyne veitchii Rolfe	*Veitchiae*	PNG	*Leiden cult. 22277* (L)
		Coelogyne asperata Lindl.	*Verrucosae*	PNG	*Leiden cult. 22279* (L)
		Coelogyne pandurata Lindl.	*Verrucosae*	unknown	*Leiden cult. 21532* (L)

Macromorphology

Pseudobulbs — One- or two-leaved pseudobulbs, consisting of one internode and living more than one growth season, are present in all taxa of Coelogyninae examined, except for *Pleione*, which has short-living pseudobulbs. In many of the taxa studied, a considerable amount of intraspecific variation is present in the shape of the pseudobulbs, which is why we did not use this character.

Leaves — The texture of dried leaves varies considerably within subtribe Coelogyninae and the genus *Coelogyne* from thin-papery to decidedly leathery. This is also the case for the shape of the leaves (varying from narrowly linear to oblong) and the number of main veins (varying from one up to nine). All these characters could not be divided unambiguously into discrete, non-overlapping states as recommended by Pimentel & Riggins (1987), and were therefore omitted.

Inflorescence — Four types of inflorescences are recognized. In heteranthous inflorescences, the vegetative shoot, from which the inflorescence sprouts, never develops leaves, and the terminal internodes never enlarge into a pseudobulb. The older inflorescences seem lateral on the rhizome. In hysteranthous inflorescences, the inflorescence develops on top of a full-grown pseudobulb with fully developed leaves. In proteranthous inflorescences, the leaf from the immature pseudobulb at the base is still hidden in the scales of the inflorescence-bearing young shoot during anthesis. In synanthous inflorescences, the inflorescence-bearing shoot has an immature pseudobulb hidden in the basal scales and the young leaf or leaves on top of this pseudobulb are partly hidden and partly extending from the scales (De Vogel, 1988; Pedersen et al., 1997). The position of the inflorescence is coded as erect when the rhachis is (almost) vertical. This was the case for most species examined. When the rhachis is distinctly curved, this is coded as pendulous. A scatter plot of flower number per inflorescence for all taxa examined for this study is shown in Fig. 3.1. The gap present in the number of flowers is considered to be distinct enough to recognize the following states in this character: flower number < 15 and flower number >15. In many of the species examined, several imbricate or isolated sterile bracts were present on the base of the rhachis. These bracts are identical with the floral bracts in shape and size, but do not accompany a flower. They are not considered to be homologous with the sterile bracts at the base of the scape in this study. Floral bracts are coded as deciduous when they fall off just after anthesis and persistent when they are still attached to the rhachis after the flower or fruit has fallen off. In inflorescences with a large number of flowers, flowers are considered to be opening simultaneously, when all flowers are expanded before the first start to wither.

Flower colour — Considerable variation in flower colour is found both at intra- and interspecific level, which is why we did not use this character, although it is used as key character for sectional delimitation within *Coelogyne*.

Flower indumentum — Small brown, black or whitish hairs are present on the ovary and lateral sepals of several of the taxa studied. The size, shape and density of hairs varies considerably. All types of indumentum are considered homologous here, which might not be justified, because their microscopic structure was not studied.

Table 3.2. Data matrix of macromorphological and anatomical characters scored. Polymorphisms are indicated by all states possible and inapplicable or unknown characters by a question mark.

character **species**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**
Arundina graminifolia	2	2	2	?	?	3	1	1	2	2	1	2	2	2	1	1	2	2	1	2	2	3	1	2	1	1	2	1	2	2	2	1	2	2	2	2	2	1	2	2	2	?	?	?	?
Bletia purpurea	2	1	2	2	2	1	1	1	1	2	1	2	2	2	1	1	2	2	1	2	2	2	1	2	1	1	3	1	2	1	2	2	2	2	2	2	2	1	2	2	2	?	?	?	?
Thunia alba	2	2	2	?	?	3	2	1	2	2	1	2	2	2	2	1	2	2	1	2	2	2	3	3	1	1	3	4	2	1	2	2	2	1	2	2	2	1	2	2	2	?	?	?	?
Bracisepalum selebicum	1	1	2	1	1	3	2	2	2	2	1	1	2	2	2	2	2	1	2	1	2	2	2	1	1	1	1	?	2	2	2	1	2	2	2	2	1	1	1	2	1	2	1	1	?
Chelonistele amplissima	1	1	2	1	1	2/3	1	2	2	2	2	?	2	1	2	2	1	2	2	2	2	2	2	1	2	2	2	1	2	2	2	1	2	1	2	2	1	2	1	2	1	?	?	?	?
Chelonistele sulphurea	1	1	2	1	1	2/3	1	2	2	2	2	?	2	1	2	2	1	2	2	2	2	1	2	1	2	2	2	1	2	2	2	1	2	1	2	2	1	2	1	2	1	2	1	1	?
Dendrochilum glumaceum	1	1	2	1	1	3	2	2	2	2	1	1	2	2	2	2	2	2	2	2	1	1	2	1	2	2	2	1	2	2	2	1	2	1	2	1	1	1	1	2	1	?	?	?	?
Dendrochilum longifolium	1	1	2	1	3	2	2	2	2	1	1	2	2	2	2	2	2	2	2	1	1	2	1	2	2	2	1	2	2	2	1	2	1	2	1	1	1	1	1	2	1	2	1	2	1
Entomophobia kinabaluensis	1	1	2	1	2	2/3	1	1/2	2	2	2	?	2	2	2	2	2	2	2	2	2	1	2	1	1	1	1	?	1	1	2	1	2	1	2	1	1	1	1	2	1	2	1	2	?
Geesinkorchis phaiostele	1	1	2	1	2	2	1	2	2	2	2	?	2	1	1	1	1	2	2	2	2	1	2	1	2	2	2	1	2	2	2	1	2	1	2	2	1	1	1	1	?	2	1	2	?
Nabaluia angustifolia	1	1	2	1	2	3	1	1/2	2	2	2	?	2	1	2	2	1	2	2	2	2	1	2	1	1	2	1	?	1	2	2	1	2	2	2	2	1	1	1	2	1	2	1	1	?
Neogyna gardneriana	1	1	2	1	2	4	1	1	2	2	2	?	2	2	1	1	1	1	1	2	2	3	2	2	1	1	2	1	2	2	1	1	2	2	2	2	1	1	1	2	1	2	1	1	1
Pholidota carnea	1	1	2	1	2	2/3	1	2	2	2	2	?	2	1	2	1	2	2	1	2	2	1	2	2	2	1	2	1	2	1	2	1	2	1	2	1	1	1	1	2	1	?	?	?	?
Pholidota imbricata	1	1	2	1	1	3	2	2	2	2	1	1	2	2	2	1	2	2	1	2	2	1	2	2	1	1	2	1	2	2	1	1	2	1	2	2	1	1	1	2	1	3	1	2	1
Pleione bulbocodioides	2	1	1	1	1	3	1	1	2	2	2	?	2	2	1	1	2	2	1	2	2	3	2	3	1	1	3	4	2	1	2	1	1	2	2	2	1	1	1	2	1	?	?	?	?
Pleione formosana	2	1	1	1	1	3	1	1	2	2	2	?	2	2	1	1	2	2	1	2	2	3	2	3	1	1	3	4	2	2	2	1	1	2	2	2	1	1	1	2	1	1	2	2	2
Coelogyne fimbriata	1	1	2	1	2	4	1	1	1	2	2	?	2	1	1	1	1	2	1	2	2	2/3	1	2	1	1	2	1	2	2	2	1	1	2	2	2	1	1	1	2	1	2	1	2	1
Coelogyne flexuosa	1	1	2	1	2	4	1	1	2	2	1	2	2	1	2	1	1	2	1	2	1	2	1	2	2	1	2	1	2	2	2	1	2	1	2	2	1	1	1	2	1	2	1	1	?
Coelogyne bilamellata	1	1	2	1	2	4	1	2	1	2	?	2	1	1	1	1	2	1	2	1	1	1	2	2	1	2	1	1	2	2	1	2	2	2	2	1	1	1	1	2	1	?	?	?	?
Coelogyne cuprea	1	1	2	1	2	4	1	1/2	2	1	2	?	2	1	1	1	1	2	1	2	1	2	1	2	1	1	2	1	2	2	2	1	2	2	2	2	1	1	1	2	1	?	?	?	?
Coelogyne harana	1	1	2	1	1	3	1	2	2	2	2	?	1	1	1	1	1	2	1	2	2	2	1	2	1	1	2	1	2	1	2	1	2	2	2	2	1	1	1	2	1	?	?	?	?
Coelogyne kelamensis	1	1	2	1	1	3	2	1	2	2	2	?	1	1	1	1	1	2	1	2	1	2	1	2	2	1	2	1	2	1	2	1	2	2	2	2	1	1	1	2	1	?	?	?	?
Coelogyne beccarii	1	1	2	1	2	3	1	1	2	2	2	?	2	1	1	1	1	2	1	2	2	3	1	2	1	1	3	2	2	2	2	2	2	2	2	2	1	1	1	2	1	2	1	2	?
Coelogyne macdonaldii	1	1	2	1	2	3	1	1	2	2	2	?	2	2	2	1	1	2	1	2	2	3	1	2	1	1	3	2	2	2	2	2	2	2	2	2	1	1	1	2	1	2	1	2	?
Coelogyne dayana	1	1	2	1	2	2/3	2	2	2	2	1	1	2	2	2	2	2	2	2	2	2	2/3	1	2	1	1	2	3	2	2	2	2	2	2	2	2	1	1	1	2	1	1	1	1	1
Coelogyne rhabdobulbon	1	1	2	1	2	3	2	2	2	2	1	1	2	2	2	2	2	2	2	2	2	2	1	2	1	1	3	1	2	2	2	2	2	2	2	2	1	1	1	2	1	1	1	1	?
Coelogyne velutina	1	1	2	1	2	1	2	1/2	2	2	1	1	2	2	2	2	2	2	1	2	2	2	1	2	1	1	2	4	2	2	2	2	2	2	2	2	1	1	1	2	1	1	1	2	?
Coelogyne pandurata	1	1	2	1	2	2/3	1	2	2	2	1	1	2	2	2	2	2	2	2	2	2	3	1	2	1	1	2	1	2	2	2	2	2	2	2	2	1	1	1	2	1	1	1	1	1
Coelogyne asperata	1	1	2	1	2	2/3	1	1/2	2	2	1	1	2	2	2	2	2	2	2	2	2	3	1	2	1	1	2	1	2	2	2	2	2	2	2	2	1	1	1	2	1	?	?	?	?
Coelogyne barbata	1	1	2	1	2	4	1	1	2	2	1	1	2	1	2	1	1	2	1	2	2	3	1	2	1	1	2	5	2	2	2	1	1	2	2	2	1	1	1	2	1	?	?	?	?
Coelogyne bicamerata	1	1	2	1	2	3	1	1	2	2	2	?	2	1	1	1	2	1	1	2	2	2	2	2	1	1	3	1	2	2	2	2	2	2	1	2	1	1	1	2	1	?	?	?	?
Coelogyne stricta	1	1	2	1	2	4	1	1	1	2	1	1	2	1	2	1	1	2	1	2	2	2	1	2	1	1	2	3	2	2	2	1	2	2	2	2	1	1	1	2	1	?	?	?	?
Coelogyne multiflora	1	1	2	1	2	3	1	2	2	2	1	1	2	2	2	2	2	2	2	2	1	2	1	2	2	1	2	3	2	2	2	3	2	1	2	2	1	1	1	2	1	1	1	1	?
Coelogyne plicatissima	1	1	2	1	1	1	1	1	2	2	1	2	2	2	2	2	2	2	1	2	2	2	1	2	1	1	2	1	2	2	2	1	2	2	2	2	1	1	1	2	1	?	?	?	?
Coelogyne veitchii	1	1	2	1	2	1	2	2	2	2	1	1	2	2	2	2	2	2	2	2	1	2	1	2	1	1	2	1	2	2	2	1	2	2	2	2	1	1	1	2	1	?	?	?	?
Coelogyne chloroptera	1	1	2	1	2	2/3	1	1	2	2	2	?	2	2	2	1	1	2	1	2	2	2	1	2	1	1	2	1	2	2	2	2	2	2	2	2	1	1	1	2	1	?	?	?	?
Coelogyne miniata	1	1	2	1	2	2/3	1	1	2	2	2	?	2	1	2	1	1	2	1	2	2	1/2	1	2	1	1	2	1	2	2	2	1	2	2	2	2	1	1	1	2	1	2	2	2	1
Coelogyne virescens	1	1	2	1	2	4	1	1	1	2	2	?	2	2	2	1	1	2	1	2	2	2	1	2	1	1	3	1	2	2	2	1	2	2	2	2	1	1	1	2	1	?	?	?	?
Coelogyne flaccida	1	1	2	1	2	1	2	1	2	2	2	?	2	1	2	1	1	2	1	2	2	2	1	2	1	1	2	1	2	2	2	1	2	2	2	2	1	1	1	2	1	2	3	2	?
Coelogyne trinervis	1	1	2	1	2	2/4	1	1	2	2	2	?	2	1	2	1	1	2	1	2	2	2	1	2	1	1	2	1	2	2	2	2	2	2	2	2	1	1	1	2	1	?	?	?	?
Coelogyne foerstermannii	1	1	2	1	2	1	1	2	2	2	1	1	2	2	2	2	2	2	1	2	2	2/3	1	2	1	1	2	4	2	2	2	2	2	2	2	2	1	1	1	2	1	?	?	?	?
Coelogyne sanderiana	1	1	2	1	2	4	1	2	2	2	1	1	2	1	2	2	2	2	1	2	2	3	1	2	1	1	3	4	2	2	2	2	2	2	2	2	1	1	1	2	1	?	?	?	?
Coelogyne cristata	1	1	2	1	2	1	1	1	2	2	2	?	2	2	2	1	2	2	1	2	2	3	1	2	1	1	3	4	2	2	2	1	2	2	2	2	1	1	1	2	1	1	1	1	1

Petals and sepals — Petals are coded as linear when they are more than ten times longer than wide, otherwise they are coded as ovate-oblong.

Lip — Morphology of the lip is very diverse within Coelogyninae and *Coelogyne*. The base of the hypochile can be spurred (*Thunia*), saccate (all genera of Coelogyninae except for *Coelogyne*) or rounded (*Coelogyne*). In *Bracisepalum* the base of the hypochile has two sac-like extensions, which might not be homologous with the saccate hypochile base of other Coelogyninae. If a saccate hypochile base is present, this is coded as one character state, although the above mentioned differences might be an indication that this approach is not justified. In addition, a sigmoid curve is present at the base of the hypochile in *Dendrochilum* and several *Coelogyne* species. A sigmoid and/or saccate hypochile base are assumed to be independent of each other here. A scatter plot of lip size for all taxa examined for this study is shown in Fig. 3.2. The variation in lip size appears to be more or less continuous. However, flower size is a very important key character for sectional delimitation within *Coelogyne*. Therefore the following (rather artificially defined) states in this character were used: flowers small (lip length <10mm), flowers of intermediate size (lip length 10–30 mm) and flowers large (lip length >30mm). The lateral lobes of the hypochile and epichile are considered to be absent when no clear distinction can be made with the blade and small when they are present on less than a quarter of the total lip length.

Column — The column is coded as short when it does not cover more than half of the total lip length. Most taxa examined have an unbranched column, but in the species of *Dendrochilum* and *Entomophobia* studied and *Pholidota carnea* it is provided with two lateral stelidia. The stelidia are of various shape, and they are positioned on the middle (*Dendrochilum*) or apex of the column (*Entomophobia* and *Pholidota*). If stelidia are present, they are considered to be homologous, although the differences mentioned above might be an indication that this approach is not justified. The anther of all Coelogyninae studied contains four pollinia, which are elliptical to orbicular in shape and have caudicles, consisting of sterile pollen. Small differences in pollinium shape were found between the taxa studied, but it turned out to be too difficult to define discrete character states due to the often vague limit between pollinium and caudicle and we did not use this character. A stipes is present in *Geesinkorchis* only. Both the rostellum and stigma show considerable variation in size and shape, also within a single species, and were not used.

Fruit — Variation in fruit shape appeared to be rather uniform for the taxa examined, and we did not use this character. The morphology of the seeds is largely unknown.

Vegetative anatomy

Leaves (surface) — Three types of trichomes are present on the leaf surface in Coelogyninae: elongate trichomes with a small base and acute top, short trichomes with a broad base and broadly rounded top, and short trichomes with a broad base and acute top (see Plate 3.1). Rosinski (1992) found a strong correlation between size of the trichome basal cells and light and temperature conditions of the habitat in Coelogyninae, that is why we did not use the size of the trichome lumen cells, but only their gross morphology.

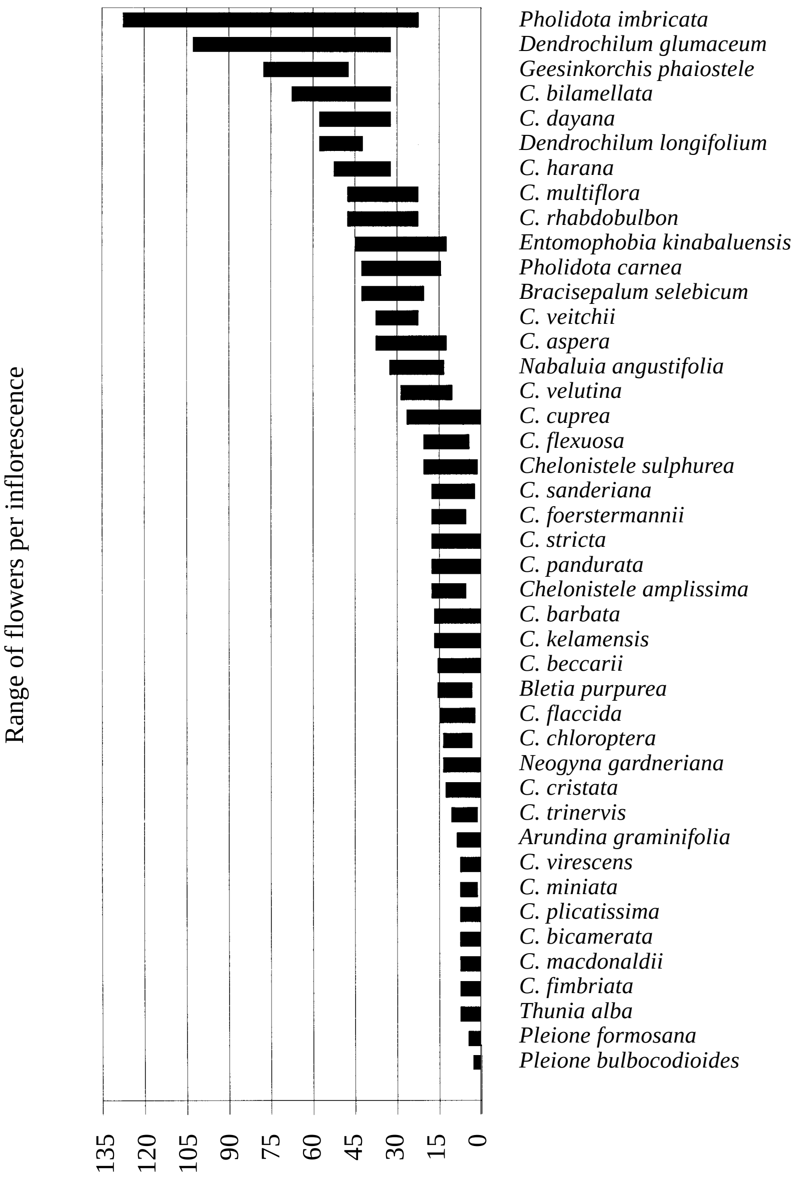


Fig. 3.1. Range of number of flowers per inflorescence for taxa studied.

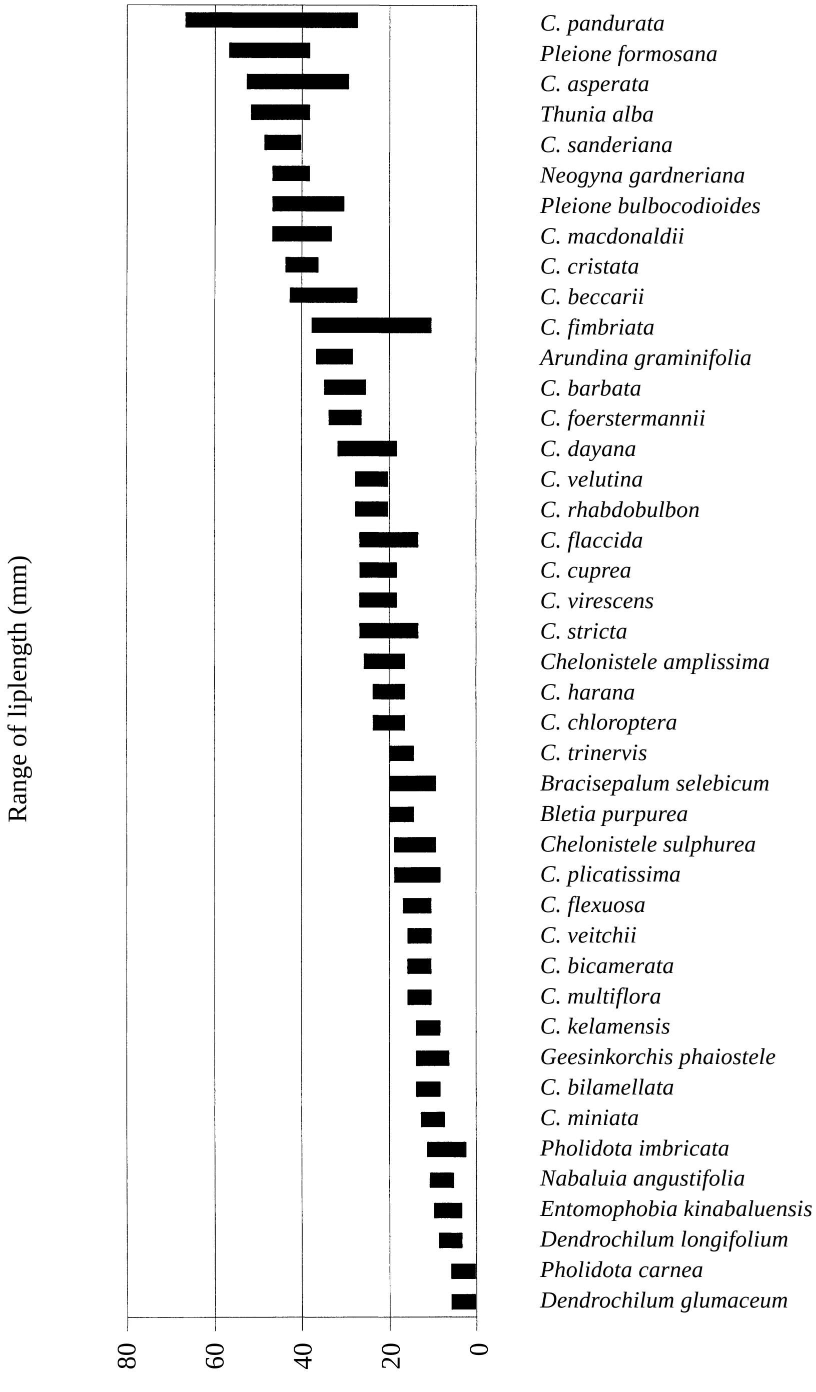


Fig. 3.2. Range of lip length (mm) for taxa studied.

Leaves (cuticle) — The size and shape of the guard cells of the stomata and the presence of a ridge around the stomata on the abaxial surface are all strongly correlated with habitat conditions in Coelogyninae according to Rosinski (1992), which is why we did not use these characters. The stomata are tetracytic (rarely with 5 or 6 subsidiary cells) (Zörnig, 1903; Solereder & Meyer, 1930; see Plate 3.1). Within Coelogyninae, the shape of the stegmata is rather uniform, only conical silica bodies, with a flat, extended base on the side of the cell adjacent to the sclerenchyma, are present (Møller & Rasmussen, 1984; Pridgeon, 1999), which is why we only coded presence/absence of this character.

Leaves (petiole) — In most of the taxa studied, a sclerenchyma sheath is completely surrounding the vascular bundles. In a few taxa, the sclerenchyma sheath appears to occur on the phloem sides only, but differences seem to be too gradual for a good delimitation of character states.

Phylogenetic analyses

Maximum parsimony (MP) analysis was performed on the morphological and molecular data with PAUP* version 4.0b64 (Swofford, 1999) using heuristic search, random addition with ten replicates and TBR swapping. *Arundina graminifolia, Bletia purpurea* and *Thunia alba* were specified as outgroups in all analyses. All multistate characters were assessed as independent, unordered and equally weighted using Fitch parsimony (Fitch, 1971). Indels were coded as missing data only. The relative robustness for clades found in each parsimony analysis was assessed by performing 1000 replicates of bootstrapping (Felsenstein, 1995), using simple stepwise additions, SPR swapping, MULTREES on, and holding only 10 trees per replicate.

RESULTS

Morphological analysis

In total, 45 characters were used, of which 41 are macromorphological and four anatomical. Of these characters, 44 are variable and 38 phylogenetically informative. The MP analysis yielded 198 most parsimonious trees (length = 166, CI = 0.34, RI = 0.64). The bootstrap consensus topology and the corresponding branch supports are indicated in Fig. 3.3.

The morphological and anatomical bootstrap consensus tree strongly supports the monophyly of the Coelogyninae (92%). Other strongly supported clades unite both *Dendrochilum* (91%) and both *Pleione* species (100%).

Molecular analysis

In total, 2722 characters were used, of which 23 are based on plastid RFLP data, 759 on ITS sequences and 1940 on *matK* sequences. Of these characters, 731 are variable and 363 phylogenetically informative. The MP analysis yielded five most parsimonious trees (length = 1840; CI = 0.59; RI = 0.56). The bootstrap consensus topology and the corresponding branch supports are indicated in Fig. 3.4.

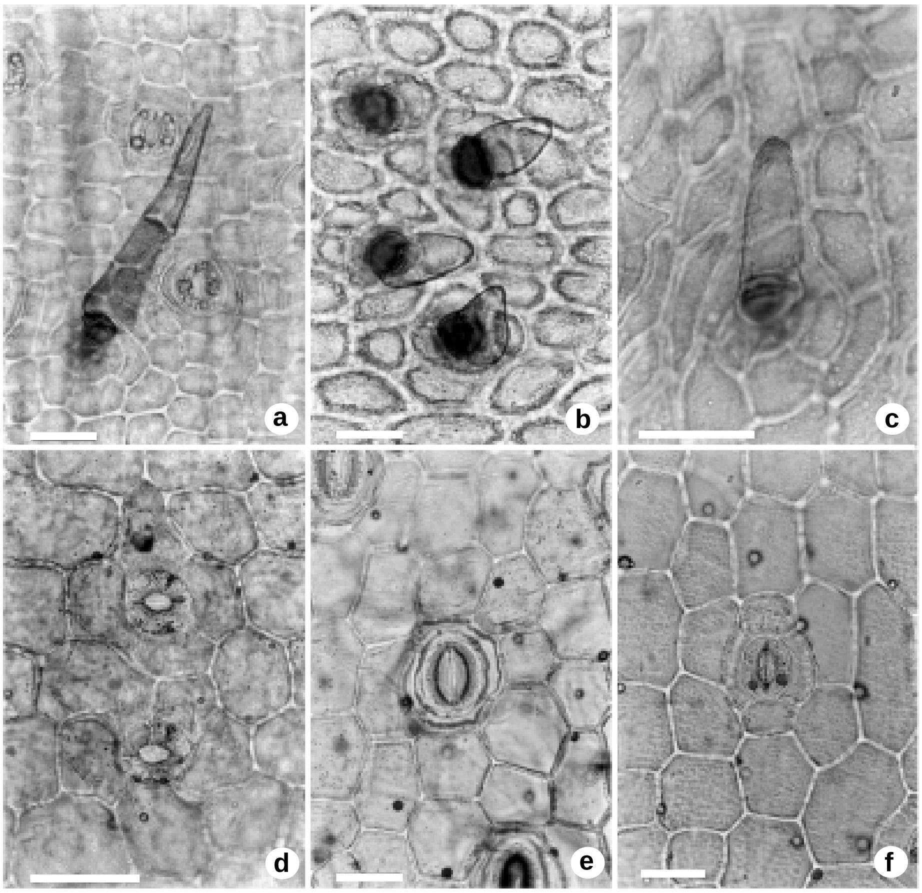


Plate 3.1. Leaf anatomical characters. – a. Elongate trichome with narrow base and acute top. *Coelogyne multiflora* Schltr. [*Leiden cult. 215747*]. – b. Short trichome with broad base and acute top. *Pholidota imbricata* Hook. [*Leiden cult. 21540*]. – c. Short trichome with broad base and broadly rounded top. *Coelogyne carinata* Rolfe. [*Leiden cult. (De Vogel) 30714*]. – d. Stomata with subsidiary cells not clearly different from unspecialised epidermal cells. *Coelogyne miniata* (Blume) Lindl. [*Leiden cult. 940710*]. – e. Stomata with subsidiary cells clearly different from unspecialised epidermal cells and almost fully submerged below guard cells. *Coelogyne flaccida* Lindl. [*Leiden cult. 940707*]. – f. Stomata with subsidiary cells clearly different from unspecialised epidermal cells. *Coelogyne speciosa* (Blume) Lindl. [*Leiden cult. 19930*]. – Scale bars: 50 µm.

The molecular bootstrap consensus tree strongly supports the monophyly of the Coelogyninae (97%). Other strongly supported clades unite both *Pleione* species (100%), all Coelogyninae except for *Pleione* (94%), *Dendrochilum* with *Bracisepalum* (100%), *Chelonistele sulphurea* and *Entomophobia kinabaluensis* (100%), *Coelogyne* sect. *Moniliformes* (100%), sect. *Moniliformes* plus *Speciosae* (91%), sect. *Tomentosae* (95%), sect. *Verrucosae* (100%), and *C. fimbriata* plus *C. stricta* (98%).

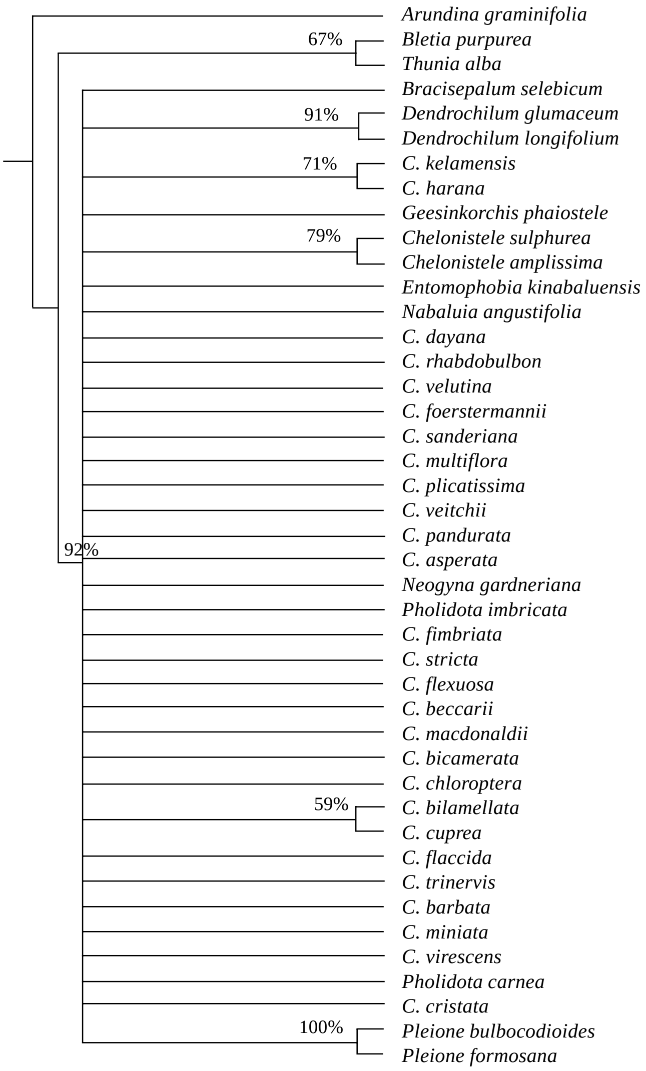


Fig. 3.3. Bootstrap consensus of 198 trees from parsimony analysis of macromorphological and anatomical data with bootstrap percentages (only percentages >50% are given).

Total evidence analysis

MP analysis yielded two most parsimonious trees (length = 2046, CI = 0.56, RI = 0.56). The two MPTs differ only in the position of both *Dendrochilum* species (in the first MPT *D. glumaceum* is sister to *Bracisepalum selebicum*, in the second MPT this is *D. longifolium*). The first MPT with corresponding branch supports is indicated in Fig. 3.5.

The total evidence tree strongly supports the monophyly of the Coelogyninae (97%). Other strongly supported clades unite both *Pleione* species (clade III in Coelogyninae) (100%), clade I and II together in Coelogyninae (93%), clade I in Coelogyninae (85%), *Dendrochilum* with *Bracisepalum* (100%), *Chelonistele sulphurea* and *Entomophobia kinabaluensis* (100%), *Coelogyne* sect. *Tomentosae* and sect. *Verrucosae* (both 100%), clade II in Coelogyninae (81%), *C. fimbriata* plus *C. stricta* (97%), *Coelogyne* sect. *Longifoliae* (92%), sect. *Moniliformes* (100%) and sect. *Moniliformes* plus *Speciosae* (83%).

DISCUSSION

The consistency index of the morphological analysis of 0.34 represents a high level of homoplasy and may be caused by the use of characters with continuous states (characters 8 and 22), polymorphic states (characters 6, 8 and 22) and many missing data (characters 42 till 45). Moreover, resolution and nodal support as defined by the number of synapomorphies is low (see Fig. 3.3 and 3.5), which may be caused by the low ratio of terminal taxa (43) to characters (45). Many recent studies have indicated that phylogenetic resolution and bootstrap percentages are improved by directly combining different data sets (De Queiroz et al., 1995; Chase & Cox, 1998; Wiens, 1998). The high level of congruence among the morphological and molecular data sets and the lower number of MPTs and higher resolution in the combined analysis strengthen the confidence in the combined tree as a good hypothesis of phylogenetic relationships of *Coelogyne* and the Coelogyninae.

Character development

Morphological characters are identified which support each monophyletic group in the total evidence tree. Also, transformation series for certain characters are reconstructed. All morphological autapomorphies and synapomorphies are depicted in Fig. 3.5.

Characters supporting subtribe Coelogyninae

Bootstrap support for the monophyly of the subtribe in the total evidence phylogeny is high (97%) and synapomorphies include the presence of pseudobulbs of one internode, a completely winged column, four pollinia and a large caudicle.

Characters supporting major clades in Coelogyninae

Characters that support clade I in Coelogyninae are the more than 15 flowers per inflorescence, presence of sterile bracts on the rhachis (with reversals in *Chelonistele*, *Entomophobia*, *Geesinkorchis* and *Nabaluia*) and presence of hairs on the ovary (with a reversal in *Geesinkorchis*). Characters, which are present in the majority of taxa in clade I are the presence of elongate trichomes with acute top on the leaf surface, synanthous inflorescences, presence of sterile bracts at the base of the rhachis, simultaneously opening flowers, persistent floral bracts, ovate-oblong petals, and hairy sepals.

The second major clade in Coelogyninae (*Coelogyne* s.s. group) is supported by caducous floral bracts (with the exception of *Neogyna*, *Pholidota*, *C. chloroptera*, *C. cristata*, *C. macdonaldii* and *C. virescens*), glabrous ovaries, linear petals (with the

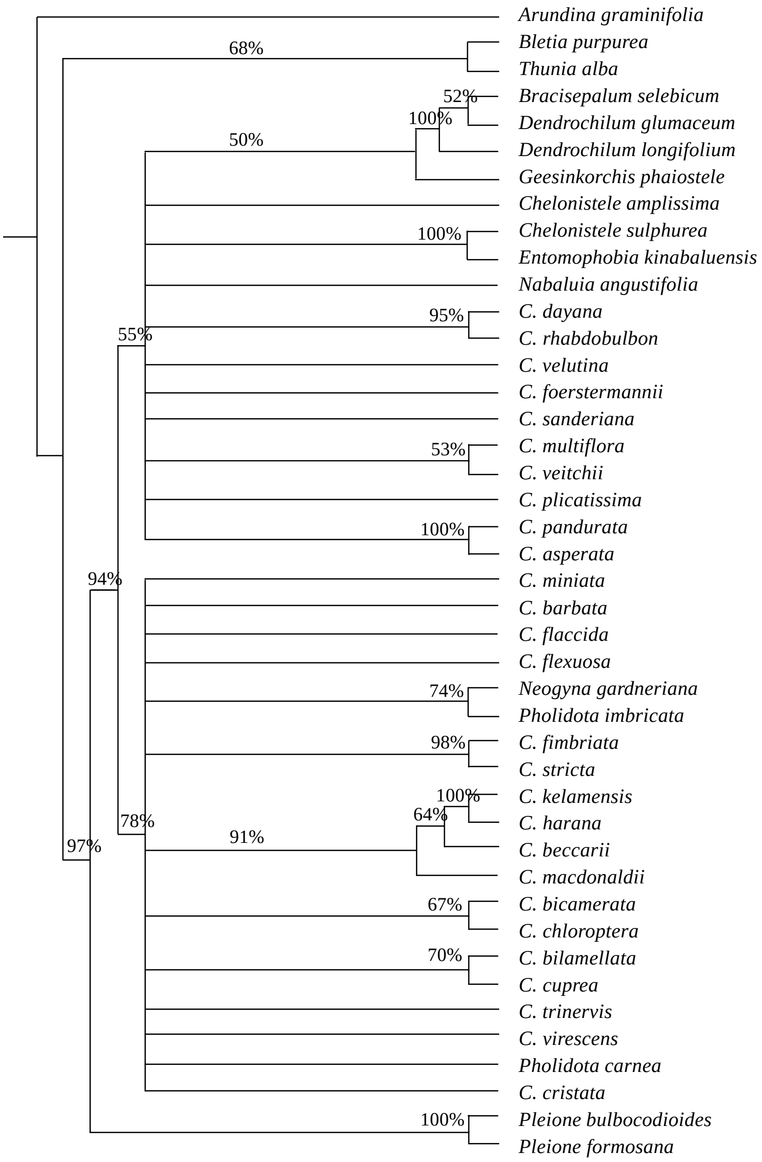
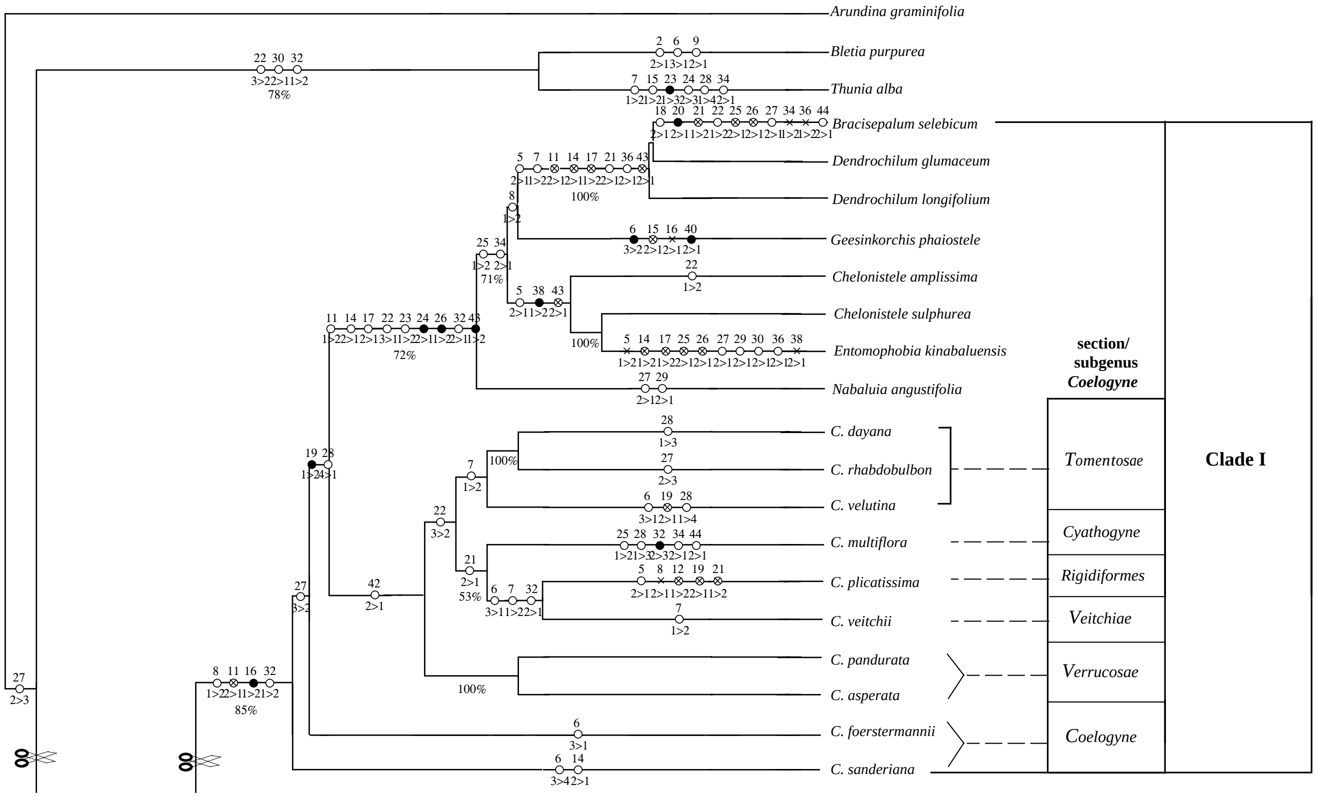


Fig. 3.4. Bootstrap consensus of five trees from parsimony analysis of combined molecular data with bootstrap percentages (only percentages > 50% are given).


Arundina graminifolia
Bletia purpurea
Thunia alba
Bracisepalum selebicum
Dendrochilum glumaceum
Dendrochilum longifolium
Geesinkorchis phaiostele
Chelonistele amplissima
Chelonistele sulphurea
Entomophobia kinabaluensis
Nabaluia angustifolia
C. dayana
C. rhabdobulbon
C. velutina
C. multiflora
C. plicatissima
C. veitchii
C. pandurata
C. asperata
C. foerstermannii
C. sanderiana
section/ subgenus Coelogyne
Tomentosae
Cyathogyne
Rigidiformes
Veitchiae
Verrucosae
Coelogyne
Clade I
78%
100%
71%
72%
100%
100%
53%
100%
85%

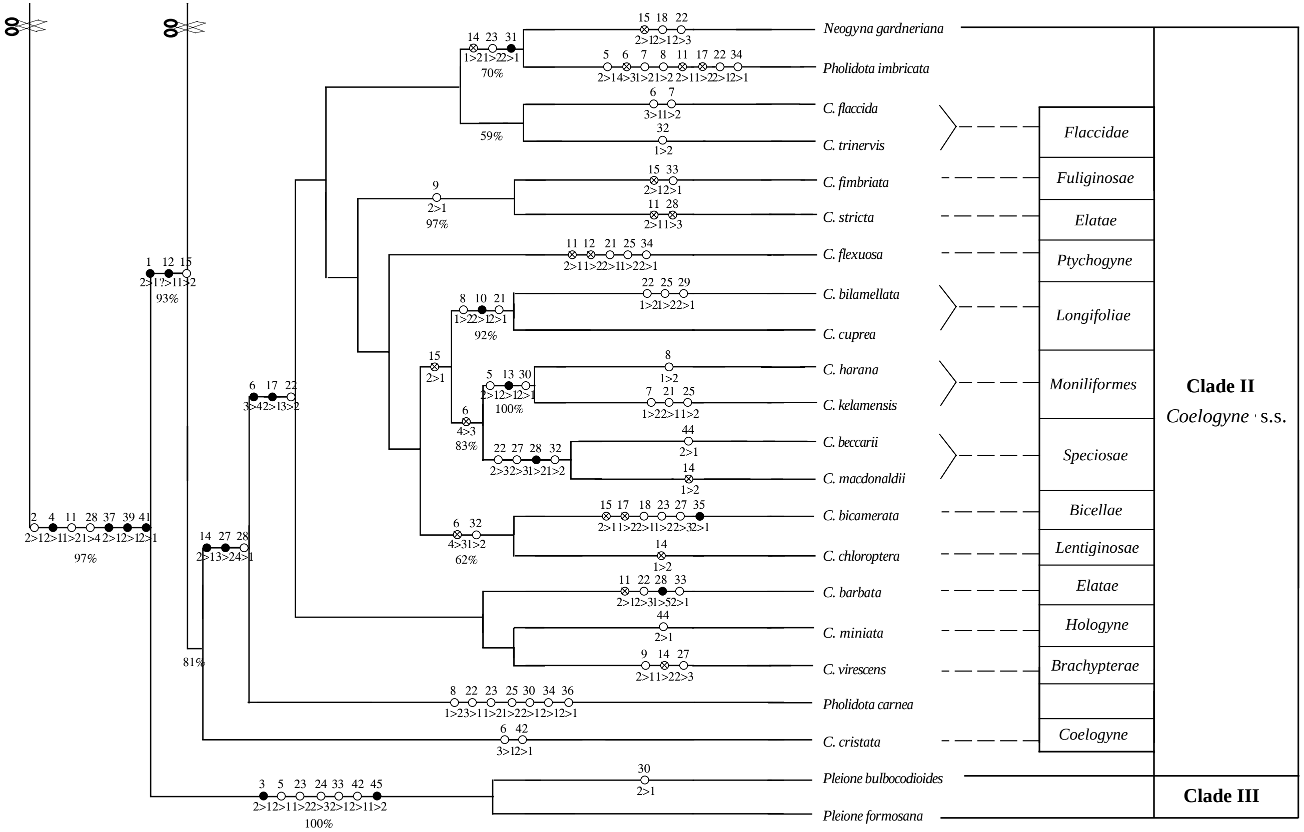


Fig. 3.5. One of the two MPTs from the total evidence analysis (only bootstraps > 50%). The state changes of the morphological characters used were traced with MACCLADE version 3.04 (Maddison & Maddison, 1992). Legends: ● = unique apomorphy; ○ = parallelism; x = reversal; ⊗ = parallel reversal.

exception of *Pholidota* and *C. cristata*) and two to three keels on the hypochile (with the exception of *C. beccarii*, *C. bicamerata*, *C. macdonaldii* and *C. virescens*), which can be plate-like, warty or consisting of projections and glabrous or fimbriate. Characters, which are present in the majority of taxa in clade II are hysteranthous inflorescences, less than 20 flowers per inflorescence, intermediate-sized flowers and less than three keels on the epichile.

The third major clade (*Pleione*) is characterized by short-living pseudobulbs, a lack of stegmata in all sclerenchymatous tissues, a hypochile without lateral lobes, and an epichile apex with fimbriate margin.

Characters with low phylogenetic information

Characters that show many reversals are the number of leaves per pseudobulb, size of the flowers, shape of the lip base and petals and presence of stelidia and calli. As these characters are very homoplasious, they should not be used for generic and sectional delimitations in Coelogyninae.

Transformation series

A rhizome arose early in the phylogeny of the subtribe, as it is absent in clade III (plesiomorphic condition) and present in clade I and II (derived condition). A synanthous inflorescence type is reconstructed as derived from a hysteranthous inflorescence type in clade II. Simultaneously opening flowers is the plesiomorphic character state and successively opening flowers are reconstructed as derived in clade II. The shape of the petals shows a general tendency to change from oblong to linear in Coelogyninae. Hairy ovaries are reconstructed as derived from glabrous ovaries in clade I. The size of the flowers shows a general tendency to change from large (plesiomorphic state) to intermediate to small (derived state) in clade I. A rounded hypochile base is plesiomorphic; a saccate hypochile base is reconstructed as a synapomorphy for part of the taxa in clade I. Narrow, discontinuous and spreading lateral lobes on the hypochile are reconstructed as derived from broad, continuous and erect lateral lobes in clade I. More than three keels on the epichile is the plesiomorphic character state and less than three keels is reconstructed as derived in clade I. However, in clade II, the opposite situation occurs: more than three keels is reconstructed as derived from less than three keels here. A long column is the plesiomorphic character state and a short column is reconstructed as derived in clade I.

Comparison with traditional classifications

Overviews of the most important classifications of Coelogyninae and *Coelogyne* are indicated in Fig. 3.6 and 3.7. They are compared with the total evidence phylogeny below.

Generic boundaries within subtribe Coelogyninae

The total evidence phylogeny indicates that *Coelogyne* as currently circumscribed is polyphyletic, with species falling into at least two well-supported clades. The possible taxonomic solutions for a new phylogenetic classification of *Coelogyne* are discussed in Chapter 2. As the type species of *Coelogyne* (*C. cristata*) belongs to clade II (*Coelogyne* s.s.), the best option for reorganizing *Coelogyne* seems to be:

1) restriction of *Coelogyne* to the *Coelogyne* s.s. clade, including *Neogyna* and *Pholidota*. These two genera were already considered to be just sections of *Coelogyne* by Lindley, Griffith and Reichenbach f. (Lindley, 1830; Griffith, 1851; De Vogel, 1988; see also Fig. 3.7). All species sampled of *Neogyna* and *Pholidota* have persistent floral bracts, a saccate hypochile base and an epichile with semi-orbicular, widely retuse lateral lobes;
2) removal of the species of *Coelogyne* sect. *Coelogyne* (in part), *Cyathogyne*, *Rigidiformes*, *Tomentosae*, *Veitchiae* and *Verrucosae*. The main morphological characters distinguishing these species from *Coelogyne* s.s. are the relatively high number of simultaneously opening flowers with persistent floral bracts, hairy ovaries and ovate-oblong petals. These characters are also present in *Bracisepalum*, *Chelonistele*, *Dendrochilum*, *Entomophobia*, *Geesinkorchis* and *Nabaluia*.

Bracisepalum seems well nested within *Dendrochilum* (100% support). Characters supporting the clade consisting of *Bracisepalum* and *Dendrochilum* are the pseudobulbs with one leaf, pendulous inflorescences, presence of sterile bracts on the base of the rhachis, persistent floral bracts and ovate-oblong petals.

Entomophobia seems well nested within *Chelonistele* (100% support). Characters supporting this clade are the pseudobulbs with one leaf, column apex with large wings and stomata with unequally sized subsidiary cells.

Sectional and subgeneric relationships within Coelogyne

From the 17 different sections of *Coelogyne* considered here, just three (with only two sampled species each) form strongly supported monophyletic groups in the combined analysis: sect. *Longifoliae* (92%), *Moniliformes* (100%) and *Verrucosae* (100%). Both species of sect. *Longifoliae* sampled have laterally flattened inflorescences with many flowers and a sigmoid shaped lip base. Both species of sect. *Moniliformes* sampled have pseudobulbs with one leaf, a rhachis with distinctly swollen internodes and an epichile without clear lateral lobes. The species of sect. *Verrucosae* sampled here have no unique characters.

Coelogyne sect. *Flaccidae* is monophyletic in all shortest trees, but bootstrap support for this clade is low (59%). This is in accordance with the few and not unique characters that define this section. *Coelogyne* sect. *Tomentosae* seems monophyletic, but support for this clade is very low (< 50%). The only synapomorphy present in all three species sampled is a pendulous inflorescence.

Coelogyne sect. *Coelogyne* and sect. *Elatae* are clearly paraphyletic. This is in accordance with the high variety in pseudobulb shape, inflorescence type, flower size and morphology of the keels on the lip in both sections. The only character that is present in all species currently assigned to sect. *Coelogyne* is the colour of the flowers: white, with yellow/brown spots. The species currently assigned to sect. *Elatae* only share the sterile bracts at the base of the rhachis and the simultaneously opening flowers, a combination of characters present in many other Coelogyninae species. A well-supported subset of species is formed *C. fimbriata* (sect. *Fuliginosae*) and *C. stricta* (sect. *Elatae*). These species share the presence of sterile bracts on the base of the scape. To investigate whether this clade warrants the status of a new section, a much larger sampling within *Coelogyne* is needed.

Bentham (1881)	Pfitzer & Kraenzlin (1907b)	Butzin (1974)	Pedersen et al. (1997)	This study (2000)
Josepha				
Earina				
Glomera				
Agrostophyllum				
Ceratostylis				
Callostylis				
Cryptochilus	*Camelostalix*			
Trichosma	*Chelonistele*		*Chelonistele*	*Chelonistele* (incl. *Entomophobia*)
Calanthe	*Chelonanthera*	*Bulleyia*	*Bulleyia*	*Bulleyia*[1]
Elleanthus	*Crinonia*	*Nabaluia*	*Nabaluia*	*Nabaluia*
Arundina	*Hologyne*	*Ischnogyne*	*Ischnogyne*	*Ischnogyne*[1]
Coelogyne	*Coelogyne*	*Coelogyne*	*Coelogyne*	*Coelogyne* (incl. *Neogyna* and *Pholidota*)
Otochilus	*Otochilus*	*Otochilus*	*Otochilus*	*Otochilus*[1]
Pholidota	*Pholidota*	*Pholidota*	*Pholidota* (including *Chelonanthera* and *Crinonia*)	
	Panisea	*Panisea* (incl. *Sigmatogyne*)	*Panisea* (incl. *Sigmatogyne*)	*Panisea* (incl. *Sigmatogyne*)[2]
	Sigmatogyne	*Zetagyne*	*Geesinkorchis*	*Geesinkorchis*
	Ptychogyne	*Forbesina*	*Entomophobia*	
	Pleione	*Pleione*	*Pleione*	*Pleione*
	Neogyna	*Neogyna*	*Neogyna*	
	Dendrochilum	*Dendrochilum*	*Dendrochilum*	*Dendrochilum* (including *Bracisepalum*)
	Gynoglottis	*Gynoglottis*	*Gynoglottis*	*Gynoglottis*[1]
		Bracisepalum	*Bracisepalum*	
		Dickasonia	*Dickasonia*	*Dickasonia*[1]

Fig. 3.6. Overview of most important subtribal classifications of Coelogyninae according to Bentham (1881), Pfitzer & Kraenzlin (1907), Butzin (1974), Pedersen et al. (1997) and this study (2000).

Notes:

1) No representatives of *Bulleyia*, *Dickasonia*, *Gynoglottis*, *Ischnogyne* and *Otochilus* could be included in this study. It is therefore not clear yet whether these genera are monophyletic groups.
2) *Panisea* was not included in the sampling of this study. According to the plastid data collected in Chapter 2, *Panisea* is nested within *Coelogyne* s.s., but nuclear sequences suggest a sister group relationship with *Geesinkorchis*. This incongruency might be caused by introgression due to hybridisation and needs further investigation.

The species of subgenus *Bicellae*, *Hologyne* and *Ptychogyne* sampled seem well nested within clade II (*Coelogyne* s.s. clade). *Coelogyne multiflora* of subgenus *Cyathogyne* is closely related with the species of sect. *Cristatae*, *Rigidiformes*, *Tomentosae*, *Veitchiae* and *Verrucosae* in clade I. It seems therefore, that these taxa do not warrant the status of subgenus, as suggested by various taxonomists (see Fig. 3.7).

In contrast with the *Coelogyne* s.s. clade, a good morphological delimitation of clade I is still difficult. Many characters, although present in most taxa of clade I, do not map perfectly on the total evidence tree due to a substantial amount of convergent evolution in this group. In addition, generic boundaries within clade I are not yet

Lindley (1854)		Reichenbach f. (1861)	Pfitzer&Kraenzlin (1907d)	De Vogel (1994); Clayton (in press)	This study (2000)	
	1	*Neogyna*				**subgenus**
		Pleione				
				Bicellae		
				Cyathogyne		
				Hologyne		
				Ptychogyne		
Erectae		*Erectae*				**section**
Filiferae		*Filiferae*				
Flexuosae		*Flexuosae*				
Flaccidae		*Flaccidae*		*Flaccidae*	*Flaccidae*	
Proliferae		*Proliferae*	*Proliferae*	*Proliferae*	*Proliferae*^{3}	
		Otochilus	*Fuscescentes*	*Fuscescentes*	*Fuscescentes*^{3}	
		Crinonia	*Lentiginosae*	*Lentiginosae*	*Lentiginosae*	
		Chelonanthera	*Longifoliae*	*Longifoliae*	*Longifoliae*	
		Chinensis	*Ocellatae*	*Ocellatae*	*Ocellatae*^{3}	
		Undulatae	*Fuliginosae*	*Fuliginosae*	*Fuliginosae*	
	2	*Imbricatae*	*Speciosae*	*Speciosae*	*Speciosae*	
		Articulatae	*Tomentosae*	*Tomentosae*		
		Camelostalix	*Verrucosae*	*Verrucosae*		
		Cymbidina	*Ancipites*	*Ancipites*	*Ancipites*^{3}	
			Elatae	*Elatae*		
			Cristatae	*Coelogyne*	*Coelogyne* (p.p.)	
			Carinatae	*Brachyptera*	*Brachyptera*	
			Venustae	*Lawrenceanae*	*Lawrenceanae*^{4}	
				Rigidiformes		
				Micranthae	*Micranthae*^{3}	
				Moniliformes	*Moniliformes*	
				Veitchiae		

Fig. 3.7. Overview of most important infrageneric classifications of *Coelogyne* according to Lindley (1854), Reichenbach f. (1861), Pfitzer & Kraenzlin (1907d), De Vogel (1994), Clayton (in press) and this study (2000).

Notes:

1) Reichenbach f. (1861) described *Neogyna*, *Pleione* and several species groups within *Coelogyne* all as sections. However, he placed *Neogyna* and *Pleione* on a higher level than the species groups within *Coelogyne*. Therefore, *Neogyna* and *Pleione* are placed under the category subgenus in this overview.
2) Section *Chelonanthera*, *Chinensis*, *Undulatae*, *Imbricatae*, *Articulatae*, *Camelostalix* and *Cymbidina* all encompass species of *Pholidota*, which Reichenbach f. (1861) reduced to *Coelogyne*.
3) Of section *Ancipites*, *Fuscescentes*, *Micranthae*, *Ocellatae* and *Proliferae* no representatives could be included in this study. It is therefore not clear yet whether these sections are monophyletic groups.
4) Section *Lawrenceanae* was not included in the sampling of this study. However, results of the molecular phylogeny of Chapter 2 suggest that sect. *Lawrenceanae* is well separated from sect. *Speciosae*, which is not in accordance with Seidenfaden (1975), who suggested they should be combined.

clear, as most internal nodes have only low support. Additional sampling is needed, not only by including more taxa, but also by sequencing more variable DNA regions to find the limits of new monophyletic groups and to justify the creation of a new genus for the species of *Coelogyne* section/subgenus *Coelogyne*, *Cyathogyne*, *Rigidiformes*, *Tomentosae*, *Veitchiae* and *Verrucosae*.

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